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Algal recruitment and reproduction in the context of reef degradation: interactions with corals, substrates, herbivores and nutrients

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Guillermo A. Diaz-Pulido

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Abstract

Recruitment and reproduction are important processes in the dynamics of ecological populations and communities. Recruitment dynamics have been shown to influence the structure of tropical fish and coral, and of temperate algal populations, but there is a significant lack of information about the recruitment of tropical algae. Coral reef degradation commonly involves overgrowth and invasion of abundant corals by abundant algae. Reduction in herbivore populations, increases in nutrient supply and coral disturbances are considered as causes of algal invasions and coral-algal phase shifts, but conceptually, for algal invasions to occur they generally require dispersal, recruitment and colonisation processes. Despite the importance of algal recruitment to such invasions, there is little information about the recruitment dynamics and reproduction of coral reef algae. The aim of this thesis was to investigate the dynamics of, and factors that affect, the recruitment and reproduction of coral reef algae and their interactions with corals, particularly in the context of reef degradation. I addressed this aim by exploring i. The variability in algal recruitment in response to substrate availability, coral disturbances, reductions in herbivory, and addition of nutrients; ii. Variability in algal fecundity in response to nutrient enhancement. I compared the outcomes in terms of both numeric responses and growth responses, and included comparisons between two taxa of brown algae with contrasting morphologies (*Sargassum* spp. and *Lobophora variegata*). The study took place in a range of inshore and mid-shelf reefs on the Great Barrier Reef (GBR), Australia.

The first study tested the ability of *Sargassum* spp. and *L. variegata* to settle and grow on healthy coral tissue, and explored the effects of interactions with prior occupants, and of abiotic substrate properties. Healthy corals prevented attachment or survival of recruits of these macroalgae. This is a significant point, since it suggests that the replacement of corals by algae may often require prior stress or death of the coral tissue. Pre-conditioning of ceramic settlement plates at different sites had some effects on growth and survival, but these were relatively minor, whereas there was considerable variation within sites. Some of this variation appeared related to the amount of turf algae or crustose calcareous algae on the plates. Recruitment was generally but not always higher on plates with rougher texture. These results indicate considerable potential for variability in outcomes of algal colonisation, with implications for the dynamics of algal invasions. Furthermore, growth and survival responded differently to substrate manipulations, emphasising the importance of using a variable appropriate to

the process being questioned. The results do not support suggestions that planktonic algal propagules can directly settle on and colonise healthy coral tissue.

The massive bleaching of corals that occurred on the GBR, in early 1998 provided an opportunity to explore the roles of coral disturbances in the recruitment of algae and shifts in dominance from corals to algae. In this study I described the composition and time course of algal recruitment on bleached corals, and the possible roles of that recruitment on the fate of the corals. Massive *Porites* corals were selected with different degrees of bleaching, and the cover of live coral tissue, and relative abundance and composition of algal recruitment, were followed in small plots over 2.5 years. The bleaching disturbance caused a major shift in abundance of corals and algae. All dead corals were colonised by a diverse assemblage of epilithic and endolithic algae, the nature and composition of which was variable and related to the stage of the succession, the severity of bleaching and reef location. Quantitative data on species composition of colonising algae are given, apparently the first such data. The epilithic algal assemblage was initially dominated by diatoms and blue-green algae, but rapidly shifted to an assemblage dominated by upright and branched filamentous algae and, on one reef, fleshy macroalgae. Algal colonisation was not the initial cause of coral tissue mortality, although it may have contributed to the failure of corals to recover after bleaching. The results thus emphasise the role of coral disturbances and substratum availability in controlling the abundance of coral reef benthic algae, in contrast to "bottom-up" and "top-down" views that assume changes in algal abundance are the major cause of changes in coral abundance. The considerable variability in outcome of bleaching damage and algal colonisation demonstrates the potential for major and variable effects on the recovery of coral populations, with implications for future reef status.

To explore the relative and interactive effects of bottom-up regulation (nutrient enhancement) and top-down control (herbivory reductions) as causes of algal invasions, I simultaneously manipulated nutrient supply to and herbivory on recruits of *Sargassum fissifolium* and *L. variegata* on a coral reef in the GBR. Herbivory strongly reduced both density and growth of recruits for both species, whereas nutrient supply had only minor effects on growth of *L. variegata* recruits and no detectable effects on *S. fissifolium* recruits. Notwithstanding the dominance of herbivory over nutrient treatments, herbivore effects were not uniform, but varied between taxa, response variables (growth and density), and were apparently stronger for nutrient-enriched plants. These results emphasise the importance of protecting herbivores for coral reef management, complement previous work with results for recruitment of tropical marine algae, and demonstrate that interpretations of the relative importance of bottom-up and top-down processes may depend on the species, circumstances, and life-history processes (survival and growth) under consideration.

It is often assumed that enhancement of nutrient levels and supply will lead to increases in area colonised by algae. In the case of algae with distinct individuals (e.g. *Sargassum* spp.), such increases must involve increases in propagule numbers, presumably by facilitating algal fecundity (or reproductive output). However, there is no experimental evidence for that assumption in tropical coral reef algae. In the final study I experimentally explored the assumption that nutrient enhancement will facilitate algal fecundity. Although by no mean a comprehensive test, the results suggest that the additions of nutrients may not necessarily lead to increased algal fecundity, since the number and biomass of reproductive structures (receptacles) decreased with nutrient additions. This indicates that increased nutrient inputs alone cannot be assumed to promote invasions of *Sargassum* spp. without further experimental evidence.

Three main conclusions arise from this thesis. Firstly, there is considerable variability in the outcomes of the algal recruitment process and in the effects of factors on recruitment. Factors that accounted for variability in the recruitment dynamics included substrate availability, coral disturbances, location and successional stage, herbivory, taxa, and the life-history processes measured (growth and survival), and to a lesser extent nutrient enhancement. This variability in recruitment is very likely to have major consequences for changes in adult algal distributions and algal invasions on coral reefs. Secondly, the distinctions between growth and numeric responses are important to the understanding of algal dynamics during phase shifts. Growth is a property of an individual whereas density is a measure of the population. As algal invasions will generally require an increase in number of individuals, density seems to be a more relevant variable in the context of those invasions. Lastly, the replacement of corals by algae through the mechanism of direct settlement of propagules from the plankton onto live coral is unlikely, but that mechanism appears important following coral disturbances. Given the fundamental importance of recruitment in the colonisation and invasion of algae on coral reefs, exploring the dynamics and variability of, and factors that affect, the recruitment and reproduction of algae is important to understanding the dynamics of coral-algal phase shifts and reef degradation.

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Statement on 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.

20-3-2002

Guillermo A. Diaz-Pulido

List of publications

The following publications resulted from this project:

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Diaz-Pulido, G. and McCook, L. J. The fate of bleached corals: patterns and dynamics of algal recruitment. Mar. Ecol. Prog. Ser., 232: 115-128.

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Chapter 1

Introduction

1.1 Overview

Supply side ecology recognises the critical roles of reproduction, dispersal, settlement, attachment, and recruitment processes in structuring natural populations and communities in both terrestrial and aquatic systems (Roughgarden et al., 1988; Underwood and Fairweather, 1989; Caley et al., 1996; Hughes et al., 2000). In marine systems, there is considerable information on the importance of other ecological processes such as disturbance, competition, predation, and resource limitation to the dynamics of organisms, particularly for fishes, invertebrates and temperate algae (Bertness et al., 2001). However, a better understanding of the processes that underlie populations and community dynamics requires knowledge of the recruitment dynamics, that is the addition of new individuals to populations. For instance, recruitment and post-settlement dynamics have been shown to strongly influence the structure of tropical fish populations (Doherty and Williams, 1988), and studies on corals and other benthic invertebrates have demonstrated the critical importance of supply-side processes (i.e. supply of propagules to a site) and the coupling of these processes to adult abundances (Roughgarden et al., 1988; Hughes et al., 2000). In temperate systems, recruitment can be a significant agent of change in macroalgal assemblages (Santelices, 1990; Menge et al., 1993; Lotze et al., 2000; Wright and Steinberg, 2001).

In coral reef ecosystems, benthic algae play fundamental roles in the overall primary productivity, in the construction of the physical structure, and in reef degradation (Littler and Littler, 1984; Adey, 1998; McCook, 1999). However, in contrast to fishes and corals and to temperate systems, very little is known about the recruitment dynamics of coral reef algae. Recruitment dynamics are conceptually important in determining the abundance of adult algal populations on coral reefs, and will therefore be critical to algal–coral dynamics, especially during coral reef degradation. The development of abundant benthic algal populations can inhibit growth and reproduction of existing corals, and may also influence the ability of coral populations to recover after disturbances, affecting either new coral recruitment or regeneration from remnant corals (Tanner, 1995; Genin et al., 1995; Connell et al., 1997; McCook et al., 2001b). Thus, algae have great potential to modify the structure and functioning of coral reefs.

Coral reef degradation due to eutrophication, reduction of herbivore populations, and coral disturbances, usually involves the replacement of live corals by benthic algae, and is usually referred to as "phase shifts" (Done, 1992; Hughes, 1994; McCook, 1999; Knowlton and Jackson, 2001). During this replacement, the colonisation, invasion and increased abundance of algal populations may lead to the development of "algal blooms" with serious implications to the overall reef status. The development of algal blooms also affects other tropical and temperate marine systems, including seagrass beds, coastal lagoons, etc (Morand and Briand, 1996; Raffaelli et al., 1998; Hauxwell et al., 2000). The development of algal blooms can clearly be very important to the overall ecosystem status.

The relative contribution of nutrients (bottom-up regulation) and herbivory (top-down control) as causes of algal blooms has been a matter of recent debate (Lapointe, 1997; Hughes et al., 1999). Recent experimental studies have demonstrated that herbivory generally exerts much greater control on algal populations than does nutrient regulation. The strength of both processes may, however, vary in space and time, and furthermore, these processes may also interact or act simultaneously to control the abundance of coral reef algae (Hatcher and Larkum, 1983; Miller et al., 1999; Thacker et al., 2001; Jompa and McCook, 2002b). However, both top-down and bottom-up perspectives have ignored the critical role of coral disturbance as a cause of algal invasions. Coral disturbances such as cyclones, crown-of-thorns starfish outbreaks, diseases and bleaching, among others, can create new free space for the colonization and invasion of algae, potentially contributing to coral-algal phase shifts (Hughes, 1994; Knowlton and Jackson, 2001; Williams et al., 2001).

The increase in abundance of algae may involve an increase in biomass per unit area, within an area already occupied by existing plants (growth increase), or it can also involve increases in area. The latter can happen by lateral vegetative overgrowth, or it can involve increased colonisation by increasing propagule numbers (numeric increase). This increased colonisation may involve increased fecundity (reproductive output) or increased recruitment (Fig. 1.1).

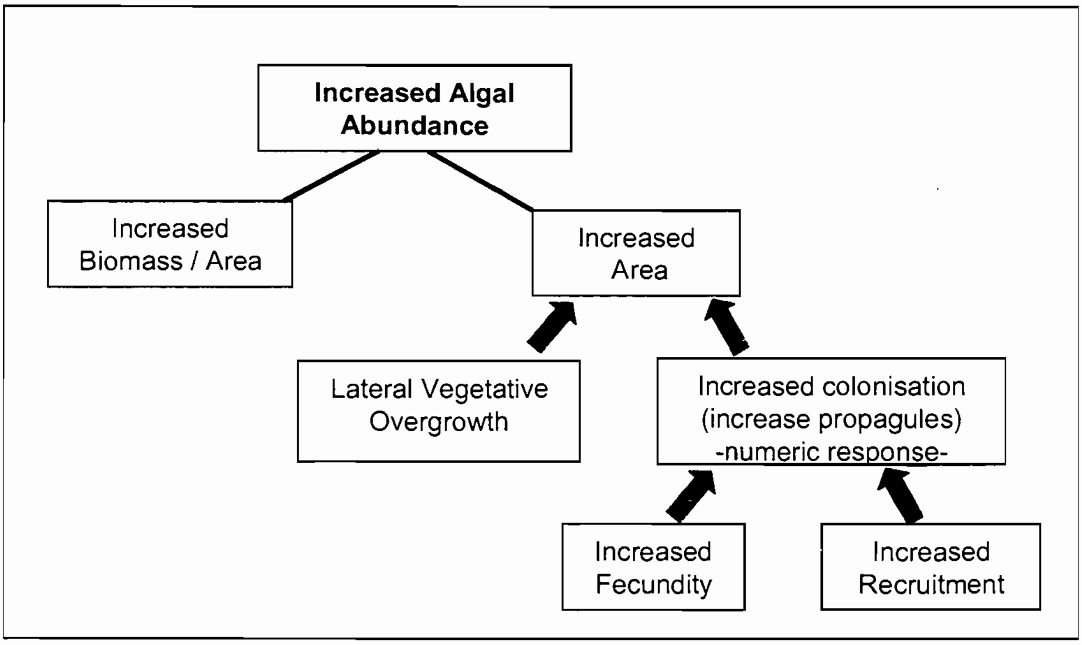


Fig. 1.1 Mechanisms of increase of algal abundance and colonisation.

In general, the delivery of propagules to a site and subsequent successful recruitment are important for algal invasions. Algal invasions can also occur in coral reefs by abundant vegetative growth of existing plants (Fig. 1.1). The latter mechanism is much more limited in distance compared to the former (Maggs and Stegenga, 1999; Davis et al., 2000). Vegetative overgrowth involves active competitive processes and the outcomes of these interactions are dictated by the properties of both corals and algae. Since the forms and species in coral reefs are highly diverse, the outcomes seem to be highly variable (McCook et al., 2001a). Clearly, the recruitment dynamics and reproductive potential of benthic algae will be critical to their ability to invade and colonise new areas during reef degradation. An important aspect of this colonisation will be the ability of algal propagules to settle on live coral tissues. As previously suggested, despite the importance of supply-side ecology during algal colonisations and invasions, and in general in coral reef degradation, the process of algal recruitment and reproductive output and the factors affecting them have been generally unaddressed in coral reef ecosystems.

Several factors may affect the recruitment of algae on coral reefs. Substrate type, nutrients, herbivory and the interactions between these factors have been shown to be important to the recruitment of benthic algae in temperate marine systems (Santelices, 1990; Vadas et al., 1992; Lotze et al., 2000; 2001). It is likely that these factors may exhibit similar importance to the ecology of early life history stages of algae on coral reefs, particularly during reef degradation. Most studies on the ecology of early life-history stages of algae on coral reefs has focused on the importance of herbivory in limiting the development of algal communities (Lewis, 1986; de Ruyter van Steveninck and Breeman, 1987; Carpenter, 1990; Hixon and Brostoff, 1996). Few have addressed the roles of nutrients and substrate type on the survival and growth of algal recruits in tropical areas (Hixon and Brostoff, 1985; 1996; Schaffelke and Klumpp, 1997b; Miller et al., 1999), and none have considered in detail the roles of coral disturbance as a critical factor for the colonisation of algae. Moreover, there is surprisingly little information on the effects of benthic occupants (e.g. including corals, algal turfs and crustose calcareous algae) on the survival of algal recruits. Finally, studies that have implications for algal invasions on coral reefs have not considered the mechanisms of increase in densities of algae (or numeric responses); one of these mechanisms, the increase in recruitment, has been scarcely studied (Fig. 1.1).

1.2 Aims and approach

The aim of this thesis is to experimentally explore the dynamics of, and factors which, affect the recruitment and reproduction of coral reef algae and its interactions with corals, particularly in the context of algal colonisations and invasions, and the potential consequences for algal populations and community structure and hence for reef degradation. I have addressed 4 major themes. 1. Variability in algal recruitment in response to substrate availability (type of material and texture, prior occupants including corals, and coral disturbance). 2. Variability in algal recruitment in response to reductions in herbivory and nutrient enhancement. 3. Responses of fecundity (another aspect of the supply-side ecology) of adult algae to additions of nutrients. 4. The role of coral disturbance, such as bleaching, as a mediator of coral-algal phase shifts and the significance of algal recruitment to the colonisation and development of adult populations.

I compared the outcomes in terms of numeric responses and growth responses since these life history properties may be affected differently by various processes. These properties include density, as a measure of survival or mortality, and growth, as a measure of increase in size of individuals. Growth is a property of an individual, while density is a property of the population and is therefore a more appropriate parameter for measuring population dynamics. Since both variables may have different responses, it cannot be assumed that they have the same implications for coral reef degradation. In addition to these variables, I considered responses at the community level, including community composition. I also tested the effects on both early stages and reproductive adult stages. I included comparisons between two taxa of brown algae with contrasting functional morphologies [*Sargassum* spp. and *Lobophora variegata* (Lamouroux) Womersley ex Oliveira], since it is very likely that different species and life history stages respond differently to ecological processes.

1.2.3 Experimental species

I choose to work with *Sargassum* spp. and *Lobophora variegata* for several reasons. Firstly, the reproductive biology and life cycles are relatively well known for both taxa, and this knowledge facilitated the experimental design and data collection in response to ecological variables. Additionally, the large size of *Sargassum* propagules facilitated methodological procedures.

Secondly, *Sargassum* spp. and *L. variegata* are abundant and have been implicated in coral reef degradation worldwide (Bouchon et al., 1992; Hughes, 1994; Bell and Elmetri, 1995). For example, Bouchon et al. (1992) registered *Sargassum* outbreaks in reefs of the eastern Caribbean and Hughes (1994) documented the progressive increase of *Sargassum* spp. during the degradation of a Jamaican reef. In the Great Barrier Reef (GBR), Australia, Bell and Elmetri (1995) suggested that the abundance of *Sargassum* may be an indicator of reef degradation. *S. muticum*, a species from temperate zones, is highly invasive and has caused important changes to benthic communities; it has been suggested that other species of *Sargassum* from tropical areas posses the same invasive potential as *S. muticum* (Paula and Eston, 1987; Critchley et al., 1990). Thus, *Sargassum* and other Fucales are ecologically important seaweeds with potential to colonise tropical reefs (Stiger and Payri, 1999a; 1999b). *Lobophora variegata* is one of the most abundant species in coral reefs of the Caribbean Sea and inshore GBR. These species have increased in abundance following the mass mortality of the herbivorous sea urchin *Diadema antillarum* in the Caribbean, and have been considered a threat to corals reefs due to an ability to overgrow and kill corals (de Ruyter van Steveninck and Bak, 1986; Hughes et al., 1987; de Ruyter van Steveninck and Breeman, 1987; McCook et al., 1997; Lapointe et al., 1997; Diaz-Pulido and Diaz, 1997; Diaz-Pulido and Bula-Meyer, 1997; McClanahan et al., 2001; Jompa and McCook, 2002a).

Thirdly, the two taxa contrast in functional morphology, biology and ecology, and therefore may have different responses to ecological factors (Littler et al., 1983; Steneck and Dethier, 1994). *Sargassum* spp. are leathery macrophytes that form dense canopies of up to several metres height, and are highly seasonal on tropical reefs. Most *Sargassum* spp. have little ability for lateral vegetative overgrowth (but see Phang and Yoshida, 1997). In contrast, *L. variegata* belongs to the functional form of corticated foliose algae and is anatomically and morphologically much simpler than *Sargassum*, and has active lateral growth. *L. variegata* may occur as understorey in inshore reefs where it forms lower canopies of generally <10 cm height with apparently less seasonal variation than *Sargassum*. Another contrasting feature of the two taxa is the conspicuous morphological plasticity of *L. variegata*, which ranges from encrusting to upright forms, while *Sargassum* spp. have only one morphological type (although there may be considerable variability in some structures, e.g. leaves, vesicles, etc). These two taxa provide a range of morphologies as a basis for a better understanding of the role of algal recruitment in phase shifts.

1.3 Thesis outline

The thesis is divided into six chapters including this General Introduction, four data chapters and a General Discussion. The following paragraphs describe the specific objectives of each of the data chapters and provide a brief summary of the results and implications of each.

Chapter 2 examines the ability of algal propagules to settle and recruit onto healthy corals in comparison to dead corals, and explores the effects of prior occupants (dead coral, algal turfs and crustose calcareous algae), together with the effects of substrate material and texture, on algal recruitment and growth. The results indicate that the replacement of corals by algae is unlikely to occur by direct settlement of algal propagules onto healthy corals from the plankton, as is commonly assumed. In this chapter, I emphasise the potential for variable outcomes of the recruitment process. Density and growth measurements (life-history properties) responded differently to substrate manipulations, emphasising the importance of using a variable appropriate to the process being questioned. The two taxa also responded differently to the different types of substrate and contributed to the observed variability. Despite the considerable variability in outcomes, algae never settled on healthy corals.

Chapter 3 took advantage of the opportunity of the 1998 GBR coral bleaching event to provide information on the consequence of this globally significant disturbance in terms of algal-coral transitions. I used the massive coral bleaching event as an example of a coral disturbance to explore the role of disturbances in general as a basis for coral to algal shifts. In this study I monitored algal recruitment and colonisation (at the community level) onto corals with different severities of bleaching damage, whilst monitoring coral survival at two inshore reefs on the GBR. I also explored the potential effects of the colonising algae on the recovery of the corals. The study lasted 2.5 years. This chapter complements the observations of Chapter 2 that algal recruitment onto healthy corals was a rare mechanism of coral replacement by algae. It emphasises the important roles of coral disturbance and substrate availability in controlling the abundance of coral reef algae, in contrast to the bottom-up and top-down approaches that assume that changes in algal abundance are the major cause of changes in coral abundance. In this chapter I suggest that the bottom-up and top-down perspectives must be expanded to include coral disturbances as causes of algal blooms on coral reefs. Chapter 3 shows that, as in Chapter 2, the outcomes are highly variable and depend on the stage of the algal succession, the severity of coral bleaching and geographical location. This study is the first to provide detailed information on the algal species succession after bleaching disturbances.

In Chapter 4, I investigated the relative and interactive effects of bottom–up and top-down processes on the survival and growth of algal recruits, using factorial manipulations of nutrient supply and herbivory, on a midshelf coral reef on the GBR. The experimental design involved the seeding of propagules of *Sargassum* and *Lobophora* onto settlement plates in aquaria, followed by transplantation to the reef to carry out the manipulations. This study significantly contributes to the current debate on the relative importance of over-fishing and eutrophication to algal overgrowth and reef decline. This debate has largely ignored the role of supply-side processes in structuring ecological communities (Fig. 1.1), and this is particularly important for algae since they have complex life-history stages which may respond differently to environmental factors. The results complement studies of adult seaweeds, supporting the widespread dominance of top-down over bottom-up effects on algal abundance on coral reefs. Despite the strong effects of herbivory, the effects were not uniform, but varied between taxa, response variables (density and size), and were stronger for nutrient-enriched plants. As in Chapter 2, this emphasises the need to address appropriate variables in relation to the process in question. These variables are the expression of different processes, i.e. density refers to survival / mortality and size to growth, and represent different measurements for populations or individuals (Fig 1.1).

In Chapter 5 I used adult *Sargassum siliquosum* seaweeds to explore the effects of nutrient enhancement on fecundity under a controlled environment. Here I argue that one of the steps by which nutrients increase algal abundance (e.g. by increasing reproductive output, Fig. 1.1) is unlikely, since the number and biomass of reproductive structures actually decreased with nutrient additions. However, it is important to recognise that this experiment is not a comprehensive test, and therefore should not be taken as unequivocal demonstration that nutrients reduced the overall fecundity of this species, but rather as demonstration that nutrient increases may not result in increased fecundity, and that further experimental evidence is required. This chapter illustrates the potential complexity of nutrient effects for algal invasions, and as illustrating the need to distinguish between effects on growth, and effects on fecundity and recruitment processes, and consequent invasion potential.

Finally, Chapter 6 is the General Discussion, which aims to integrate the outcomes of the individual data chapters. Two main points are emphasised. First, there were considerable differences between the algal life-history parameters measured, such as density (survival or mortality) and sizes (growth), as well as between species, in response to factors involved in reef degradation. I argue that the identification of this variability is critical in understanding the dynamics of algal colonisations and invasions in phase shifts, because each life-history parameter measures different processes, i.e. growth is a measure of the individuals while density is a measure of the population. In general, for an algal invasion to occur, there is a need for a numeric increase in algal populations. Thus density appears to be a more appropriate parameter to understand the dynamics of algal colonisations. Secondly, I propose a mechanistic framework to understand phase shifts dynamics, in which I identify four basic mechanisms by which algae can replace corals. Of these mechanisms, the replacement of corals by algae through direct settlement of propagules from the plankton onto live coral is unlikely. In contrast, the replacement of corals by algae mediated by coral disturbances seems to be a very important mechanism.

Chapter 2

Algal Recruitment on Corals, Interactions with other Coral Reef Benthos, and Effects of Substrate Type

2.1 Introduction

The recruitment of benthic organisms is an important ecological stage that affects the abundance of adult populations and community structure, and is potentially a critical bottleneck for population dynamics. Populations of many invertebrates, fishes and temperate algae, are to a large extent regulated by their supply side ecology (e.g. recruitment dynamics, Underwood and Fairweather, 1989; Santelices, 1990; Caley et al., 1996; Hughes et al., 2000; Wright and Steinberg, 2001). However, there is very little information available on the supply-side processes of tropical algae (Ang, 1985b; Clifton, 1997; Stiger and Payri, 1999b).

The recruitment of algal populations is especially critical during coral reef degradation, which usually involves the replacement of hard corals by benthic algae (Hughes, 1994; McCook, 1999). During this replacement, algal recruitment is a key but under-recognised step in the invasion and colonization of adult algal populations. For example, there is a widespread perception that algae, such as *Sargassum* on the Great Barrier Reef (GBR), can and will colonise live corals, if conditions such as nutrients or herbivory are suitable (Bell and Elmetri, 1995). Previous studies of tropical algal recruitment and colonization have looked at the effects of herbivory on the development of epilithic algal communities (Lewis, 1986; Scott and Russ, 1987; de Ruyter van Steveninck and Breeman, 1987; Carpenter, 1990; McCook, 1997; Miller et al., 1999; Smith et al., 2001). However, very few experimental studies have explored the ability of algal propagules to settle and recruit onto healthy coral tissue, or the interactions with prior benthic occupants on tropical reefs. There is, however, considerable literature from temperate ecosystems suggesting that interactions between algal propagules and prior occupants are important to net recruitment and hence to final community structure (Johnson and Mann, 1986; Reed, 1990; Brawley and Johnson, 1991; Benedetti-Cecchi and Cinelli, 1992; McCook and Chapman, 1993; Van Tamelen and Stekoll, 1997; Figueiredo et al., 1997; Worm and Chapman, 1998).

The settlement and recruitment of algal propagules to benthic communities may require both suitable substrate, and competition with prior occupants (Worm and Chapman, 1998). Substrate texture, material, or chemical composition have been shown to affect the survival of germlings and productivity of algal communities (Norton and Fetter, 1981; Santelices, 1990; Amsler et al., 1992; Fletcher and Callow, 1992; Carpenter and Williams, 1993). On coral reefs, interactions between early stages of macroalgae and the major benthic groups, corals, crustose calcareous algae and algal turfs, will be of critical importance during algal settlement and recruitment, especially after disturbance to corals (see Chapter 3).

In this study I tested the ability of algal propagules to recruit onto healthy coral tissue, in comparison to recruitment on dead coral plates, and onto substrates pre-conditioned with different epilithic algal communities at different sites. I also explored the relationship between abiotic properties of the substrate (i.e. surface texture and material) and algal recruitment and growth. The specific hypotheses tested include:

1) Propagules of Fucales and *Lobophora variegata* cannot recruit onto healthy coral tissue, but can settle and recruit onto dead corals.

2) Recruitment of Fucales and *L. variegata* is influenced by the presence and type of prior occupants on the substrate.

3) Recruitment of Fucales and *L. variegata* is influenced by the surface texture and material of the substrate.

The study focussed on two taxa of brown seaweeds, Fucales (predominantly *Sargassum* spp.), and *Lobophora variegata*. Throughout this study, I use the term algal recruitment to refer to the combination of propagule settlement, attachment and post-settlement survival (or mortality) and growth (prior to my census; Santelices, 1990).

2.2 Methods

2.2.1 General approach and study site

To investigate the effects of competitive interactions with coral tissue and other benthic organisms, I compared the algal recruitment onto 1) healthy coral tissue and dead coral plates, 2) settlement plates pre-conditioned on different reefs, and clean settlement plates (as controls) and 3) settlement plates of different textures and materials (ceramic and carbonate), on the reef flat of an inshore coral reef on the Great Barrier Reef (GBR), Australia. I pre-conditioned plates at two different reefs to provide a range of pre-existing benthic occupants, of epilithic algal communities (EAC) in particular. In all, there were 7 substrate treatments (full details of treatments are summarised in the horizontal axes of most figures).

The experimental site is on a very inshore island, Goold Island (18°10' 85 S; 146° 10' 05 E), in the central section of the GBR. Turbid waters (max 5-8 m visibility) prevail most of the time. The reef flat and slope are covered by luxuriant populations of Fucales seaweeds including *Sargassum* spp. (*S. siliquosum, S. baccularia, S. polycystum, S. fissifolium, S. oligocystum, S. swartzii* and *S.* sp.), *Turbinaria* spp. and *Hormophysa* spp., as well as other fleshy macroalgae, algal turfs, and corals (McCook, 1999; pers. obs.). *L. variegata* is often abundant as understorey of *Sargassum* beds.

The species of *Sargassum* in this area are highly seasonal, with peaks of biomass, maturation of reproductive structures, settlement, and recruitment during the warmer months of December through May (Price, 1989; Martin-Smith, 1993; pers. obs.). To ensure abundant propagules, the experiments were run during the peak of *Sargassum* recruitment, April-May (1999). *L. variegata* seems to have a more complex temporal pattern of recruitment, but clearly recruited during the experimental period.

Because of the limited dispersal shadows of *L. variegata* and *Sargassum* spp. propagules (de Ruyter van Steveninck and Breeman, 1987; Kendrick and Walker, 1995), I located the plates in a well developed *Sargassum* bed with abundant understorey thalli of *L. variegata*, within a relatively small area to minimise variations in propagule supply. All settlement plates were 11 x 11 cm side with 9 replicate plates per treatment, randomly allocated to positions within the site. Settlement plates were bolted to the substratum using stainless steel screws and masonry plugs and located as close to the substrate as possible. The plates were left in the reef for a period of one month, then retrieved and examined in the laboratory.

2.2.2 Effects of live coral and of other benthic occupants on algal recruitment

To explore the ability of propagules of Fucales and *L. variegata* to recruit onto live coral tissue I marked areas of live coral tissue (11 x 11 cm, with no dead tissue) on small colonies from a range of the most abundant species at the study site. Coral species used included massive *Porites australiensis* (3 colonies), *Favites russelli* (2 colonies), *Galaxea astreata*, *Cyphastrea chalcidicum*, *Goniastrea retiformis*, and *Astreopora listeri* (one colony each). Colonies were collected, maintained under water, and the surface of the coral tissue examined for algal recruits using a stereomicroscope, then colonies were returned to the reef. Algal recruitment onto the live coral was compared to control settlement plates (11 x 11 cm) made of dead massive *Porites* corals (*P. australiensis* or very similar species).

To explore the effects of competitive interactions with the EAC, I compared algal recruitment between settlement plates pre-conditioned on two different reefs, and clean settlement plates (as controls). Smooth terracotta ceramic settlement plates of 11 x 11 cm side were placed in reef areas with scarce or absent populations of *Sargassum* spp. and *L. variegata*, two months immediately prior to the experiment. Pre-conditioning sites included the reef slope of an inshore island (Great Palm Island; 18° 40' 943 S; 146° 35' 397 E) at 6-8 m depth, and the reef crest of a mid-shelf reef (Rib Reef; 18° 28' 422 S; 146° 52' 783 E) at 4 –5 m depth. These plates were retrieved, checked for recruits of Fucales and *L. variegata* under a stereomicroscope, the percent cover of algal turfs, CCA, and bare substrate estimated using a 100 point grid, and the height of the algal turf canopy measured. Plates were then deployed at the experimental site at Good Island. Percent cover of major benthic groups was also recorded at the end of the experiment (one month later).

At the beginning of the experiment, pre-conditioned plates had developed epilithic algal communities dominated by filamentous algal turfs, crustose coralline and other calcareous algae (CCA) and microbial film (Fig. 2.1). On plates pre-conditioned at Palm Island, the cover of algal turfs was higher than CCA, both at the beginning and end of the experiment. Plates pre-conditioned at Rib Reef initially had less cover of algal turfs than CCA, although the cover of these two groups was similar by the end of the experiment. The percent cover of algal turfs was not significantly different between reefs, but the percent cover of CCA was higher in the plates pre-conditioned at Rib Reef (Fig. 2.1, *t*-test). Algal turfs generally had a canopy height of < 5 mm and included species of brown algae (*Sphacelaria*, *Hincksia*), green algae (*Enteromorpha*, *Cladophora*, *Derbesia*), red algae (*Polysiphonia*, *Jania*, *Ceramium*), blue-green algae, and diatoms. The CCA assemblage generally consisted of species of non-geniculate coralline algae, but did include some small individuals of *Peyssonnelia*.

2.2.3 Effects of substrate texture and material on algal recruitment: "Abiotic" effects

Comparisons were made between ceramic settlement plates of two different textures, and between dead coral plates of two different textures. I did not compare coral and ceramic plates statistically. The coral plates had intrinsic texture or micro-porosity at a range of scales (difficult to quantify), so that any comparison of coral and ceramic materials is intrinsically confounded by differences in texture, and so should be interpreted cautiously. In particular, rough and smooth textures are not comparable between coral and ceramic plates.

Rough ceramic plates had surface pits of 0.5 – 2 mm size and 0.1 – 0.3 mm depth, while smooth ceramic plates had little significant rugosity greater than 0.005 mm. Rough coral plates were created by cutting grooves of 1.5 – 2.5 mm wide and 1.5 – 2.0 mm depth into similar plates to those used as controls for live coral ("smooth"). The surface of the coral plates was very porous, with micro cavities of 0.13 – 0.25 mm size and 0.1 – >3.8 mm depth.

2.2.4 Variables and data analyses

The main response variable was density (number of recruits per plate), as a measure of recruitment, but I also measured length and width, as measures of growth. Length (from base to apex) and width (longest dimension perpendicular to the length of the largest branch) were measured for five, randomly selected recruits per plate for each taxon (i.e. Fucales and *L. variegata*). Density and size measurements were made at the end of the experiment, using a stereomicroscope and a 10 x 10 cm grid as a guide. Size measurements were averaged between the five recruits to obtain a single value per plate.

Since the individuals of the dominant Fucales (*Sargassum* spp., *Turbinaria* spp. and *Hormophysa* spp.) are difficult to distinguish from each other during early stages (<2 mm), I refer to them collectively as Fucales. However, due to the high abundance of adult *Sargassum* spp. compared to other Fucales at my site, it is likely that most Fucales recruits on the plates were in fact *Sargassum* spp.

Data were analysed separately for each effect (live coral, other occupants and substrate texture and material), because the treatments were not factorial combinations. The comparison between live and dead coral did not require statistical comparison. The density and mean size of recruits of Fucales and *L. variegata* were compared between pre-conditioned and clean, ceramic control plates, using one-way ANOVAs and Bonferroni post-hoc comparisons. As well as simply comparing plates pre-conditioned on the two different sites, I also explored the potential effects of turfs and CCA using simple linear regressions. However is important to recognise that, since both pre-conditioning treatments had algal turfs and CCA in varying amounts, it is difficult to separate the effects of these algal groups on recruitment. The effects of texture were analysed within type of material using *t*-tests. Both density and size data were transformed ($\log_{10}$) for homogeneity of variance, based on Cochran's test for homoscedasticity, and were checked for normality of residuals (graphically). Minor transgressions of Cochran's test were accepted where these were unlikely to influence the conclusions.

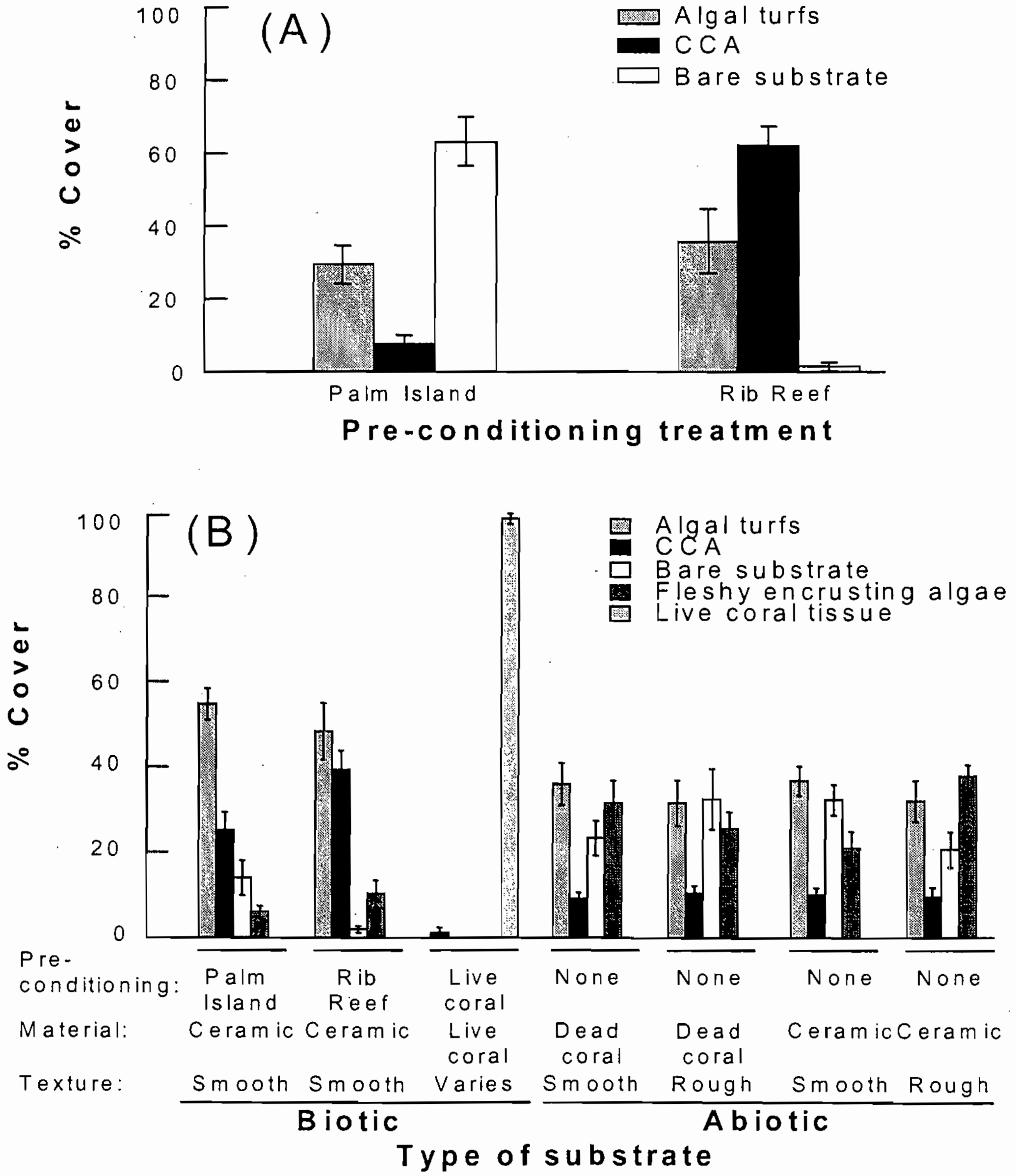


Fig. 2.1 Mean percent cover of benthic organisms and bare substrate on settlement plates. (A) Cover in two pre-conditioning treatments (Palm Island and Rib Reef) at the beginning of the experiment. (B) Cover in all treatments at the end of the experiment (± 1 SE, N = 9).

2.3 Results

2.3.1 Algal recruitment onto healthy coral tissue

Healthy corals apparently excluded algal recruitment of Fucales and *L. variegata* in this study. Recruits were never found on healthy coral tissue of any of the species. In contrast, none of the other plates had no recruits and dead coral settlement plates had approximately 100 and 10 recruits of Fucales and *L. variegata* per plate respectively (Figs. 2.2 and 2.4). I occasionally observed recruits of both taxa growing on small areas of dead coral tissue (< 2 cm^2) beside the healthy coral tissue.

2.3.2 Effects of pre-conditioning sites, algal turfs and CCA

2.3.2.1 Fucales

The recruitment of Fucales propagules was not significantly different between plates from the two pre-conditioning sites and control plates which had not been pre-conditioned (all smooth ceramic plates; Fig. 2.2, Table 2.1). Interestingly, recruits were distinctly longer and wider on plates pre-conditioned at Rib Reef (Fig. 2.3), although the difference was not statistically significant (Table 2.1).

Fucales recruits were frequently observed growing both among algal turfs (between the filaments), and on CCA, as well as on bare substrate (with associated microbial films). Regression analyses indicated a significant, positive relationship between the cover of algal turfs and the density ($r^2 = 0.244$, $P = 0.037$), length ($r^2 = 0.581$, $P = 0.001$) and width ($r^2 = 0.486$, $P = 0.001$) of Fucales recruits on pre-conditioned plates. The height of the algal turf canopy was not significantly related to the density of Fucales recruits ($P = 0.114$) but was weakly, positively related to the length ($r^2 = 0.263$, $P < 0.001$) of Fucales recruits. CCA showed a significant negative relationship with the density ($r^2 = 0.274$, $P = 0.026$), and no clear relationship with the length ($r^2 = 0.14$, $P = 0.637$) or width ($r^2 = 0.041$, $P = 0.422$) of recruits on pre-conditioned plates.

2.3.2.2. *Lobophora variegata*

The recruitment of *L. variegata* recruits was not significantly different among pre-conditioned plates and control plates (Fig. 2.4; Table 2.1). Although recruitment was slightly, but not significantly, lower in the pre-conditioned plates from Rib Reef, the recruits on those plates grew significantly more than those in any other treatment. They were 114 % larger and 165 % wider than recruits from the plates pre-conditioned at Palm Is. and from the control plates (Fig. 2.5; Table 2.1).

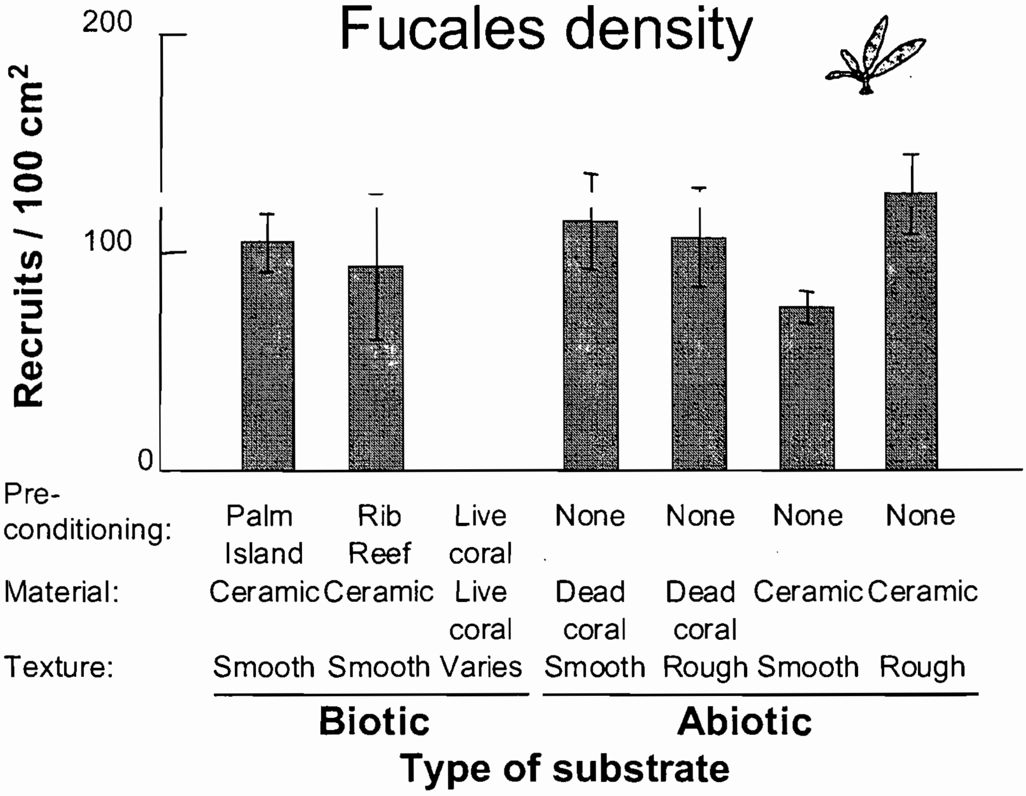


Fig. 2.2 Mean density of recruits of Fucales (mainly *Sargassum* spp.) across pre-conditioning treatments, healthy live coral tissue, and coral and ceramic plates with different textures (± 1 SE, N = 9). Comparison of live and dead coral shows that live coral tissue prevented the recruitment of algal propagules. Comparison of plates pre-conditioned at Palm Island, at Rib Reef and control (smooth ceramic) plates shows that pre-conditioning sites had minimal effects on recruitment. Comparison of smooth and rough ceramic plates shows that increased rugosity enhanced algal recruitment; comparison within the dead coral plates suggests that the differences in coral texture in this experiment had little effect on recruitment.

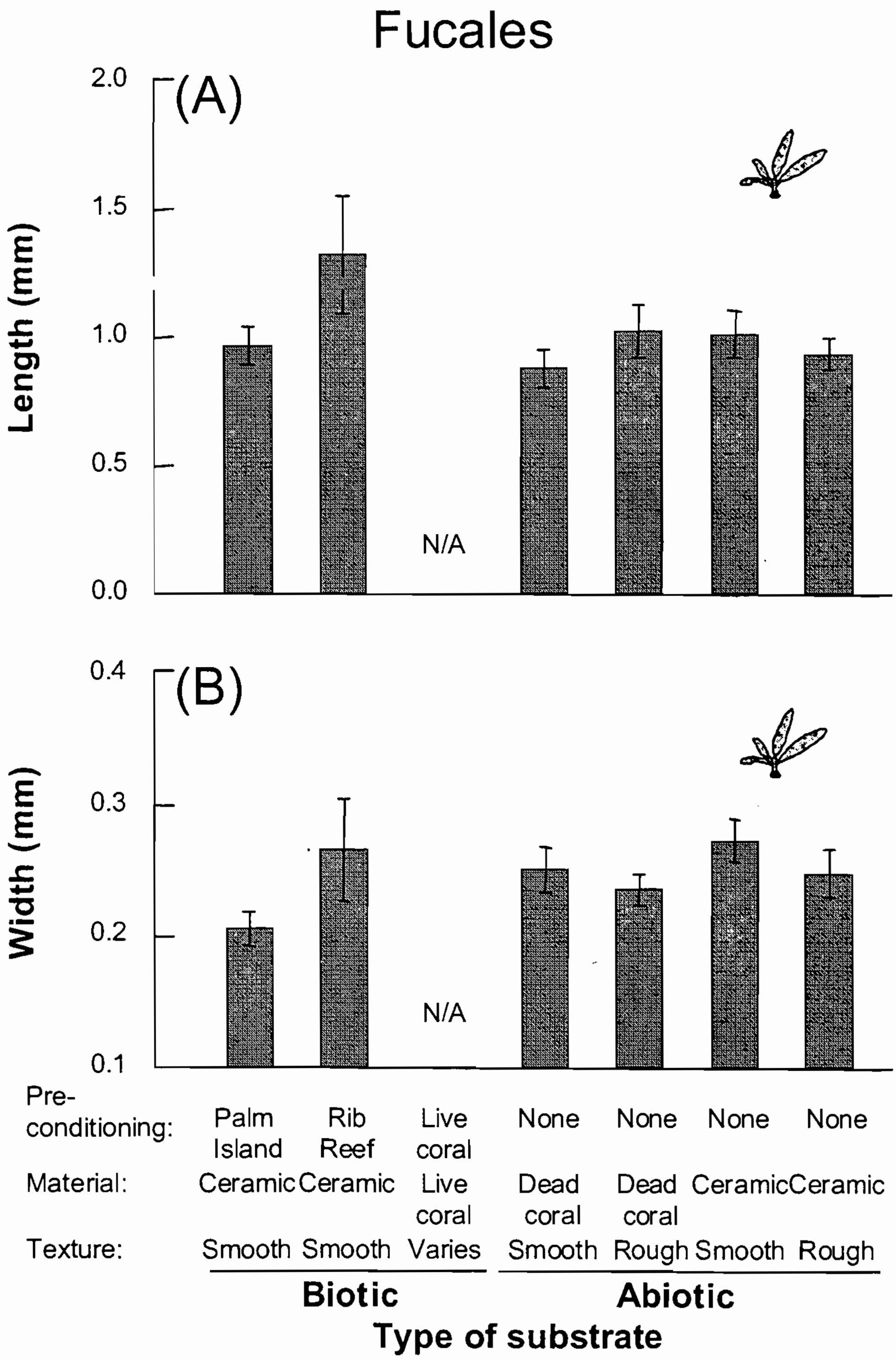


Fig. 2.3 Mean (A) length and (B) width of Fucales recruits (mainly *Sargassum* spp.) for treatments as in Fig. 2.2. N/A: not applicable.

Table 2.1 One way ANOVAs for effects of substrate pre-conditioning on the density and sizes of early stages of two brown macroalgae: Fucales spp. and *Lobophora variegata*. R: Rib; P: Palm; C: Control.

Source of variation	df	MS	*F*	*P*	Conclusion
Fucales					
Density					
Pre-conditioning	2	0.184	1.286	0.295	n.s.
Error	24	0.143			
Length					
Pre-conditioning	2	0.021	0.788	0.466	n.s.
Error	24	0.027			
Width					
Pre-conditioning	2	0.036	3.006	0.068	n.s.
Error	24	0.012			
L. variegata					
Density					
Pre-conditioning	2	0.105	0.812	0.456	n.s.
Error	24				
Length					
Pre-conditioning	2	0.157	8.353	0.004	$R > P \approx C$
Error	14	0.019			
Width					
Pre-conditioning	2	0.232	9.014	0.003	$R > P \approx C$
Error	14	0.026			

Lobophora variegata recruits were also frequently observed growing both among algal turfs (between the filaments), and on CCA, as well as on bare substrate (with associated microbial films). There was no significant relationship between the density or sizes of *L. variegata* recruits and the cover of algal turfs ($r^2 < 0.02$, $P > 0.5$). The cover of CCA was not related to density of *L. variegata* recruits ($r^2 < 0.01$, $P > 0.8$), but was moderately and significantly positively related to growth ($r^2 > 0.56$, $P < 0.01$ for both length and width).

2.3.3 Effects of texture and material on Fucales and *L. variegata* recruits

Comparison of rough and smooth ceramic plates indicated that roughness significantly enhanced the density of Fucales and *L. variegata* recruits (Figs. 2.2 and 2.4). Recruitment was 65 % and 177 % higher on rough ceramic plates than on smooth ceramic plates for Fucales ($t = 2.97$, df = 16, P = 0.009), and *L. variegata* ($t = 2.06$, df = 16, P = 0.055) respectively. No differences were observed in the size of Fucales recruits

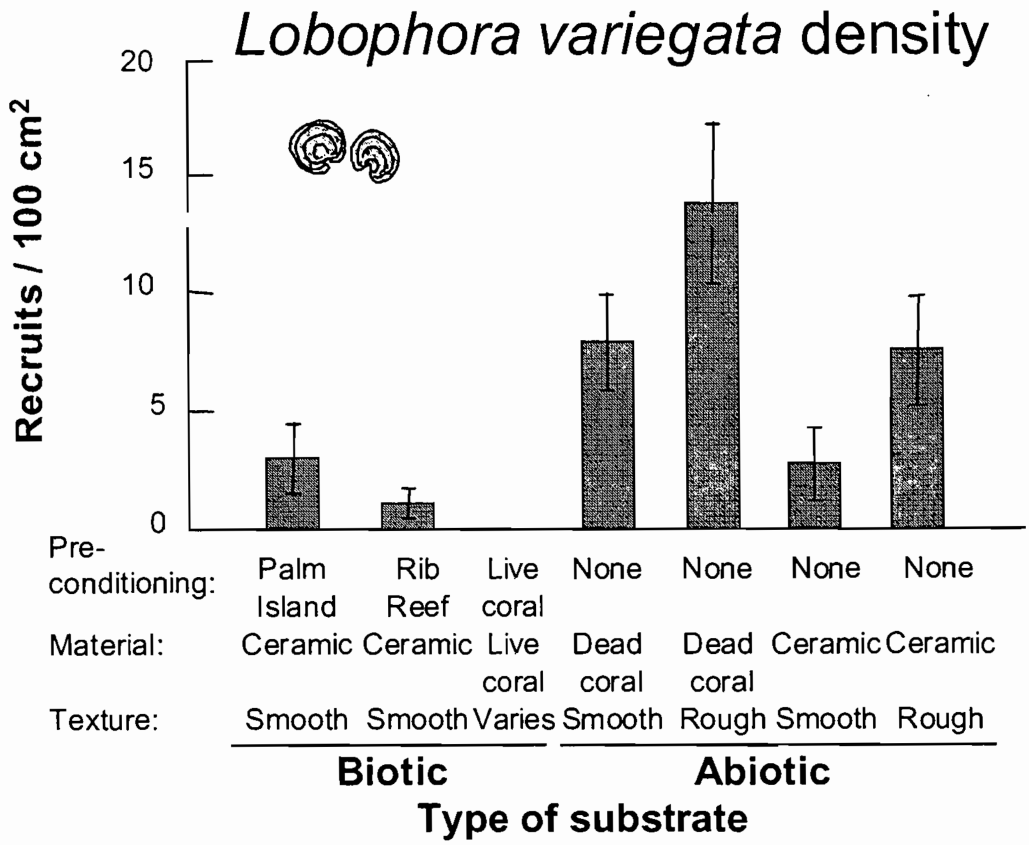


Fig. 2.4 Mean density of recruits of *Lobophora variegata* for treatments as in Fig. 2.2.

across abiotic substrates (t = -0.61, df = 16, P = 0.547 for length; t = -1.07, df = 16, P = 0.3 for width; Fig. 2.3). In contrast, recruits of *L. variegata* from rougher surfaces were significantly smaller than those from smoother surfaces (Fig. 2.5; t = -3.51, df = 11.7, P = 0.005 for length; t = -3.29, df = 11.4, P = 0.007 for width).

Within the dead coral plates, the density of Fucales recruits was not affected by the grooves cut into the rough treatment (t = -0.27, df = 16, P = 0.791; Fig. 2.2). The survival of *L. variegata* on roughened dead coral plates was higher (74 %) than on ordinary dead coral plates, but the difference was not significant (t = 1.54, df = 16, P = 0.144). No differences were observed in the size of recruits of both taxa between texture treatments of dead coral (t-test, P > 0.05; Figs. 2.3 and 2.5). In general, dead coral plates had more recruits of *L. variegata* than ceramic plates (120 % higher; Fig. 2.4).

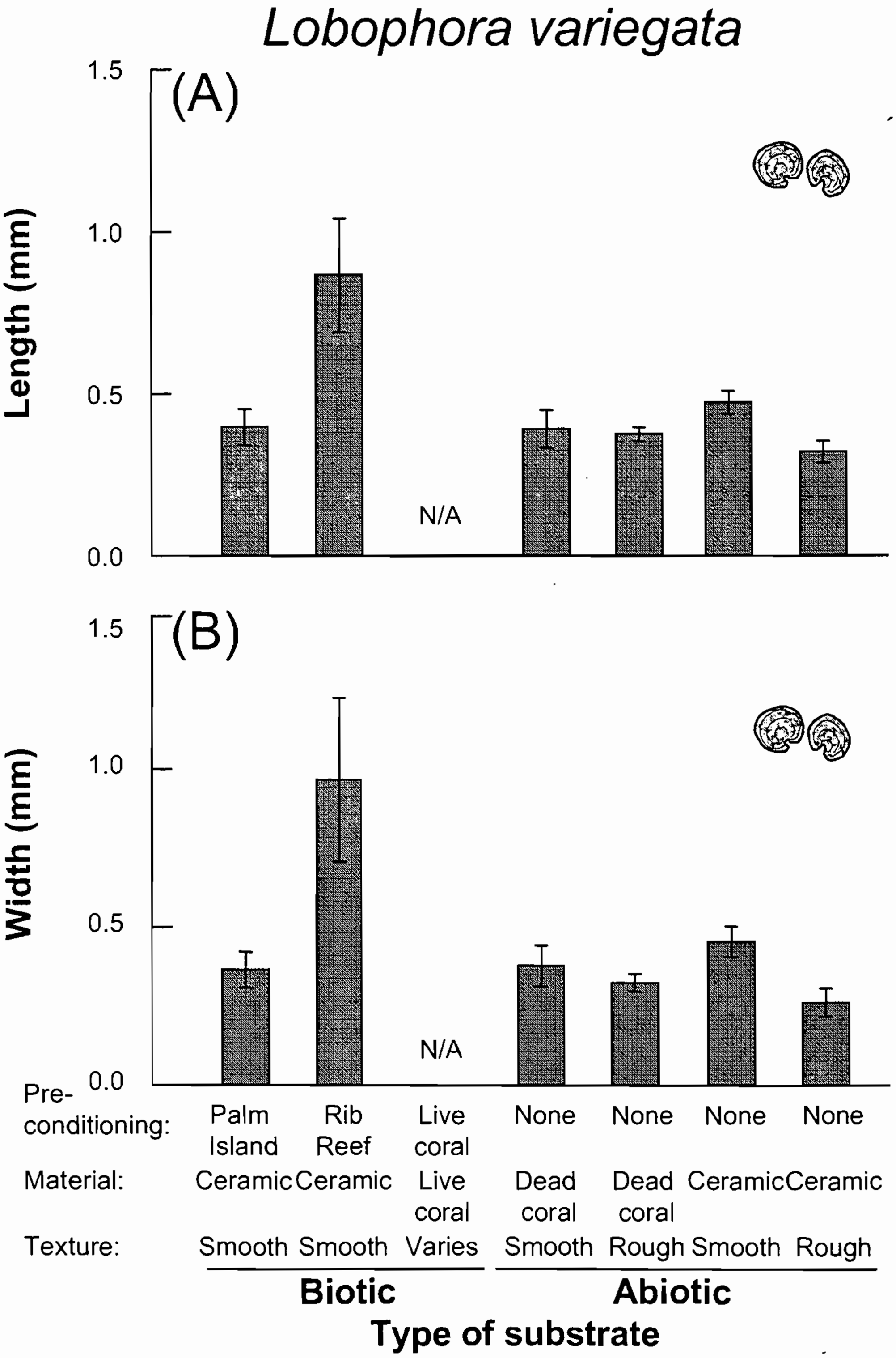


Fig. 2.5 Mean (A) length and (B) width of *Lobophora variegata* recruits as in Fig. 2.3 (except N=6).

2.4 Discussion

The nature of the substrate had considerable influence on the recruitment success of the two coral reef macroalgae studied. These effects were, however, variable and depended on the type of substrate, the species, and the type of response measured. Despite this variability, algal propagules did not recruit onto healthy live coral tissue.

2.4.1 Algal recruitment onto healthy coral tissue

The most important outcome of this study was the demonstration that algal propagules of Fucales and *L. variegata* did not settle on healthy live coral tissue (Figs. 2.2 and 2.4), independent of the coral species. Algal recruits were never found on healthy coral tissue of any of the coral species examined, supporting findings for massive *Porites* corals from nearby reefs (Chapter 3). Although I observed occasional recruits of both species growing on small dead tissue areas beside healthy coral tissue, the pattern of dead coral tissue was never consistent with algal settlement as the cause of coral tissue death, but was generally indicative of physical or other injuries (Fig. 2.6). The strong and consistent contrast between recruitment on live corals and dead coral plates strongly suggests that the absence of recruits on live coral tissue represents defensive exclusion by the coral. The strength of this exclusion is emphasised by the contrast with CCA (and algal turfs), since both Fucales and *L. variegata* were observed growing directly on CCA (and among turfs). Thus the ability of corals to exclude algal recruitment is impressive, not only in comparison to dead substrata, but also in comparison to other organisms, including calcified organisms.

This conclusion has important implications in terms of the competitive interactions between benthic algae and corals, particularly in the context of reef degradation. The replacement of corals by algae may occur by three processes: 1. Settlement and growth of algal propagules from the plankton onto the healthy coral tissue; 2. Competitive vegetative overgrowth from adjacent algal thalli; 3. Coral disturbance, injury, stress or tissue mortality, followed by either of the above processes. The mechanism of replacement due to algal settlement from the plankton onto healthy coral tissue seems to be rare for a range of algal groups and forms (Chapter 3). The second mechanism, replacement by vegetative overgrowth has been documented for fleshy macroalgae (including *L. variegata*) and filamentous algal taxa, both on nearby islands of the GBR (Jompa and McCook, 2002a; 2002b) and in the Caribbean (Hughes, 1994; Littler and Littler, 2000). Algal settlement and colonisation is a rapid and almost universal consequence of coral tissue death, or even injury or stress (Chapter 3; Done, 1992; McCook et al., 2001a). Thus it appears that the replacement of healthy corals by algae is more likely to involve either lateral, vegetative overgrowth by competing algae or coral disturbance and subsequent algal colonisation, than settlement of algal propagules directly from the plankton.

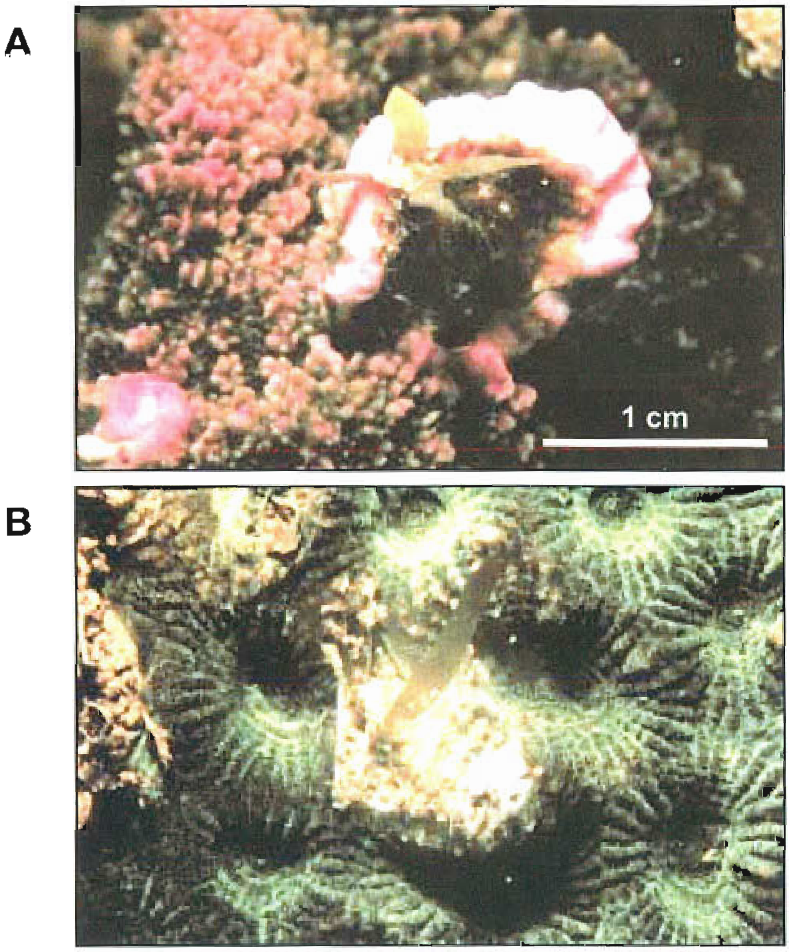


Fig. 2.6 Photographs of *Sargassum* spp. recruits growing on small dead tissue patches beside healthy coral tissue of (A) *Montipora* sp. and (B) *Favites* sp. at the experimental site at Goold Island.

The mechanisms by which live corals competitively inhibit the settlement of algal propagules (i.e. space pre-emption) are not clear from my study. However, likely processes include mucus secretion, cleaning activity of tentacles, allelochemicals or ingestion of algal propagules (see reviews in Lang and Chornesky, 1990; McCook et al., 2001a). Algal propagules that settle onto coral surfaces may get trapped on the mucus layer, which may be subsequently removed by tentacle activity or water movement. Filter feeding benthic organisms, such as mussels, can ingest algal propagules and may have the potential to modify rates of macroalgal settlement to benthic communities (Santelices and Martínez, 1988). However, there is a lack of experimental evidence supporting possible ingestion of algal propagules by the corals, although some corals may include microalgae in their diet (Fabricius et al., 1995). Further experiments are needed to determine the contribution of different potential mechanisms to the inhibition of algal settlement and recruitment.

2.4.2 Effects of pre-conditioning sites, algal turfs and CCA

In general, variations in density of Fucales and *L. variegata* recruits (Figs. 2.2 and 2.4) among pre-conditioning treatments or sites were not significant, notwithstanding the increased growth of *L. variegata* recruits on plates from Rib Reef (Fig. 2.5). To some extent the lack of significant differences appears to reflect variation within treatments (limiting experimental power). Pre-conditioning treatments are unlikely to have strong effects except those caused by the colonising biota, and the abundance and height of turf algae in particular varied considerably within treatments. On this basis, the relationships between recruitment and components of the EACs may be more informative than the lack of significant differences among treatments.

The contrasting relationships between CCA and Fucales or *L. variegata* are intriguing. Previous work has generally found that CCA inhibited the recruitment of algal propagules (Steneck, 1997; Littler and Littler, 1997; Keats et al., 1997; Figueiredo et al., 1997), either by epithelial sloughing or enhanced grazing on the surface of the CCA (but see Kendrick, 1991; Airoldi, 2000, for different effects of CCA on algal turfs). These processes could explain the weak negative relationship between Fucales recruitment and cover of CCA. However, this contrasts markedly with the increased growth of *L. variegata* on plates conditioned at Rib Reef, which presumably reflect the higher abundance of CCA on those plates (Fig. 2.1A), since there was a clear positive relationship with cover of CCA. The underlying cause of this pattern remains obscure, although Santelices and Varela (1994) found that calcium carbonate facilitated rhizoidal attachment in the fleshy red alga *Gelidium chilense*, perhaps explaining an apparent association between this alga and CCAs.

It is also intriguing to speculate on the contrasting relationships between CCA and Fucales or *L. variegata* and the contrasting distributions of these taxa across the continental shelf. Although the abundance of both taxa is apparently strongly regulated by herbivory (de Ruyter van Steveninck and Breeman, 1987; Morrison, 1988; McCook, 1996; 1997; Jompa and McCook, 2002b), *Sargassum* spp. are virtually absent from offshore reefs, whereas *L. variegata* is widespread, and generally common but low in abundance on offshore reefs (McCook et al., 1997; pers. obs.). As CCA are ubiquitous and most abundant on offshore reefs (McCook et al., 1997; Fabricius and De'ath, 2001), it may be that the differing distributions of *Sargassum* and *L. variegata* are to some extent due to differing effects of CCA.

The relationships between algal turfs and algal recruitment were also contrasting, being positively related for Fucales, but unrelated for *L. variegata*. Previous experimental studies have shown a range of effects for turf algae on recruitment of Fucales and kelps, including facilitation by both small, filamentous algal turfs (< 1 cm height; Ang, 1985b; McCook and Chapman, 1993) and large algal turfs (Brawley and Johnson, 1991; Benedetti-Cecchi and Cinelli, 1992), and competitive inhibition of survival of macroalgal recruits by algal turfs (Reed, 1990; Chapman, 1990; Worm and Chapman, 1998). The mechanisms mediating the facilitation interaction may include refuges against desiccation, grazing, and water displacement (above refs). The presence of a bacterial film has been also suggested to enhance recruitment of marine algae (Ang, 1985b; Santelices, 1990). Although the relationships in my study are only correlative, as I did not directly manipulate algal turfs, causal interpretations are strengthened by the nature of the pre-conditioning, which took place prior to and in a different place to the recruitment. It may be that the turfs facilitated attachment of Fucales recruits, with little subsequent inhibition of these taller taxa, but did not competitively inhibit the prostrate *L. variegata* juveniles. Overall, the effects of algal turfs and CCA on algal recruitment can not be considered to be homogeneous among taxa.

2.4.3 Effects of texture and material

Substrate rugosity of ceramic plates enhanced the survival of Fucales and *L. variegata* recruits, and reduced the growth (size) of *L. variegata*. Rougher surfaces had up to 165 % more recruits than the smoother surfaces (Figs. 2.2 and 2.4). Among plates made from dead coral, although my attempt to increase rugosity had no effects on Fucales recruitment, there was a large but not significant increase in *L. variegata*. I suggest that the lack of significant effects of rugosity among coral plates reflects the high intrinsic micro-rugosity or porosity of the coral skeleton. Higher survival of macroalgal recruits on rougher textures is consistent with reports on the literature (Harlin and Lindbergh, 1977; Norton, 1983; Hixon and Brostoff, 1985; Fletcher and Callow, 1992; Amsler et al., 1992; McCook and Chapman, 1993; Johnson, 1994; Anderson and Underwood, 1994). Rougher textures and porous materials have been suggested to protect algal recruits from dislodgment by wave action, water currents, and grazing activity and to increase surface area available for settlement and recruitment (refs. above).

It is interesting that substrate rugosity increased the density but decreased the growth of *L. variegata* recruits (Fig. 2.5). This may reflect increased competition with other organisms, such as fleshy crustose algae (Fig. 2.1B), the recruitment of which was also enhanced by the texture. Whatever the explanation, the contrasting effects on density and growth demonstrate that effects on recruitment may vary markedly among different life-history parameters.

Recruitment of *L. variegata* was affected more by rugosity (and perhaps by material) than that of Fucales. This variability may reflect a relationship between propagule size and optimum surface rugosity (Fucales propagules are substantially larger than those of *L. variegata*), or differences in post-settlement mortality, since effects on the two stages can not be separated in this study (Fletcher and Callow, 1992; as discussed by Amsler et al., 1992). However, they again emphasise the variability, this time between taxa.

Although it is not possible to directly compare recruitment on coral and ceramic plates in a factorial analysis, it is worth noting that density of *L. variegata* recruits was significantly less on ceramic plates than on coral plates. Whether this is due to physical or chemical differences in the plates is unclear, although the micro-porous nature of the coral skeleton did allow the rhizoids of *L. variegata* to penetrate deeper and anchor better than did the ceramic material (pers. obs.; see also Hardy and Moss, 1979 for

Fucus). Barnes and Topinka (1969) noted enhanced growth of *Fucus* germlings on carbonate substrates, in contrast to our results for both taxa.

In summary, the abiotic and biotic characteristics of the substrate may be important to the recruitment of these two taxa of brown algae. However, the outcomes of these interactions were variable and complex, and depended on the type of substrate, organisms already present, the species involved, and the life history processes (attachment, survival or growth). Despite the heterogeneity in outcomes, it is clear that algal settlement via propagule dispersal will rarely occur onto healthy coral tissue. The variability in outcomes is important in terms of subsequent development of algal populations, especially, for example, during putative invasions by *Sargassum* of inshore reefs of the GBR.

Chapter 3

The Fate of Bleached Corals: Patterns and Dynamics of Algal Recruitment

3.1 Introduction

Coral bleaching is an important cause of coral mortality, potentially resulting in large scale declines in coral populations, which amount to reef degradation (Glynn, 1993; Hoegh-Guldberg, 1999). Several mass-bleaching events have been recorded on coral reefs around the world during the last 20 years, and there is concern that such events may be increasing in frequency (Brown, 1997; Hoegh-Guldberg, 1999). The most recent mass bleaching, in early 1998, was one of the strongest bleaching events on record for the Great Barrier Reef (Berkelmans and Oliver, 1999). Research on coral bleaching has largely focussed on the climatological and physiological causes of bleaching, behaviour of zooxanthellae, and, importantly, the recovery of zooxanthellae (Brown, 1997; Hoegh-Guldberg, 1999). However, there has been little work addressing the fate of bleached corals that fail to recover their zooxanthellae (Brown, 1997).

Bleached coral tissue may either regain its zooxanthellae and recover, or may die, in which case it is generally rapidly colonised by benthic algae. Large scale, mass bleaching events may result in massive algal overgrowth of the newly available substratum provided by the dead coral skeleton (Wellington and Victor, 1985; Glynn, 1990). These changes may thus amount to a partial or extensive phase shift, in which abundant benthic algae replace abundant corals, potentially amounting to or contributing to long-term reef degradation just as severe as that caused by diseases, eutrophication or over-fishing (Birkeland, 1987; Glynn, 1993; Aronson and Precht, 1997; McCook, 1999; McClanahan et al., 2001). Despite the importance to such changes, very little is known about the dynamics of algal colonisation of bleached corals.

The composition and type of algal colonisation may be important to the consequences of coral bleaching both in terms of the severity of disturbance, and the potential for future reef recovery. The severity of the disturbance may be influenced by the effects of the colonising algae on the ability of corals to recover from bleaching. The composition and successional trajectory of the colonising algae may also influence the ability of coral populations to re-establish on algal dominated substratum, either by recolonisation by surviving corals, or by new recruitment. The outcome of the competitive interaction between corals and benthic algae may depend on the species of coral and alga involved and the mechanism mediating the interaction (McCook et al., 2001a), with consequences for the processes of reef phase shifts and recovery from disturbances (McCook, 1999). For example, Bak et al. (1977) reported that filamentous turfing algae delay the regeneration of coral tissue after mechanical damage. In contrast, Meesters and Bak (1993) found that filamentous algae did not affect coral recovery, and in one instance, canopy-forming *Sargassum* beds were found to protect corals from bleaching damage (Jompa and McCook, 1998).

This study explores the patterns of algal colonisation of bleached corals, and the potential interactions with the corals. The study addressed four specific questions:

- What are the patterns and variations in coral tissue recovery or mortality, subsequent to different degrees of bleaching damage?
- What are the nature, composition and trajectory through time of algal colonisation of bleached corals?
- Does that colonisation depend on the severity or degree of the bleaching?
- Does the algal colonisation influence the fate of the bleached corals and the chances of coral recovery?

To address these questions I examined the abundance and species composition of algal recruitment, and cover of live coral tissue, on massive corals (*Porites* spp.) with different severities of bleaching, over a period of 2.5 years.

3.2 Methods

3.2.1 Study Sites

The study was carried out at Orpheus Island and Pandora Reef, which are located 30 km apart on the inshore central section of the Great Barrier Reef (GBR; Fig. 3.1). By late February and early March 1998, coral reefs of this area had suffered severe and extensive coral bleaching associated with raised seawater temperatures (Sweatman et al., 1998; Baird and Marshall, 1998; Berkelmans and Oliver, 1999, pers. obs. for this site). The 1998 coral bleaching event affected coral reefs around the world and was linked to an El Niño event (Wilkinson, 2000). Offshore reefs of the GBR were also affected by the bleaching event, but to a lesser extent than inshore reefs, where coral mortality was up to 80% at sites on some inshore reefs (Berkelmans and Oliver, 1999). Corals at the study sites recovered their zooxanthellae by June-August (4-6 months after the bleaching) but a large proportion of coral tissue died and was replaced by algae. The study site at Orpheus Island was on the reef crest on the sheltered, western side of the island (Pioneer Bay: 18° 36’ 422 S; 146° 29’ 365 W), where the fringing reef between 1 m to 7 m depth is dominated by large massive colonies of *Porites* spp. (*P. australiensis, P. lobata* and *P. lutea*). Pandora Reef is a shingle covered bank reef. The study site was on the southern, windward side of the reef (18° 49’ 009 S; 146° 26’ 035 W) at 3-6 m depth. The reef here is also dominated by large colonies of massive *Porites* spp., and stands of dead branched Acroporids and fleshy macroalgae (also Done, 1982; Done and Potts, 1992).

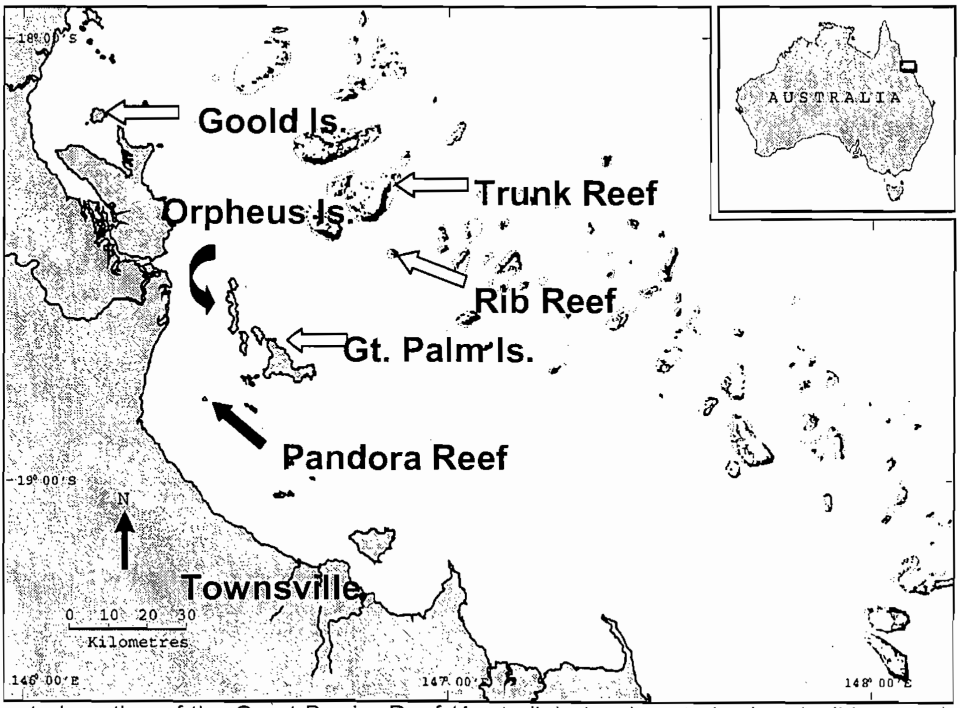


Fig. 3.1 Central section of the Great Barrier Reef (Australia) showing study sites (solid arrows). Qualitative observations were made at a range of inshore and mid-shelf sites over the period of this study (open arrows).

3.2.2 Sampling design and methods

Coral survival and mortality and algal colonisation were monitored using a combination of detailed, quantitative small-scale measurements over a range of conditions, and qualitative observations at larger scales (Fig. 3.1). To determine whether the trajectory of algal colonisation onto bleached corals depended on the severity of bleaching, I monitored benthic algal recruitment in three different "bleaching categories" over 2.5 years. I defined three categories to represent different levels in a gradient of bleaching damage to corals: "healthy" (chosen as initially having 100 % cover of unbleached, live coral tissue), "bleached" (started with 100 % cover of recently bleached, live coral tissue with no dead tissue and no algal colonisation; Fig. 3.7A.1) and "severely bleached" (i.e. coral tissue/skeleton areas partially overgrown by a thin algal turf layer, but clearly identifiable as bleached during this event). To explore the extent to which algal recruitment was location specific, bleaching treatments were replicated on two reefs (Orpheus and Pandora). To investigate the extent to which the patterns of algal colonisation were specific to bleached corals, 8 smooth ceramic settlement plates (11 x 11 cm) were fixed to the substratum in the study area at Orpheus Island, for comparison with coral substrates.

The bleached and severely bleached corals were found subtidally, between 2-5 m depth. However, at Orpheus Island, bleaching damage at these depths was so severe that no healthy corals could be found, so control, healthy corals were chosen deeper (6 m). Thus, these comparisons may be confounded by the depth difference. Massive *Porites* colonies were chosen because they are particularly common on the inshore reefs and are the most important reef-building corals on the inshore GBR (Hopley, 1982).

For each of the bleaching categories, 8 plots of 10 x 10 cm were marked on horizontal surfaces on the top of massive colonies of *Porites* spp. and the fate of the bleached coral in these plots was monitored by measuring percent cover of live coral tissue and benthic algae (at both species and functional group levels), using both direct observations and photographs. Where sufficient suitable coral colonies were available, I selected one plot per colony, using colonies with fairly homogeneous bleaching damage (although most colonies had less bleaching on the sides than the tops of the colonies). Cover of live corals, benthic algal groups (algal turfs, fleshy macroalgae and crustose coralline algae – CCA) and species of fleshy macroalgae were estimated by projecting the photographic slides onto a grid of 100 quadrats. Photographic sampling at Orpheus Island was carried out on 11 dates at intervals of 1 to 4 months between April 1998 and August 2000. At Pandora Reef restricted access in bad weather meant that photographic sampling was only possible on 7 dates in the same period.

The species composition and abundance of settled algal turfs were monitored by scraping areas approximately 1 cm^2 to a depth of 1-2 mm (therefore including endolithic taxa) adjacent to each coral plot. Sampling dates included autumn (April-May 1998, 1999 and March 2000) and winter (July 1998 and 1999). Algal turf samples were decalcified with 10 % HCl and stained with a solution of aniline blue (Price and Scott, 1992), then spread homogeneously over 2 x 2 cm on a microscope slide, and scanned with a compound microscope, recording all algae taxa present. The relative abundances of algal taxa were estimated by determining the percent cover in 5 microscopic fields at 100x. Representative specimens of the most abundant taxa are lodged at the JCU herbarium (JCT). Endolithic taxa were separated based on direct observations of growth habit and published records (Le Campion-Alsumard et al., 1995).

Data analyses included one-way ANOVAs and Tukey's HSD (using Systat ™ 8.0), to compare the means in cover of corals and algal groups amongst treatments (fixed factor) at each date. Patterns of species abundances and composition in relation to bleaching treatments, locations, date and height of the overall algal turf canopy were analysed using principal component and redundancy analyses (using CANOCO 4, ter Braack and Šmilauer, 1998) and using time-series plots for more abundant taxa (details not presented). Bleaching treatment, location, date and algal turf height were treated as "environmental variables" in the redundancy analysis (ter Braack and Šmilauer, 1998). Cover of coral and algal groups was arc-sin transformed and algal turf species cover was $\log_{10}$ transformed before statistical analyses, to homogenise variances.

3.3 Results

3.3.1. Overall patterns

The sequence of events following the coral bleaching is summarised in Fig. 3.2. In general, coral tissue that recovered zooxanthellae within 4-6 months after the bleaching survived, whereas tissue that did not recover zooxanthellae within this period died and was rapidly colonised by thin algal turfs. Algal colonisation occurred between 1 to 6 months after the bleaching, and no further replacement of corals by algae could be attributed to bleaching damage after approximately 7 months (September 1998). At the beginning of the bleaching event (February-April 1998), many corals produced an abundant layer of mucus. This mucus accumulated together with a fine film of sediment, and provided substrata for settlement and growth of algal propagules, even when overlying bleached live coral polyps. In some cases, this thin mucus-sediment-algal layer (< 2mm thick) was sloughed off, often followed by recovery of the corals. In other cases, the algae were apparently able to attach to the coral skeleton. Algal turfs dominated algal colonisation for more than 2.5 years, although fleshy macroalgae and crustose coralline algae (Figs. 3.3 and 3.4) overgrew some turfs during later stages of the succession. Subsequent grazing on algal turfs and corals by parrotfishes created bare substratum that was again colonised by algal turfs (Fig. 3.2). Qualitative observations at a range of reefs in the central GBR (Fig. 3.1) suggest widespread patterns of change similar to those documented in detail here, although coral mortality at Orpheus Island and Pandora Reef was apparently particularly severe.

3.3.2 Time-course of coral and algal cover in relation to degree of bleaching

The trajectories of live coral tissue cover and benthic algal cover indicated that coral death was always followed by a rapid colonisation by algal turfs composed of microalgae and filamentous algae (Figs. 3.3 and 3.4). In bleached and severely bleached plots, the cover of live coral tissue declined over the first 6-7 months, and was replaced by algal turfs. All healthy corals (i.e. plots chosen as initially having 100 % cover of unbleached, live coral tissue) remained healthy through the study period at both locations. Algal cover on healthy coral tissue was never more than 5 %, and was always much lower than bleached and severely bleached corals (Figs. 3.3 and 3.4; maximum P < 0.037, Tukey's test).

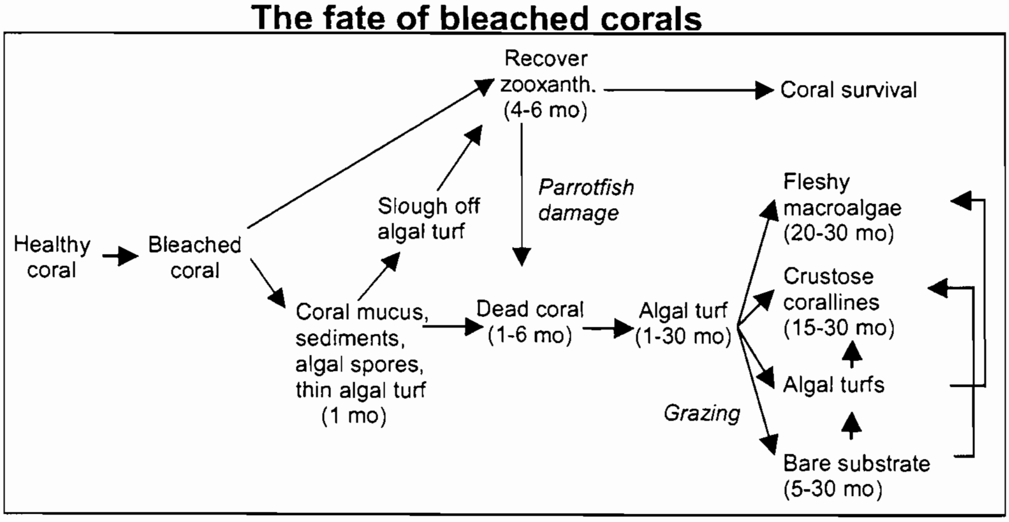


Fig. 3.2 Diagram summarising events following coral bleaching over a period of 30 months.

There were some differences in trajectories between bleached and severely bleached plots, but these were largely quantitative: the more bleaching the more coral death and consequently more algal turf overgrowth. Bleached coral plots exhibited higher live coral tissue cover (maximum $P < 0.04$, Tukey's test) and lower algal colonisation (maximum $P < 0.03$ Tukey's test) than the severely bleached corals during the first 6 months (note that in general, severely bleached plots initially had some algal colonisation, whereas bleached plots were chosen to have 100% cover of bleached but living coral tissue). However, from 7 months (September 1998) until the end of the study (August 2000), although patterns of coral and algal cover remained similar, the differences between bleached and severely bleached plots were generally not significant ($P > 0.05$ Tukey's test). In the bleached treatment, cover of live coral tissue decreased to less than 30 % after 7 - 9 months and then remained relatively constant (Figs. 3.3 and 3.4). Algal turfs reached 50 - 60 % cover in the first 3 months and remained high over 2.5 years, with relatively minor subsequent changes. Photographs show that some of the decline in coral cover in bleached plots at Orpheus Island between 5 and 7 months after bleaching was due to parrotfish grazing on recently recovered bleached corals (12% decline in coral cover, with related increases in bare substratum and then algal turfs). Successional trajectories varied considerably within bleached treatments, both between plots and between dates (Figs. 3.3 and 3.4).

In the severely bleached plots (which were chosen as initially having partial colonisation by algal turfs), the cover of live coral declined from 30 % to less than 5 % in one month at Orpheus Island and from 60 % to 12 % in 3 months at Pandora Reef (Figs. 3.3 and 3.4). Percentage of cover of live coral subsequently remained low. As dead coral was always colonised by algal turfs, turfs increased to 95 % and 70 % cover after 3 months at Orpheus Island and Pandora Reef respectively. Fleshy macroalgal and CCA cover remained low throughout the study at Orpheus Island. However, at Pandora Reef, fleshy macroalgae, including *Asparagopsis taxiformis, Sargassum spp., Lobophora variegata* and *Dictyosphaeria versluysii,* became slightly more abundant in the later stages of the study. There was some temporal and spatial variation in successional trajectories within severely bleached plots, although less than in bleached plots (Figs. 3.3 and 3.4).

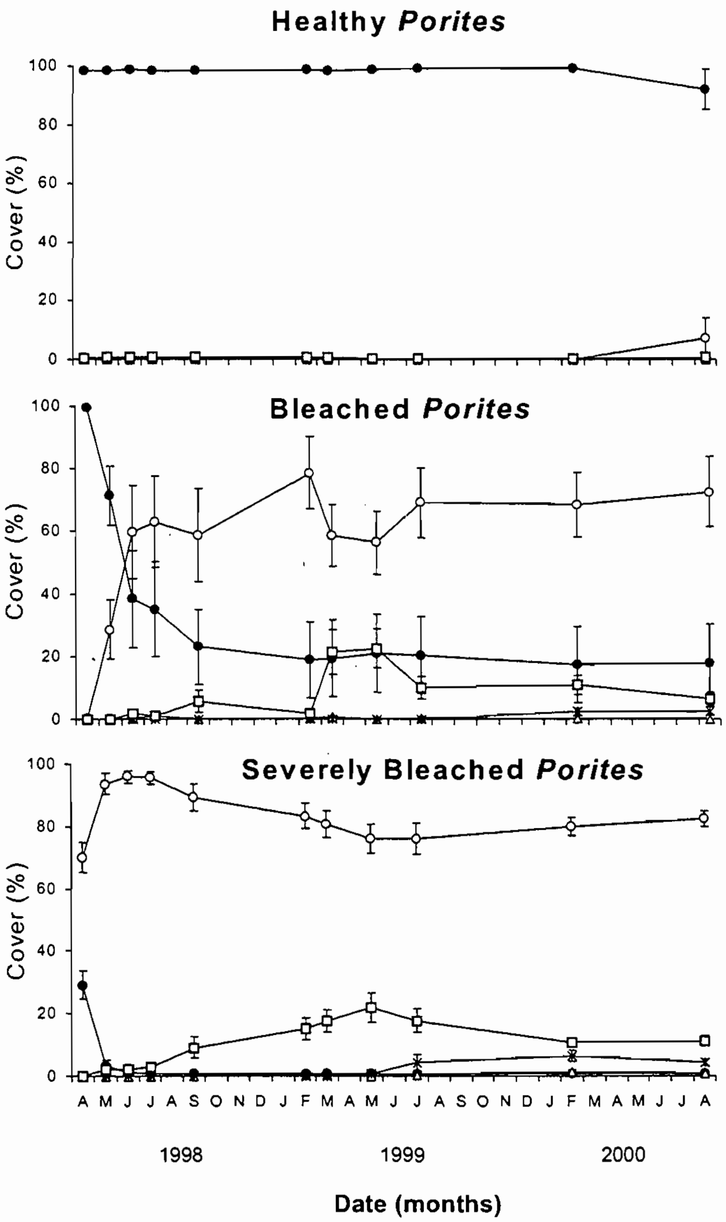


Fig. 3.3 Trajectories of coral and benthic algal cover (mean ± SE, n=8) through time in 3 bleaching categories at Orpheus Island. All areas had 100 % live coral cover before the bleaching event. (●) Coral, (O) algal turfs, (▲) fleshy macroalgae, (*) crustose coralline algae, bare substratum (□).

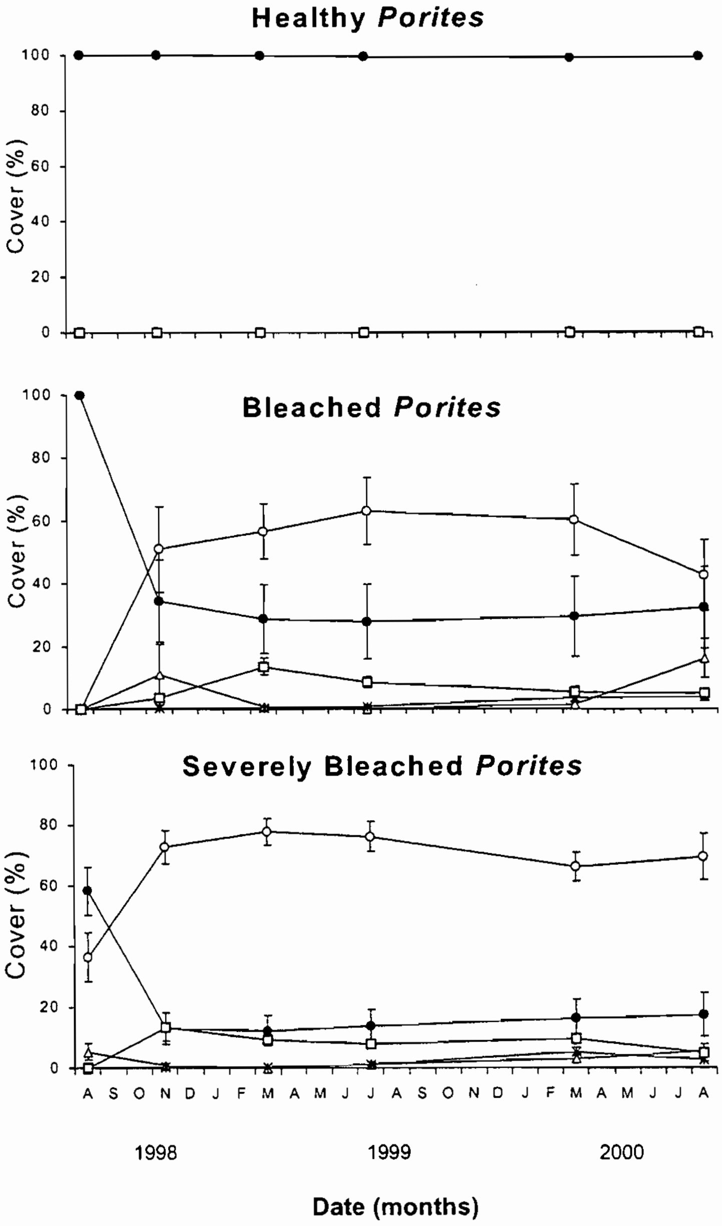


Fig. 3.4 Trajectories of coral and benthic algal cover (mean % ± SE, n=8) through time in 3 bleaching categories at Pandora Reef. All areas had 100 % live coral cover before the bleaching event. (●) Coral, (O) algal turfs, (▲) fleshy macroalgae, (*) crustose coralline algae, (□) bare substratum. (Note that although standard error bars are small, standard deviations would be approximately 3 times larger, indicating moderate variation among plots).

3.3.3 Trajectory of algal species composition during succession

The species composition of the algae recruiting to the bleached and severely bleached corals varied over the time-course of the succession and between plots (within categories and dates). Early stages of the algal succession of severely bleached corals (ca. < 3 months after the bleaching) were characterised by mixed thin algal turfs composed of up to twenty taxa from five algal phyla (Table 3.1). Pennate diatoms and coccoid and filamentous blue-green algae (*Spirulina subsalsa* and *Plectonema terebrans*) dominated the early stages with up to 50 % of relative abundance. The brown alga *Hincksia mitchelliae* and the green endolithic algae *Ostreobium* spp. were also abundant during the early stages of the succession. Mid to late stages of the succession were dominated by a diverse epilithic and endolithic assemblage of blue-green algae and turfing algae of more complex morphologies, including red *(Polysiphonia scopulorum*, *Anotrichium tenue*), brown (*H. mitchelliae*, *Sphacelaria rigidula* and *S. tribuloides*) and green algae (*Ostreobium* spp.). Algal species richness increased slightly early during the succession but was highly variable during later stages (Table 3.1).

Redundancy analyses clarified several patterns in the time-course of the turf assemblage. For example, several pioneer species occurred almost exclusively at the beginning of the succession (e.g. *Spirulina subsalsa*; top of Fig. 3.5A). Similarly, several taxa appeared predominantly at later successional stages (*Hyella* spp., *Polysiphonia upolensis*, *Taenioma nanum* and *Entocladia robusta*; bottom of Fig. 3.5A; Table 3.1). Juvenile (Table 3.1) and adult (Table 3.2) stages of fleshy macroalgae such as *Asparagopsis taxiformis*, *Sargassum* sp., *Lobophora variegata, Dictyota* spp. and *Dictyosphaeria versluysii*, were mainly recorded in later stages of the algal succession.

Although the structure of the algal assemblage on severely bleached corals 3 months after the bleaching was very similar to that observed after 24 months, there were considerable changes during the intervening period (Fig. 3.6). However, in both bleached and severely bleached plots, algal community structure apparently "stabilised" 15 months (May 1999) after the bleaching event, with only minor changes apparent in the last 10 months.

Table 3.1 Mean relative % abundance (see methods; n=8) of turf algae that colonised each of the bleaching categories (S = severely bleached corals; B = bleached corals) and clay plates (C) at two locations in April, May and August 1998 and March 1999 and 2000.

Algal Taxon	Orpheus											Pandora				
	Apr 1998		May 1998			Mar 1999			Mar 2000			Aug 1998	Mar 1999		Mar 2000	
	B	S	B	S	C	B	S	C	B	S	C	S	B	S	B	S
Pennate Diatoms		17.1	2.0	1.5	16.2	2.6	2.0	9.1	4.5	3.1	4.8	9.5	2.9	3.1	2.7	3.6
Blue green algae																
Calothrix crustacea		<0.1	0.7	2.8	0.7	1.2	5.6	2.2	1.1	1.7	3.2	0.2	0.5	1.6	0.1	0.1
Coccogonales spp.		3.6	12.0	1.9	20.2	3.2	2.0	15.0	1.7	3.2	5.3	2.8	2.7	1.4	0.6	0.4
Hyella spp.							1.4		0.1	0.7						
Mastigocoleus testarum						0.1	3.7	0.1	0.7	2.7	<0.1		5.0	4.7	2.4	2.7
Oscillatoriales spp.		5.2	2.2	5.7	3.1	4.7	5.4	5.2	2.3	2.2	6.9	5.9	17.4	12.5	2.1	5.9
Plectonema terebrans		14.7	37.8	15.4	2.6	1.6	3.5	3.2	12.1	10.9	4.6	3.2	2.7	1.3	2.7	5.8
Spirulina subsalsa		9.5	3.7	0.3	<0.1	<0.1		0.1	0.3			5.0	0.1	0.4		0.1
Undetermined sp.												0.3				
Red algae																
Acrochaetium spp.				0.03							<0.1				0.1	
Amphiroa sp.															<0.1	
Anotrichium tenue		1.0	2.7	7.0	0.5	0.7	0.9	0.1	9.9	9.3	8.5			0.6	<0.1	<0.1
Asparagopsis taxiformis															11.6	0.6
Centroceras apiculatum					<0.1											
Centroceras clavulatum		4.3	3.0	4.9	10.1	0.1	0.1	0.1	1.0	2.9	1.3	18.3		14.2	<0.1	0.9
Ceramium codii		<0.1	0.4	0.1	1.2		0.1	0.7		0.1		0.1			<0.1	<0.1
Ceramium flaccidum		0.7	1.6	0.3	2.3							7.1	2.8	5.3	1.1	2.0
Ceramium punctiforme				0.2	1.0											
Chondria sp.						<0.1	0.9									
Corallophila huysmansii		3.3		2.8	1.8	1.8	0.3	7.2	4.5	5.1	0.8					
Crustose corallines			6.0	0.7	<0.1	<0.1	0.6	1.0		<0.1	1.3	0.3				
Gelidiella pannosa		7.1	<0.1	1.9		4.3	13.9	0.6	1.1	<0.1	8.1		0.7	1.5	0.6	1.9
Gelidiopsis intricata									<0.1	0.8						0.2
Griffithsia heteromorpha		0.1		1.6	0.1						0.5					

Table 3.1 Continued

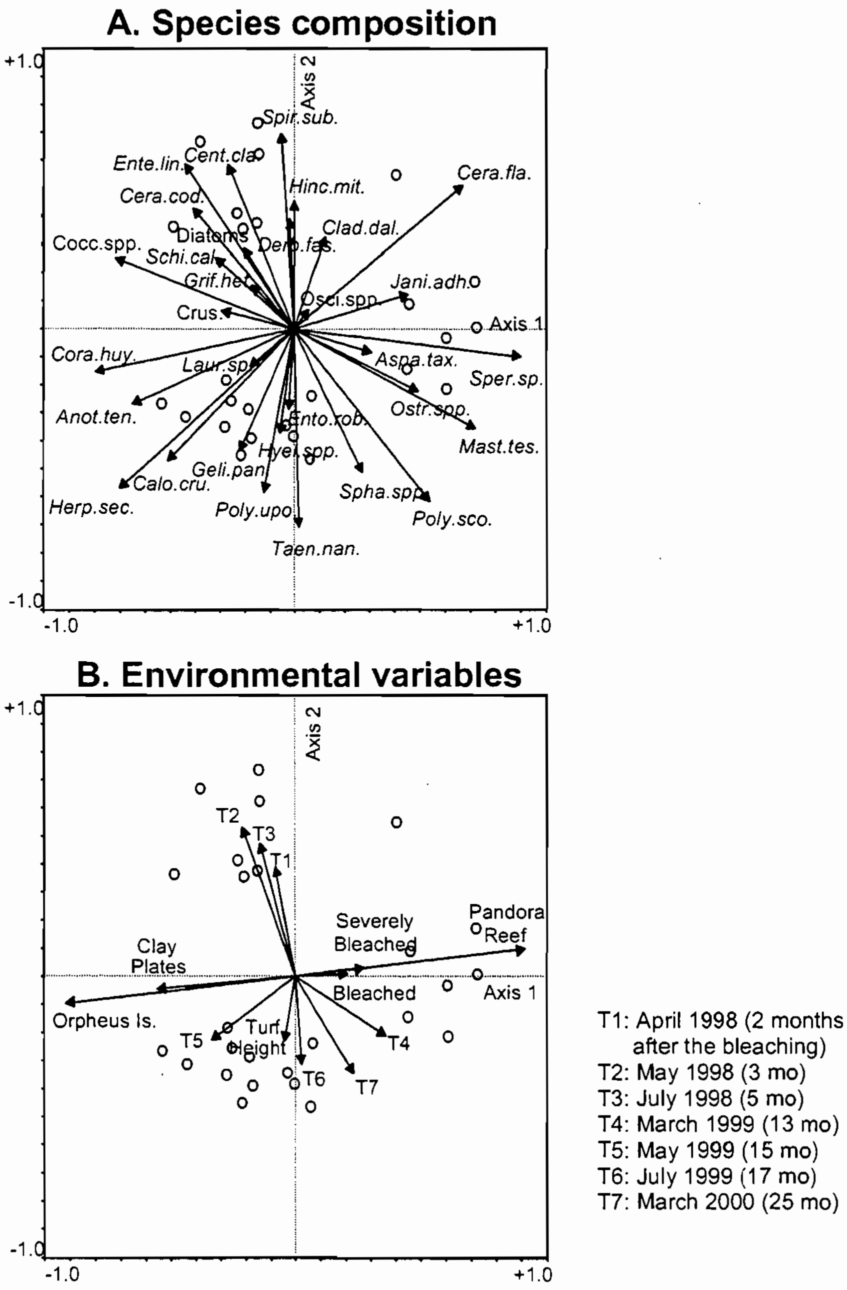
Algal taxon	Orpheus											Pandora				
	Apr 1998		May 1998			Mar 1999			Mar 2000			Aug 1998	Mar 1999		Mar 2000	
	B	S	B	S	C	B	S	C	B	S	C	S	B	S	B	S
Herposiphonia secunda f. sec.		0.2	<0.1	5.4	2.7	1.0	5.0	12.0	8.3	6.0	8.0			<0.1		0.7
Hypnea spinella				<0.1												0.2
Jania adhaerens				<0.1			<0.1					1.8		<0.1	1.2	2.3
Laurencia sp.			<0.1	0.1	0.1				<0.1	<0.1	2.5	<0.1				<0.1
Polysiphonia scopulorum		0.1	1.2	10.6	1.3	15.2	15.1	22.3	17.3	7.2	18.2	5.7	32.5	17.4	36.0	20.0
Polysiphonia upolensis									6.2	2.4	2.5					3.6
Pterocladia caerulescens															0.3	
Spermothamnion sp.				0.4	<0.1	0.7	0.1		0.5	1.6		2.4	3.7	8.7	8.8	7.7
Spyridia filamentosa										0.2						0.7
Taenioma nanum						2.5	2.4	4.4	1.6	0.7	3.6			1.5	6.6	2.0
Undetermined sp.				<0.1												
Brown algae																
Dictyota sp.										0.9					0.2	
Hincksia mitchelliae		7.8	8.5	4.3	15.4	21.9	1.3	0.3	10.5	7.7	<0.1	32.2	0.9	1.6	0.2	2.8
Lobophora variegata											0.6					
Sphacelaria spp. (*trib. & rig.*)		5.9	3.0	15.0	2.2	13.0	16.2	13.2	6.1	10.3	17.1	3.2	19.6	11.8	13.3	26.2
Green algae																
Acetabularia (*Polyphysa*) sp.											<0.1					<0.1
Blastophysa rhizopus											0.8					
Cladophora dalmatica		6.7	1.5	1.5	3.7	0.8	0.2	2.6	0.2	0.4	0.7	<0.1	1.0	3.4	1.0	2.8
Derbesia marina									0.3							
Derbesia fastigiata			2.8	4.9	0.4										0.6	0.4
Enteromorpha linza		5.8	10.1	1.1	14.4	0.5	0.7	0.6	0.2	0.4	0.3		0.1	<0.1	0.1	0.1
Entocladia robusta									1.9	1.6	0.1					
Ostreobium spp.		7.0	0.8	9.7		24.2	19.8		7.8	18.1	0.5	2.0	7.4	9.0	7.6	6.5
Udotea sp.										<0.1						
Species richness		20	21	29	24	22	24	20	26	29	27	19	16	21	26	30
Total abundance		100	100	100	100	100	100	100	100	100	100	100	100	100	100	100

3.3.4 Species composition in relation to extent of bleaching and substratum type

The species composition of colonising algae differed between bleached and severely bleached plots (Fig. 3.6), although this variation was relatively minor, compared to temporal changes, as indicated by the close overlap of vectors for the two categories in the redundancy analysis (Fig. 3.5B). The differences were most pronounced during early stages of succession and at Orpheus Island, where species composition on severely bleached plots during early stages was apparently in a "more developed" successional stage than that in the bleached plots. These differences were largely due to a higher abundance of coccoid cyanobacteria in bleached plots, and a higher abundance of *Ostreobium* spp. and *Herposiphonia secunda* in severely bleached plots (Table 3.1). The algal composition in the two categories converged after about 1.5 to 2 years (Fig. 3.6). On Pandora Reef the variation in species composition during early stages was apparently not related to the extent of bleaching.

Table 3.2 Mean absolute % cover of fleshy macroalgae that colonised *Porites* corals at two locations over time (data were obtained photographing 10 x 10 cm plots; n=16). Since there were no significant differences in % cover of fleshy macroalgae between bleached and severely bleached coral categories, the percentages of both bleaching categories were averaged.

Algal taxon	Orpheus				Pandora			
	Jul 1998	Mar 1999	Feb 2000	Aug 2000	Aug 1998	Mar 1999	Mar 2000	Aug 2000
Asparagopsis taxiformis								5.4
Sargassum spp.			<0.1				1.1	3.5
Lobophora variegata		0.5	0.3	0.5	0.3	0.3	0.6	1.5
Laurencia spp.	0.5		0.2	0.1	0.9			
Dictyota spp.					1.4	0.1	0.1	
Dictyosphaeria versluysii		0.1						0.3
Acetabularia (*Polyphysa*) sp.							0.3	0.1
Chlorodesmis fastigiata			0.2					
Galaxaura rugosa			0.2					
Padina sp.	0.1		<0.1					
Pterocladia caerulescens							0.1	
Valonia sp.								0.1



T1: April 1998 (2 months after the bleaching)
T2: May 1998 (3 mo)
T3: July 1998 (5 mo)
T4: March 1999 (13 mo)
T5: May 1999 (15 mo)
T6: July 1999 (17 mo)
T7: March 2000 (25 mo)

Fig. 3.5 Ordination plots based on the redundancy analysis (RDA) of abundance data for 48 species of turfing algae. Circles represent averages of 8 samples. (A): RDA plotting species (arrows) and sample averages (circles). Taxa names are abbreviated according to Table 3.1. Rare species with <1% total abundance were excluded from the plot. The arrow lengths are proportional to the proportion of variance of the species explained by the 2 axes. (B): The same RDA showing environmental variables (arrows) and sample averages (circles), where the lengths of arrows are proportional to the strength of association between variable and ordination. Axes 1 and 2 of the RDA explain 43.5% of the variance in the species abundance and 61.8% of the variance in the correlations of species with respect to the environmental variables. The eigenvalues of axes 1, 2 and 3 (the latter not displayed) are 0.240, 0.194 and 0.097 respectively; the sum of all canonical eigenvalues is 0.703. The P-value of the Monte Carlo test of all canonical axes is 0.005.

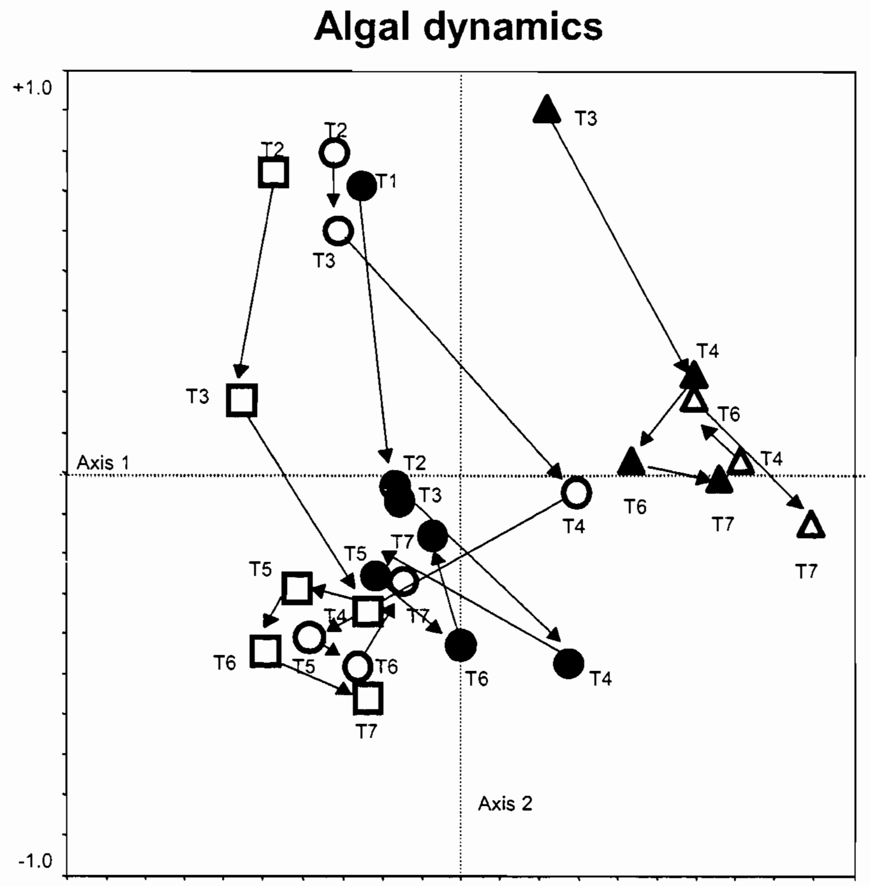


Fig. 3.6 Ordination plot based on the principal component analysis (PCA) of the algal turf species abundance data, showing temporal dynamics for different substrata and locations. Arrows show trajectories through time of algal colonisation. T1 – T7 indicate dates (as in Fig. 3.5). Symbols represent sample averages. Orpheus Island: (O) bleached corals, (●) severely bleached corals, (□) clay plates; Pandora Reef: (Δ) bleached corals, (▲) severely bleached corals. The first and second axes of the diagram explain 26% and 23 % of the variance in the species data, and the third axis (not shown) explains 11% of the variance.

The redundancy and principal component analyses indicate distinct differences in algal composition between substratum types (bleached and severely bleached coral substrates versus clay plates; Figs. 3.5 and 3.6). The vector representing clay plates is opposite to the coral substratum vectors in the redundancy analysis (Fig. 3.5B), and in the PCA all clay plate samples are located on the left-most side of the plot (Fig. 3.6). Characteristic species of coral substrates include the endolithic algae *Ostreobium* spp. and *Mastigocoleus testarum* (right side of Fig. 3.5A). To determine whether the differences in species composition between substrates were due only to the endolithic forms, I repeated the redundancy analysis excluding the endolithic taxa. This analysis (details not included here) showed that the differences persist, due to higher abundance of early successional taxa (pennate diatoms and coccoid cyanobacteria) on the clay plates (Table 3.1).

3.3.5 Differences between locations and the outcome of algal colonisation

There were marked differences in algal composition between the two locations, indicated by the length and opposite directions of vectors in the redundancy analysis (Fig. 3.5B) and by the distinct separation of locations in the PCA (Fig. 3.6). In particular, the red algae *Spermothamnion* sp. and juvenile stages of *Asparagopsis taxiformis* were found almost exclusively on Pandora Reef (Fig. 3.5), whereas the red filamentous algae *Corallophila huysmansii* and *Anotrichium tenue* occurred mainly on Orpheus Island. The locations also differed in the presence at Pandora Reef of a distinct assemblage of fleshy macroalgae dominated by adult *A. taxiformis*, juvenile *Sargassum* spp. (<2-10 cm height) and *Dictyota* spp. (Table 3.2).

3.3.6 Algal colonisation and the recovery of bleached corals: apparent competition

Recovery rates for *Porites* were very low in this study. Two and a half years after the bleaching event, only 20 to 30% of bleached and 1 to 15% of the severely bleached coral areas remained alive, at Orpheus Island and Pandora Reef respectively (Figs. 3.3 and 3.4). Bleaching was clearly an important source of tissue mortality for massive *Porites* at these sites.

Although not directly tested, there is some indication that algal colonisation influenced the recovery of the bleached corals, but that this effect was variable (Fig. 3.7). Plots where algal turfs were present initially (severely bleached treatment) had consistently higher coral tissue mortality (i.e. lower cover) than plots that initially had no algae present (bleached treatment). Bleached coral tissue that was not colonised by algal turfs uniformly regained zooxanthellae and recovered. In contrast, few bleached and severely bleached coral plots which were overgrown by turf algae were able to exclude the epilithic algae and recover (Figs. 3.3 and 3.4), presumably due to competitive inhibition by the algae (Fig. 3.7A). However, photographic sequences showed that even after coral tissue death and algal turf colonisation, the outcome was not uniform. In some plots, areas of dead coral tissue that had been colonised by algae did recover, as surrounding healthy coral tissue overgrew the algal turfs (Fig. 3.7B). This recovery apparently occurred by a competitive process.

3.4 Discussion

The results of this study document several significant aspects of coral bleaching events, including: (i) bleaching as the cause of a major shift in abundance of coral and benthic algae; (ii) detailed description of the patterns and composition of algal colonisation of bleached corals; (iii) variability in algal colonisation, in particular amongst degrees of bleaching, locations, successional stages and substratum types; (iv) potential contributions of algal colonisation to coral tissue mortality. This section discusses each of these points in turn, and suggests that overall, interactions between benthic algae and corals may be critical to understanding the consequences of coral bleaching events.

3.4.1 Bleaching disturbance as the cause of a major shift in abundance of corals and benthic algae

The 1998 mass bleaching of corals resulted in a significant shift in abundance of corals and benthic algae. Coral mortality was widespread, both regionally and globally (Pers. obs., Baird and Marshall, 1998; Berkelmans and Oliver, 1999; Wilkinson, 2000; McClanahan et al., 2001). Coral mortality at my sites was high (Figs. 3.3 and 3.4, qualitative observations) indicating that this bleaching event was a major disturbance, as massive *Porites* spp. are considered highly resistant to bleaching and other injuries (van Woesik, 1998; Sweatman et al., 1998; Berkelmans and Oliver, 1999; Marshall and Baird, 2000). Importantly, in the present study, all corals that died from bleaching were colonised by algal turfs, with higher algal overgrowth on more severely bleached corals but no colonisation on healthy corals. Algal overgrowth of corals was clearly a consequence of the bleaching event. Although caution is required in applying results from relatively small quadrats to larger scale processes, my larger-scale, qualitative observations on these and other reefs in the area, suggest that the results are representative of general patterns on bleached corals. Rapid colonisation by algae after coral disturbances is a general phenomenon, documented following extreme low tides (Fishelson, 1973), crown of thorn starfish predation (Price, 1975), mechanical injuries (Meesters and Bak, 1993) and bleaching events (Wellington and Victor, 1985; Glynn, 1993; Hoegh-Guldberg, 1999).

The replacement of coral by algae in this study depended on the prior death or debilitation of the corals by bleaching (see also Chapter 2). This shows how disturbance to corals and substratum availability may be critical mediators of shifts in dominance from coral to algal dominated systems. Much attention has focussed on the relative importance of eutrophication (bottom-up) and over-fishing of herbivores (top-down) as direct causes of macroalgal blooms on coral reefs (Lapointe, 1999; Hughes et al., 1999). In both of these perspectives decreases in coral abundance are assumed to be caused by increases in algal abundance (due to increased algal competitiveness). However, disturbances such as bleaching may result in similar relative changes in abundance of coral and algae but with reversed causality: the decline in coral abundance is the cause of increased algal abundance. Such distinctions may have significant implications, in particular if human impacts limit the recovery of reefs from natural disturbances, rather than or as well as directly causing coral mortality (Glynn, 1993; Aronson and Precht, 1997; McClanahan and Muthiga, 1998; McCook, 1999; McCook et al., 2001b).

3.4.2 Successional trends in recruitment

Coral mortality due to bleaching generally results in algal colonisation, yet the details of that colonisation have not been investigated, although reef algal succession has been documented in other circumstances (Price, 1975; Carpenter, 1990; McClanahan, 1997). Algal colonisation of bleached corals in this study followed a typical successional pattern, with dominance of diatoms and blue-green algae in early stages followed by taxa with more complex morphologies during later stages (Table 3.1). The shifts in composition towards a more mature epilithic turf assemblage, dominated by upright and branched filamentous algae, is consistent with studies of algal succession in tropical (Carpenter, 1990; Hixon and Brostoff, 1996) and temperate areas (McCook and Chapman, 1993; 1997; Lopez-Rodriguez and Perez-Cirera, 1998). The changes in composition after 15 months may reflect normal community dynamics, such as seasonality and herbivore-grazing effects, as well as continuing successional changes.

The species composition of later stages in this study is similar to other coral reef epilithic turf communities in this area (Scott and Russ, 1987) and elsewhere (Belk and Belk, 1975; Steneck and Dethier, 1994 and above refs), with abundant *Sphacelaria* spp., *Polysiphonia* spp., *Hincksia* spp. and species of Oscillatoriales. In contrast to Hixon and Brostoff (1996), who found that early successional forms were quickly replaced by encrusting algae on Hawaiian coral reefs, encrusting algae were scarce in my study, although also increasing over the course of the succession. Fleshy macroalgae occurred

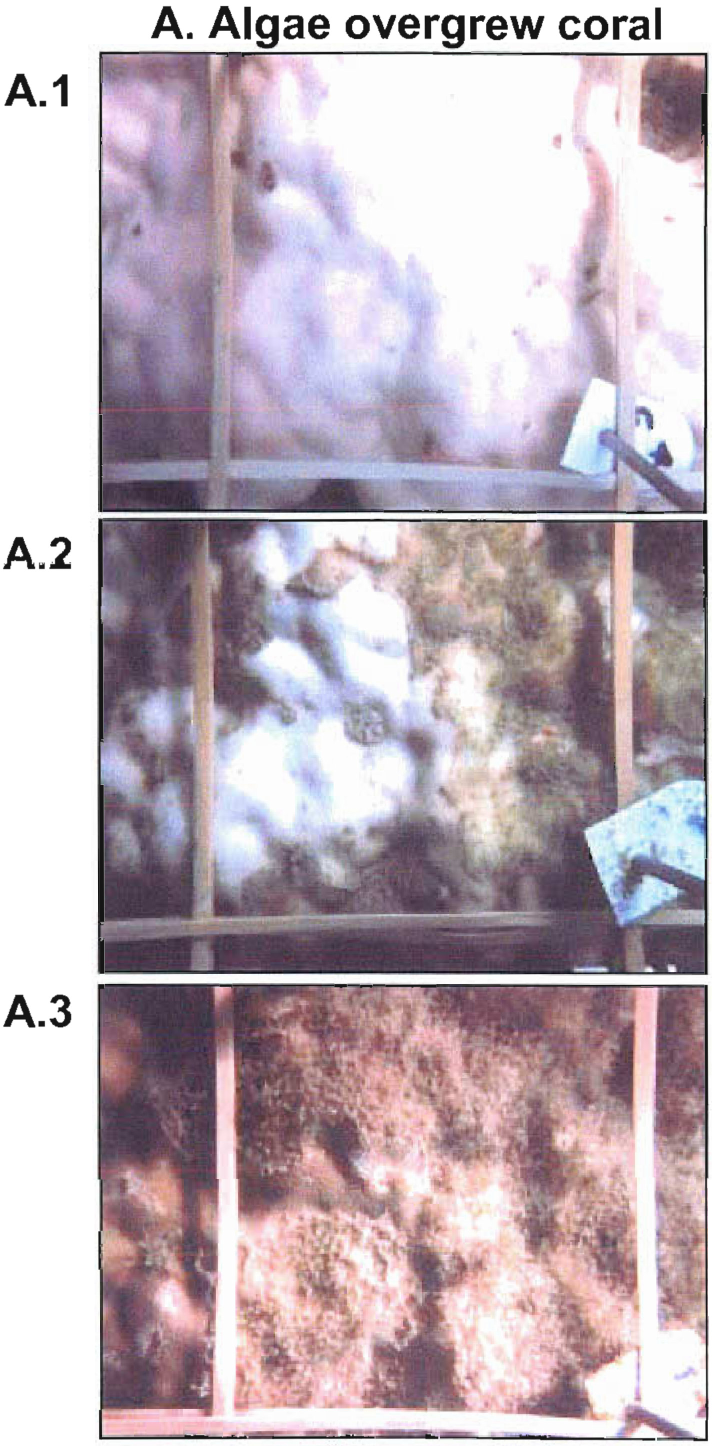


Fig. 3.7 Photographic sequences for two *Porites* plots (10 x 10 cm) after the bleaching event in early 1998, illustrating the variability in outcomes of coral recovery. In (A), the coral did not recover from algal overgrowth (plot from Orpheus Island), remaining dominated by algal turfs until August 2000. (A1) April 1998, (A2) May 1998, (A3) July 1998. In contrast, in (B) the coral recovered successfully from the algal turf colonisation (plot from Pandora Reef). (B1) November 1998, (B2) July 1999, (B3) August 2000. Both corals started with 100% bleached coral cover and were subsequently partially overgrown by algal turfs.

Fig. 3.7 Continued.

predominantly in the final stages of this succession (both in small plots and in larger-scale, qualitative observations), reflecting their slower colonisation rates, and could be expected to play a greater role in dynamics over longer time periods.

The endolithic algal assemblage that developed on bleached *Porites* in my study was very similar to those found on other tropical reefs (Le Campion-Alsumard et al., 1995; Hixon and Brostoff, 1996; Le Bris et al., 1998). In Le Campion-Alsumard's et al. (1995) study of endolithic microbial colonisation of blocks cut from dead massive *Porites*, they observed that *Ostreobium* spp. dominated later in the succession (second year), whereas, in my study, *Ostreobium* appeared soon after the bleaching event. Since *Ostreobium* populations are known to live in healthy corals (Le Campion-Alsumard et al., 1995), these differences probably reflect delays in colonising newly cut coral blocks, compared to recently bleached corals, where *Ostreobium* may have already been present.

3.4.3 Variability in algal colonisation and composition between bleaching categories, substratum types and locations

Algal colonisation of bleached corals was not uniform, but varied considerably both in overall patterns and in species composition. Although much of that variability could be accounted for in terms of differences between dates, bleaching categories, locations, and substratum types, there was also considerable variation even among plots under similar conditions. Importantly, much of that variability persisted through time, with differences remaining 25 months after the bleaching event.

The severity of bleaching damage to corals apparently affected both the trajectory and outcome of algal colonisation. Corals with more severe bleaching suffered more extensive tissue mortality and consequent algal overgrowth. Although these differences persisted to the end of the study, they were not statistically significant at the later stages. However, this may simply reflect the high variability in bleached plots, which results in decreased experimental power (i.e. possible type II error). Within the areas overgrown by algae, differences in species composition of the algae between bleaching categories were also greatest early in the study (Fig. 3.6). More severely bleached plots supported a more mature assemblage during early and intermediate stages, but the differences decreased as succession progressed in the less severely bleached plots. Presumably, the early differences simply reflect slower coral tissue mortality in less severely bleached plots, and consequent delay in initiation of the succession.

The composition of algal assemblages differed markedly between substratum types. These differences persisted to the end of the study period. Dead coral plots supported more later successional taxa, and endolithic forms were absent from clay substrates (Table 3.1). Hixon and Brostoff (1996) also found that natural substrates supported a later successional stage than artificial substrates. It is likely that endolithic algae could not penetrate the clay plates, although substratum chemistry and texture may also be important (as in Chapter 2; Harlin and Lindbergh, 1977).

Reef location accounted for more variation in algal composition than any of the other factors considered here. These differences were marked in both turfing taxa and larger fleshy macroalgae, and persisted over 2.5 years. In particular, fleshy macroalgae were more abundant and different in composition at Pandora Reef than at Orpheus Island, where they were essentially absent (Table 3.2). The extent of these differences between two inshore reefs is intriguing. Factors that might contribute to the differences in larger, fleshy macroalgae include: (i) lower levels of herbivory at Pandora Reef compared to reefs located more offshore (Scott and Russ, 1987; Klumpp and McKinnon, 1992); (ii) potentially higher availability of propagules due to the proximity of dense populations of fleshy macroalgae at Pandora Reef; (iii) different physical and chemical conditions. For example, nutrients and sediment inputs could be higher at Pandora Reef due to its more inshore location and the potential for resuspension of muddy bottom sediments (Russ and McCook, 1999). However, differences in turf composition are difficult to explain in terms of between reef differences in herbivory or proximity of propagule supply, and may simply reflect different species pools on the two reefs, due to physical or chemical condition, or to stochastic variations.

The extent of variability in amount and composition of algal recruitment on bleached corals, and the diversity of contributing factors provide strong evidence that the consequences of bleaching mortality should not be assumed to be uniform, but may vary considerably depending on the severity and timing of the disturbance, the location, and substratum. This is especially important because different patterns of algal colonisation may have different effects on the potential for later recovery of coral populations. For example, different fleshy macroalgae (e.g. *Asparagopsis taxiformis*, *Sargassum* spp. or *Lobophora variegata*) may have very different effects on coral recruitment or regrowth compared to algal turfs, due to different mechanisms involved in the interaction (McCook et al., 2001a). Previous work in this area found algal turfs to have little effect on growth of massive *Porites* (McCook, 2001), whereas fleshy macroalgae may strongly inhibit coral recovery by smothering, abrasion, shading, etc (Jompa and McCook, 2002a). Colonisation by abundant crustose coralline algae might even facilitate coral recruitment (Heyward and Negri, 1999). Fleshy macroalgae, once established, may persist and dominate for long periods, markedly changing habitat structure (Hatcher, 1984 for *Asparagopsis*).

3.4.3 Potential interactions between benthic algae and coral bleaching

Although it is clear that algae were not the initial cause of coral tissue mortality (section 3.4.1), it is possible that algal colonisation contributed to the failure of corals to recover from the disturbances (Results section 3.3.6). It is difficult to determine the extent of this contribution, since unequivocal demonstration of a contribution by algae would require direct experimental removal of the colonising algae (Underwood, 1986; McCook et al., 2001a), technically very difficult to achieve without confounding damage to the corals. Certainly, the poor recovery of severely bleached corals is presumably largely intrinsic to the tissue stress caused by the bleaching damage, potentially compounded by tissue shrinkage, or the sequestering of metabolic resources between areas within a colony (effectively sacrificing some more stressed tissue areas). However, it is possible that processes of the disturbance-induced stress and algal competition synergised, with more stressed corals more vulnerable to algal overgrowth, and algal overgrowth enhancing the stress. Even where bleaching stress was not sufficiently severe to kill the coral tissue, the stressed corals may have reduced ability to clean themselves or to avoid algal competitors. Production of a mucus layer apparently serves as a defensive mechanism against sediment accumulation and epibiotic colonisation (Lang and Chornesky, 1990), and it is likely that nutritional deficiency caused by the loss of zooxanthellae (Szmant and Gassman, 1990; Meesters and Bak, 1993; Glynn, 1993) reduced the ability of the corals to defend themselves in this manner. Meesters and Bak (1993) have previously shown that bleached corals were more easily overgrown by algae than healthy corals when injuries were inflicted to the tissue.

The consequences of algal colonisation were not uniform. Although in most cases algal overgrowth of dead coral tissue was persistent, in some instances the coral was able to regain lost ground, apparently by competitive overgrowth (Fig. 3.7). Algal colonisation has been suggested previously to delay and inhibit recovery after coral disturbances and pre-empt space that may inhibit future coral settlement and recruitment

(Birkeland, 1977; Bak et al., 1977; Hughes, 1996; Connell et al., 1997). In contrast, there are also examples of competitive superiority of corals over algal turfs, both on inshore reefs in this region of the GBR (McCook, 2001) and in other regions (Fishelson, 1973; Meesters and Bak, 1993; Littler and Littler, 1997; van Woesik, 1998). Algae may not prevent coral recovery after small-scale damage (Meesters and Bak, 1993), although the ability of corals to heal injuries that have been overgrown by benthic algae decreases as the size of the lesion increases (van Woesik, 1998). In my study, the low proportional recovery after overgrowth by algal turfs probably reflects the combined extent and severity of bleaching damage.

Overall, benthic algae have the potential to interact significantly with various stages of the bleaching process, with potentially very different consequences. The presence of abundant macroalgal canopy has been shown to reduce damage to corals at the time of bleaching, apparently by shading (Jompa and McCook, 1998). Algal colonisation subsequent to bleaching may increase the impact of bleaching stress to corals (previous paragraph). Finally, long-term patterns of algal colonisation and succession on dead coral substrates may influence the ability of coral populations to recover, either by new recruitment, or by regeneration of surviving tissue (section 3.4.3; Fig. 3.7B; see also Glynn, 1993). The marked contrast between the apparently beneficial effects of shading and the competitive effects, in combination with the potential variability within each of these effects, suggests that these interactions may have considerable consequences for the outcomes of coral bleaching events.

3.4.4 Recurrent future bleaching events and the importance of benthic algal interactions and dynamics

Recent predictions suggest that coral bleaching events will become more frequent and even more severe (Brown, 1997; Hoegh-Guldberg, 1999). Under such a scenario, it is inevitable that coral reefs will have increased and increasingly variable cover of benthic algae, with considerable potential to influence future reef recovery. As emphasised above, differences in the type and abundance of algae that overgrow bleached corals, both initially and in the long-term, are likely to be critical to reef dynamics and trajectories. There has been debate about the consequences of the predicted increases in bleaching damage, with suggestions that coral populations may adapt or may recover by means of reseeding from more resistant populations (Glynn, 1993). However, the success of such scenarios depends on the ability of remnant corals to vegetatively overgrow substrata occupied by algae, or the ability of coral larvae to successfully settle and recruit once they arrive at a damaged reef. The substratum on that reef is likely to be dominated by various forms of benthic algae. Understanding, predicting and managing the consequences of future bleaching events will depend on better understanding, not only of coral physiology, climatology, and coral recruitment dynamics, but also better knowledge of algal recruitment dynamics and coral-algal interactions after disturbances.

Chapter 4

Top-down Processes Overwhelm Bottom-up Effects on Recruits of two Coral Reef Seaweeds

4.1 Introduction

The relative importance of, and interactions between, "bottom-up", "top-down" and "supply-side" processes in structuring populations and communities is a major issue in ecology. "Bottom-up" refers to factors, such as resource limitation (e.g. by nutrient supply), which act on basal trophic levels; "top-down" refers to factors, such as herbivory and predation, which act from higher trophic levels; "supply-side" refers to processes, such as fecundity, dispersal, settlement and recruitment, which affect the supply of organisms to a site or population. There is now considerable evidence demonstrating critical roles for, and interactions between, all three types of process, in terrestrial, freshwater and temperate marine ecosystems, and there is considerable evidence for critical roles of supply-side processes in tropical fish and invertebrates (Hunter and Price, 1992; Caley et al., 1996; Menge et al., 1999; Menge, 2000; Hughes et al., 2000; Worm et al., 2001). However, there is very little information available on the ecology of early post-settlement stages of tropical marine plants (Ang, 1985b; Kendrick, 1991; Belliveau and Paul, 2002).

In terrestrial ecosystems, it has been suggested that bottom-up processes generally outweigh top-down processes, but that the relative contributions of both can vary in space and time and with the species or ecosystems involved (Hunter and Price, 1992; Dyer and Letourneau, 1999; Forkner and Hunter, 2000). Experimental work in both freshwater and marine ecosystems indicates that nutrient limitation and herbivory processes can act independently, simultaneously, or interactively, to control the abundance of primary producers (Rosemond et al., 1993; Hillebrand et al., 2000; Lotze et al., 2001; Hillebrand and Kahlert, 2001). There is also evidence that variations in supply-side processes may overwhelm both bottom-up and top-down effects (Underwood and Fairweather, 1989; Worm et al., 2001).

Much of the work on supply-side ecology in marine systems has focussed on animals rather than plants (see reviews by Underwood and Fairweather, 1989; Caley et al., 1996) although available evidence indicates that recruitment may also be critical to the dynamics of seaweed populations and communities (Santelices, 1990; Reed, 1990; Vadas et al., 1992; Kendrick and Walker, 1994; Wright and Steinberg, 2001). Further, most evidence supporting the roles of resources or herbivores in controlling aquatic plant populations comes from studies of adult plants. However, benthic algae have several life-history stages that may respond differently to environmental pressures. Algal propagules are released into the water column, dispersed via a pelagic phase, then settle, attach and enter microscopic benthic communities, where they may spend some time in propagule banks, before recruitment to the macroscopic communities (Santelices, 1990). Nutrient limitation and herbivory have been shown to have critical effects on the development of early life stages of seaweeds within temperate systems (Worm et al., 2001; Lotze et al., 2001), but these processes and interactions may act very differently in the highly diverse ecosystems of tropical coral reefs.

Coral reef degradation, as with many tropical and temperate systems, often involves "blooms" of benthic algae, usually at the expense of previous occupants (such as corals) (Hughes, 1994; McCook, 1999; Hauxwell et al., 2000). Clearly, the recruitment dynamics of benthic algae will be critical to their ability to invade and colonise new areas during reef degradation (Chapter 3). There has been considerable controversy over the relative importance of nutrient limitation and herbivory in preventing overgrowth of corals by benthic algae on coral reefs (e.g. Lapointe, 1997; Hughes et al., 1999). However, there have been few studies that simultaneously consider more than one process, especially using factorial experiments. Such experiments not only provide direct comparisons of the relative importance of each process, but clarify the interactions between them and hence the mechanisms involved (Hatcher and Larkum, 1983; Miller and Hay, 1996; Miller et al., 1999; Thacker et al., 2001; Smith et al., 2001; McCook et al., 2001a; Jompa and McCook, 2002b). These studies indicate that the effects of nutrient supply are often small relative to those of herbivory, and often depend strongly on levels of herbivory (but not vice versa). Importantly, the nutrient supply / herbivory dichotomy ignores the potential roles of several other key processes, including coral-algal competition, and disturbance-recruitment-recovery processes, in regulating the relative abundances of corals and algae (Hughes, 1994; Jompa and McCook, 2002b; Chapter 3). Further, most of this work focuses on effects on adult algae. For example, it has been suggested that differences in herbivores, rather than nutrient supply, explain *Sargassum* distributions within and between reefs, based on experiments using adult plants (McCook, 1996; 1997). However, effects on adult stages could be countered by bottom-up effects on recruitment. Nutrients have been shown to enhance growth of *Sargassum* recruits in physiological experiments (Schaffelke and Klumpp, 1997b), but the relative importance of nutrients and herbivores to the recruitment stage of coral reef algae has not been tested in an ecological context.

In this study I investigated the relative and interactive effects of nutrient limitation and herbivory on the survival and growth of algal recruits, using factorial manipulations of nutrient supply and herbivory, on a midshelf coral reef on the GBR. The study used two species, *Sargassum fissifolium* and *Lobophora variegata.*

4.2 Methods

4.2.1 Approach and experimental site

Zygotes of *S. fissifolium* (Mertens) Agardh and spores of *L. variegata* were seeded together onto settlement plates in aquaria, and then transplanted to an offshore reef for factorial experimental manipulations of herbivory and nutrients for a period of 40 days. The experimental site was on the reef slope of Rib Reef (Fig. 4.1: 18° 28' 422 S; 146° 52' 783 E), between 6-9 m depth. I chose an offshore reef with relatively low nutrient supply (Devlin et al., 2001) and high abundance of herbivorous fishes (c.f. to inshore reefs; refs in McCook, 1996), in order to maximise the potential effects of the nutrient and herbivore manipulations.

4.2.2 Recruits collection - seeding

Algal recruits were seeded by placing reproductive adults of *S. fissifolium* and *L. variegata* in 10^3 L outdoor aquarium tanks with terracotta settlement plates (11 x 11 cm side with rough texture) on the bottom. Algal propagules were released into the water and settled onto the plates (Fig. 4.1). Adult algae were collected from 3-6 m depth on the fringing reef on a nearby inshore island (Goold Is, 18°10' 85 S; 146° 10' 05 W). Zygote release of *S. fissifolium* was enhanced by short periods (30 mins) of desiccation followed by shaking the plants in the tank. Adult plants were removed from the tanks after 10 days, and the plates maintained for another 40 days to allow attachment. Tank seawater was replaced every 5 days to avoid excess growth of diatoms. Plates were then transplanted to the experimental site and bolted to steel frames (40 x 40 cm) previously anchored to the substratum (Fig. 4.2). Seven replicate plates were randomly allocated to each treatment combination and distributed over an area of ca. 2500 m^2.

4.2.3 Herbivore treatments

I used three levels of herbivore treatment: (1) open, uncaged plots that allowed free access to large herbivores; (2) caged plots that excluded large herbivores; and (3) partial-cage plots intended to control for cage artifacts (Fig. 4.2). Open plots simply consisted of a steel frame and recruitment plate. Herbivore exclusions consisted of steel frames covered by a cage (40 x 40 x 25 cm high) made of 12mm polyethylene mesh. Partial cages were identical to full cages except that two sides of the cage were removed to allow partial access for large herbivores. It appears in retrospect that the partial cages had limitations as procedural controls, as they were too small to allow full access to large herbivores (data for partial cages were consistently intermediate between those of open and caged plots, although consistently more similar to open plots than full cages). Although these patterns may indicate some cage artifacts, most such artifacts (e.g. reduced light and water flow) would be expected to reduce algal growth relative to open plots, not enhance it. Importantly, any differences between partial and full cages can nonetheless be unambiguously attributed to herbivory.

4.2.4 Nutrient treatments

Nutrient manipulations were carried out following a nutrient pulse protocol involving addition of nutrients for a 24 h period every 10 days for 40 days (during June – July 2000), using reagent-grade ammonium-chloride and sodium-dihydrogenphosphate (Schaffelke, 1999; Jompa and McCook, 2002b). I applied three nutrient concentration treatments: (1) Ambient, untreated controls, using running seawater from the lagoon of Rib Reef (average levels ranged between 0.03 – 0.16 µM NH_4 and 0.05 – 0.28 µM PO_4); (2) Medium, with ≈ 5µM of NH_4 and 0.5 µM PO_4; and (3) High, with ≈ 10 µM NH_4 and 1 µM PO_4. These nutrient concentrations are relevant to the range of values recorded on the GBR (Schaffelke and Klumpp, 1997b; Devlin et al., 2001), and were confirmed using three replicate samples of filtered water (0.45µm Sartorium Minisart), frozen immediately after collection and later analysed in an autoanalyzer at AIMS (Ryle et al., 1981). During each nutrient pulse, all settlement plates were retrieved from the experimental site, nutrient treatments applied in individual 10 L plastic buckets on board the research vessel, and then plates were returned to the field (and continuing herbivore treatments). Seawater (ambient and enriched) was replaced every 4-6 hours during the 24 h pulse. The nutrient pulse protocol was preferred over a continuous delivery of nutrient for several reasons. Firstly, reefs on the GBR are subjected to episodic, pulsed nutrient inputs, so that the pulse protocol more realistically simulates the field situation (as discussed in Schaffelke, 1999). Secondly, reliable, continuous nutrient applications are logistically difficult to sustain in an open reef field experiment.

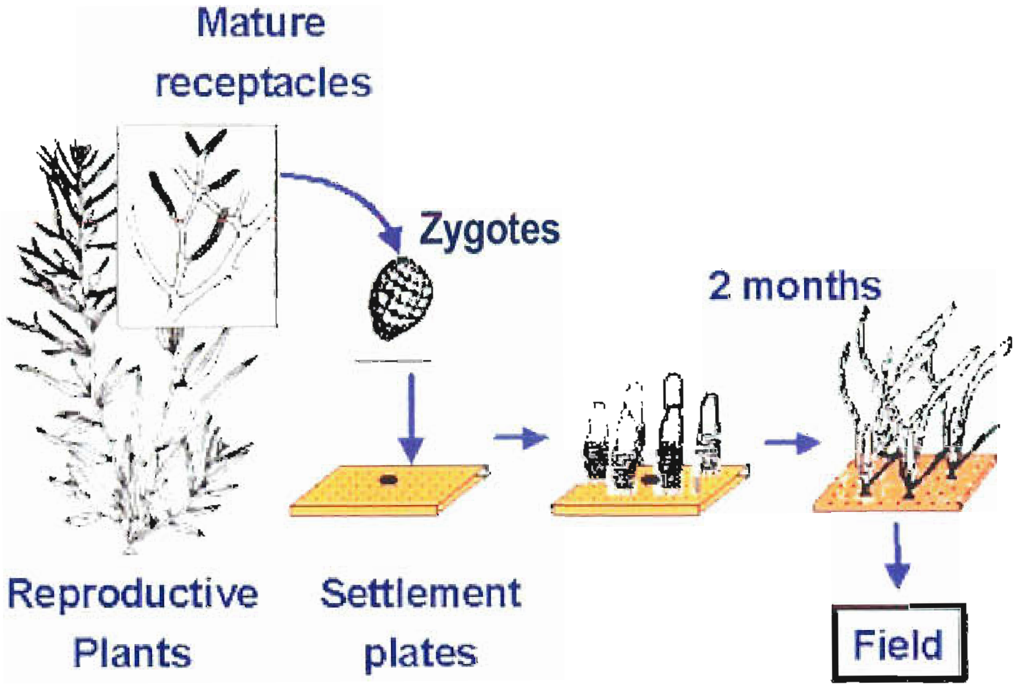


Fig. 4.1 Diagram showing method of seeding *Sargassum* recruits onto ceramic settlement plates in aquarium tanks prior to transplantation to the study site for nutrient and herbivore manipulations.

To test the effectiveness of the nutrient manipulations, I measured tissue nutrient concentrations in *S. fissifolium* recruits at the end of the experiment. Algal tissue was removed from 12 supplementary caged settlement plates (4 per nutrient treatment), dried at 60°C for 48 h, ground, and the concentrations of C and N determined with a Perkin Elmer CHN Analyzer. P was determined using ICP analysis (Ryle et al., 1981). Tissue N and P levels of *S. fissifolium* in the high nutrient enrichment treatments were significantly higher than that of the unenriched, ambient control treatments (one way ANOVA, $P<0.001$), and medium nutrient treatments were intermediate (Fig. 4.3). Although there was insufficient biomass of *L. variegata* for nutrient analyses in this experiment, Jompa and McCook (2002b) found significant enhancement of tissue nutrients in *L. variegata* using the same nutrient enhancement protocol.

Open plots

Full cages

Partial cages

Fig. 4.2 Photographs showing herbivore treatments. Settlement plates were attached to steel frames and left exposed to herbivores (open plots), protected from herbivores (full cages) or placed in partial cages intended as procedural controls.

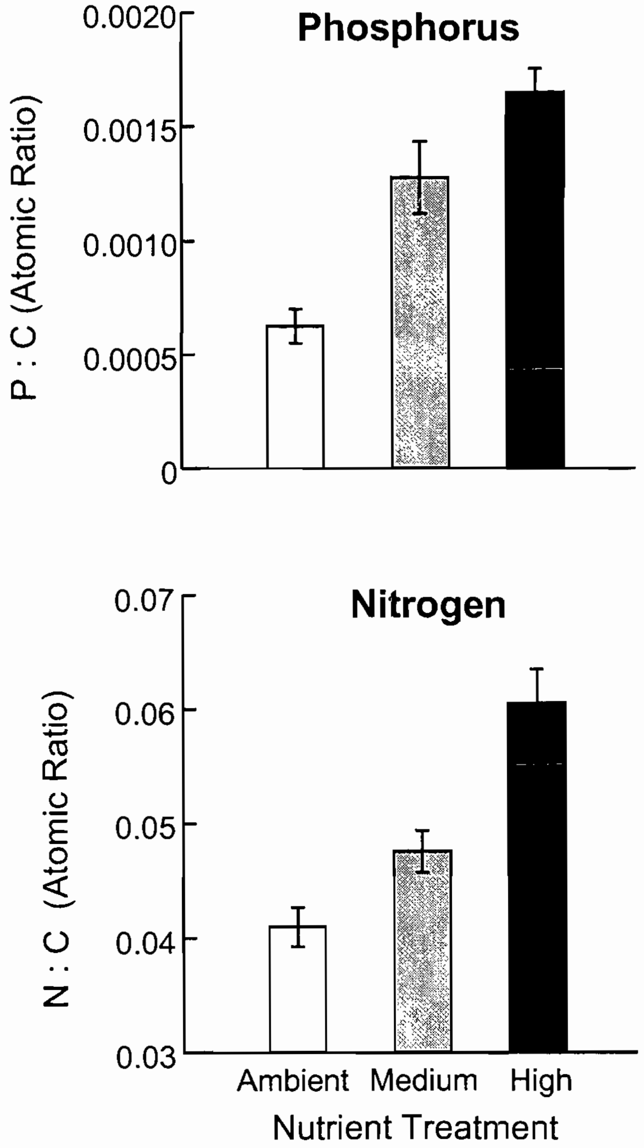


Fig. 4.3 Tissue nutrient levels (phosphorus and nitrogen) of *Sargassum fissifolium* recruits across nutrient treatments (N = 4).

4.2.5 Response variables and data analyses

The response variables included the number of recruits per plate, as a measure of survival, and the length (from base to apex), width (longest dimension perpendicular to the length), and number of branches (for *S. fissifolium* only), as measures of growth. The number of injured recruits of *S. fissifolium* (i.e. with no primary or secondary branches or fronds, apparently removed by grazers) was also recorded as a proportion of total final density; this parameter provided a measure of grazing intensity, as distinct from total density of recruits (a measure of survival). Length, width and branch number were measured for 25, randomly selected recruits per plate for each species. All measurements were taken at the end of the experiment, using a stereomicroscope. Density and size of *S. fissifolium* recruits were also estimated at the beginning of the experiment to preclude large, confounding initial differences among treatments. The initial density of recruits was similar across treatments (average densities ranged between 1422 – 1549 recruits per plate; ANOVA by treatments, $p > 0.69$).

Density data were analysed using a factorial ANOVA with levels of nutrients and herbivores as fixed factors and plates as replicates. Length, width and number of branches were analysed using a factorial, nested ANOVA, with nutrients and herbivores as fixed factors and 25 plants (= recruits) nested within plates. Post-hoc comparisons used Tukey's tests. Data were transformed ($\log_{10}$) for homogeneity of variance, and checked for homogeneity of variance (Cochran's test) and for normality of residuals (graphically).

4.3 Results

4.3.1 Effects of herbivores and nutrients on *Sargassum fissifolium* recruits

Herbivore exclusion strongly enhanced the survival (density) and growth (length, width and number of branches) of *Sargassum fissifolium* recruits, whereas nutrient enhancement had no significant effects on these variables (Figs. 4.4A-C, 4.5, 4.6; Table 4.1). The density of recruits was sevenfold higher and the height and width of recruits were fourfold larger when protected from herbivores in full cages than when they were exposed to herbivores in the open plots, and these results were consistent among nutrient treatments. The number of branches per plant was higher in recruits protected from herbivores than in partial cages and open plots (mean ± SE: 5.1 ± 0.09; 2.4 ± 0.25; 1.6 ± 0.14 respectively). Although density and number of branches of recruits in partial cages were higher than in open plots (and not significantly so for height and width), they were consistently intermediate between open and caged plots, and much more similar to open plots than cages (Fig. 4.4). This pattern among treatments suggests that the major effect of the cages was indeed due to herbivory (rather than artifact). The only possible nutrient effect on *S. fissifolium* growth involved a small, non-significant enhancement of width (but not length) in the high nutrient treatment within full cages (Fig. 4.4C).

Interestingly, there was a significant interaction between herbivore and nutrient effects on the proportion of remaining recruits that were injured. This proportion was negligible in herbivore exclusion cages, for all nutrient treatments (Fig. 4.4D, Table 4.1), consistent with the interpretation of injury as a herbivore effect. In contrast, in open plots with uninhibited herbivore access, this proportion was significantly increased by nutrient enhancement. Although this pattern was not consistent within partial cages, it may indicate that recruits were more intensively grazed in nutrient enriched treatments than the unenriched recruits.

4.3.2 Effects of herbivores and nutrients on *Lobophora variegata*

Herbivores also strongly reduced the survival (density) and size of *Lobophora variegata* recruits. The density was sixfold higher and the size 1.3 times higher in recruits that were protected from herbivores than those exposed to herbivores in open plots (Figs. 4.7A-C). Nutrient enhancement did not significantly affect the survival (density) of *L. variegata* (Fig. 4.7A), although, in contrast to *S. fissifolium*, growth (length and width) of *L. variegata* recruits were consistently and significantly higher in nutrient enhancement treatments than ambient controls (Figs. 4.7B-C, Table 4.1). The effects of nutrients were, however, small compared to the effects of herbivores: recruits grew <10 % more in the high nutrient treatment than in the unenriched treatment, but were 30% larger when protected from herbivores (Figs. 4.7B-C). The density and size of recruits within partial cages were significantly higher than in the open plots, but were generally significantly lower than in the full cages (Table 4.1; similar to *S. fissifolium*).

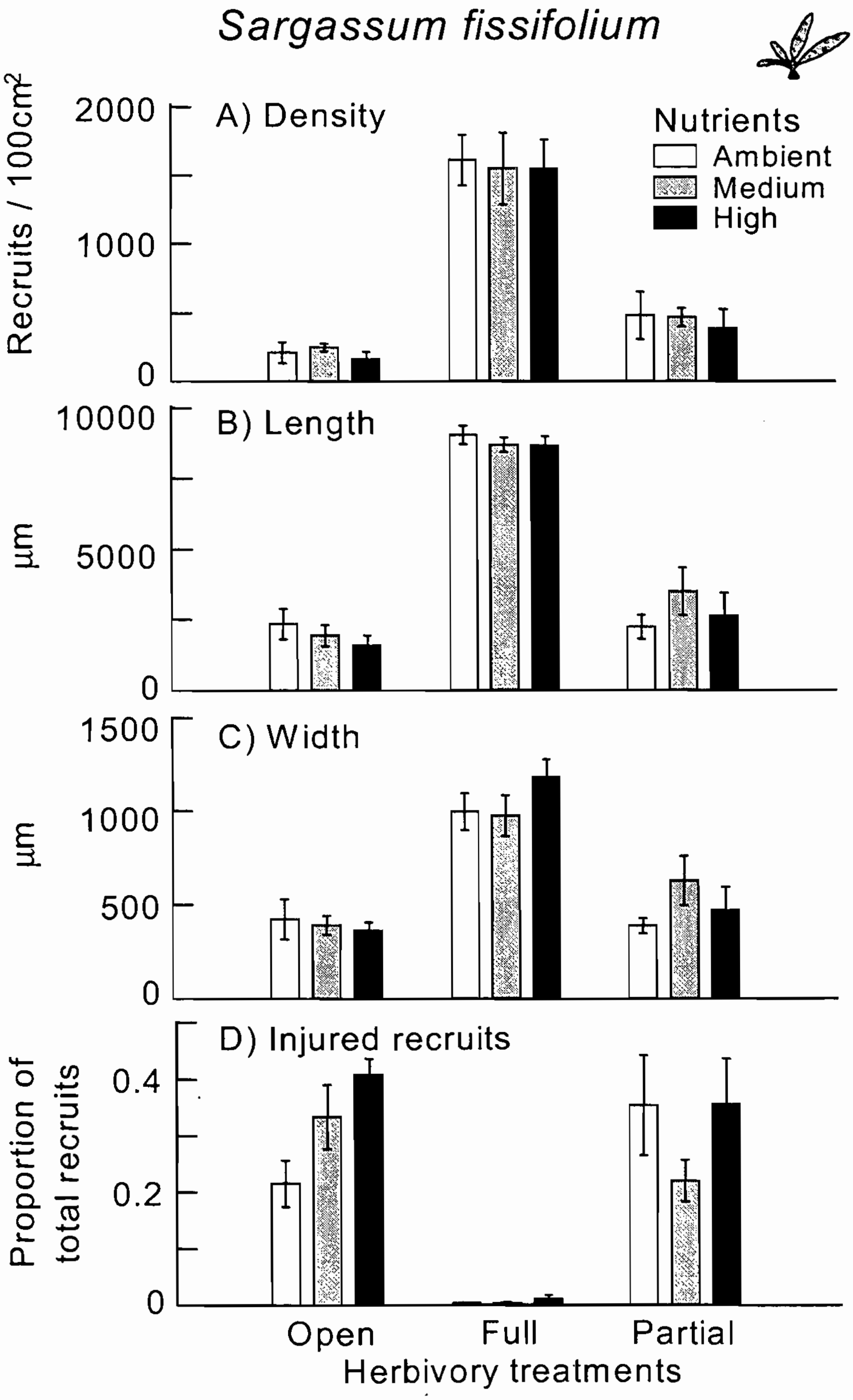


Fig. 4.4 Mean recruit density (A), length (B), width (C), and proportion of injured recruits (D) of *Sargassum fissifolium* across herbivory and nutrient treatments (± 1 SE, N = 7).

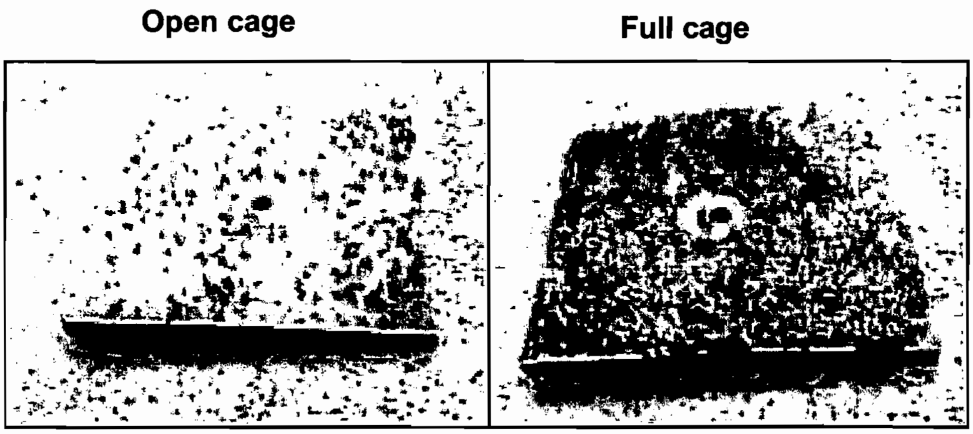


Fig. 4.5 Photographs of plates showing *Sargassum* recruits after 1 week in open plots, exposed to herbivores, and full cages, protected from herbivores.

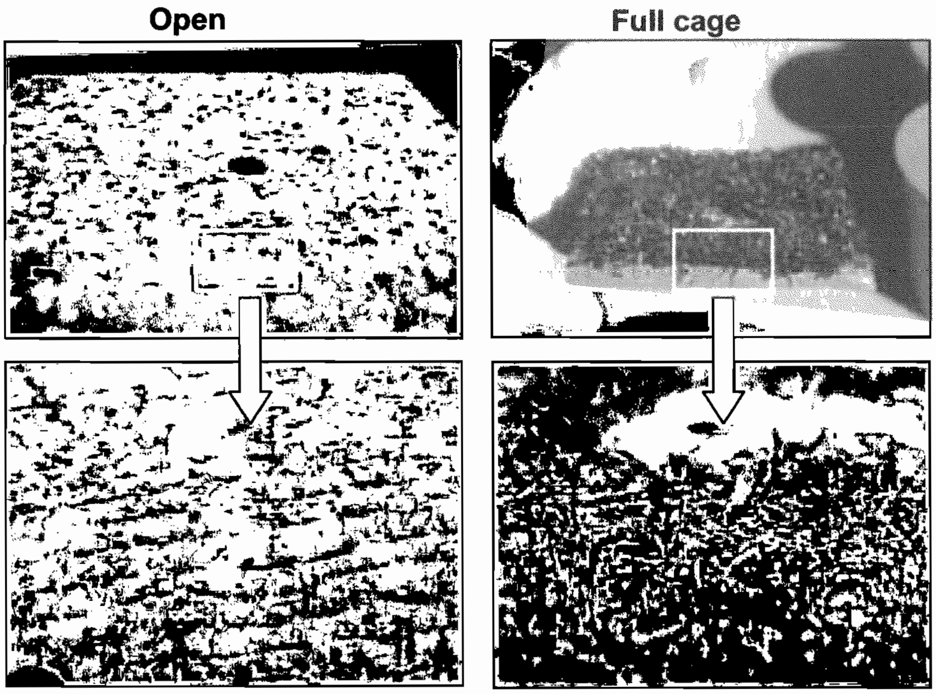


Fig. 4.6 Photographs showing settlement plates and close-up views of plates from open plots and herbivore exclusion cages after 40 days on the study reef. Note the presence of damaged holdfasts in the open treatment, apparently due to herbivore removal of upright thalli.

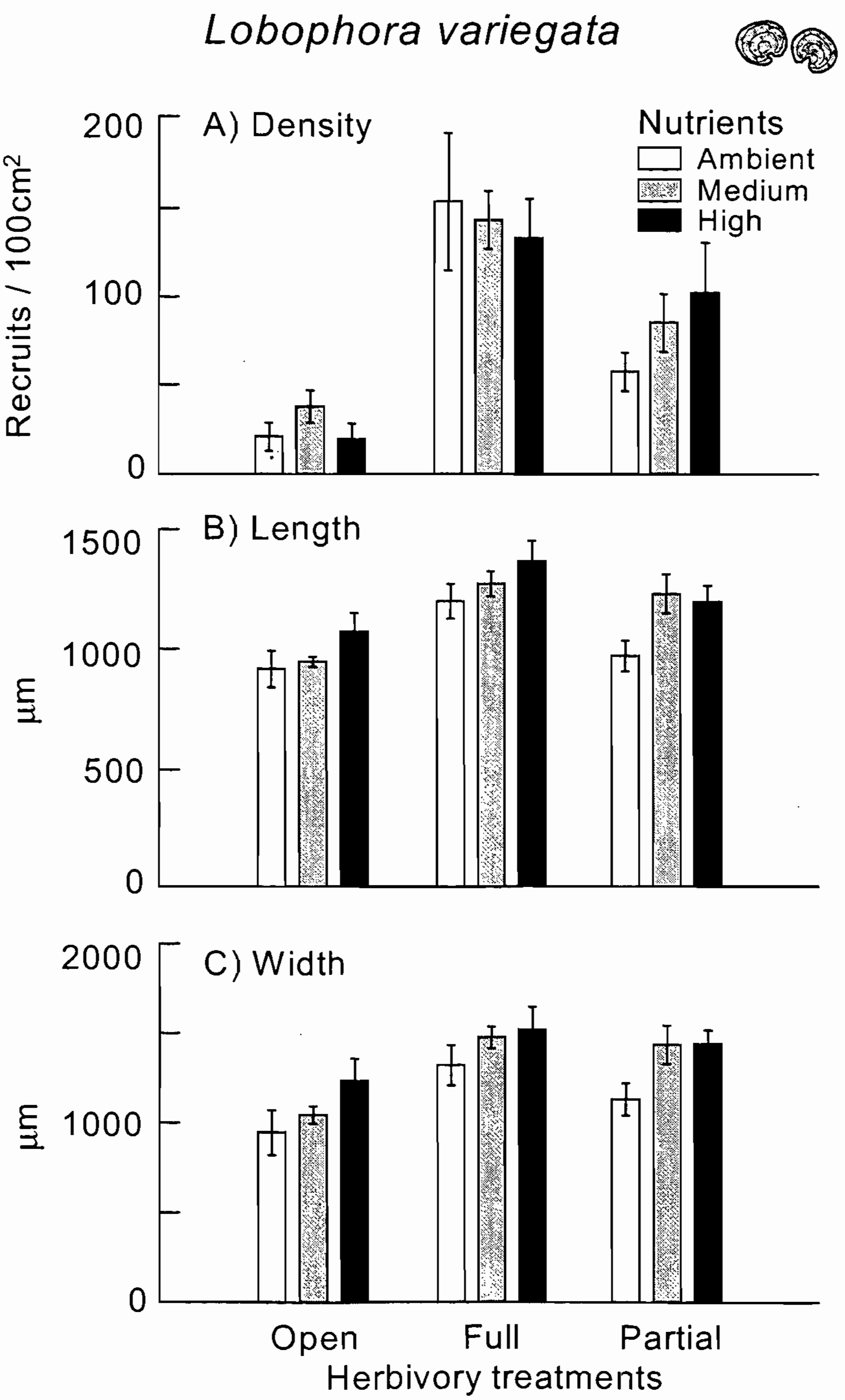


Fig. 4.7 Mean recruit density (A), length (B), and width (C) of recruits of *Lobophora variegata* across herbivory and nutrient treatments (± 1 SE, N = 7).

Table 4.1 Factorial ANOVAs for effects of herbivore exclusion and nutrient enhancement on early stages of two coral reef seaweeds.

		Sargassum fissifolium				*Lobophora variegata*			
Source of variation	df	MS	*F*	*P*	Tukey's test	MS	*F*	*P*	Tukey's test
Density									
Herbivory (H)	2	4.943	52.149	<0.001	F>P>O	3.721	47.891	<0.001	F>P>O
Nutrients (N)	2	0.175	1.847	0.168	A≈M≈H	0.148	1.900	0.159	A≈M≈H
H x N	4	0.051	0.536	0.710		0.096	1.233	0.308	
Error	54	0.095				0.078			
Length									
Herbivory (H)	2	103.492	100.794	<0.001	F>P≈O	1.098	13.812	<0.001	F>P>O
Nutrients (N)	2	0.923	0.899	0.413	A≈M≈H	0.374	4.705	0.013	A≈M; M≈H; H>A
H x N	4	0.886	0.862	0.492		0.097	1.217	0.314	
Error	54	1.027				0.080			
Width									
Herbivory (H)	2	27.467	60.069	<0.001	F>P≈O	1.269	8.214	0.001	F>O; P>O; F≈P
Nutrients (N)	2	0.245	0.537	0.588	A≈M≈H	0.677	4.381	0.017	A<M≈H
H x N	4	0.550	1.203	0.320		0.101	0.654	0.627	
Error	54	0.457				0.154			
Branch No.									
Herbivory (H)	2	23.204	91.893	<0.001	F>P>O				
Nutrients (N)	2	0.094	0.373	0.690	A≈M≈H				
H x N	4	0.179	0.711	0.588					
Error	54	0.253							
Injured recruits									
Herbivory (H) [1]	2	0.090	66.867	<0.002	F<P≈O				
Nutrients (N) [2]	2	0.004	2.797	0.006	A≈M; M≈H; H>A				
H x N	4	0.004	2.917	0.029					
Error	54	0.001							

Notes: Nested analyses (length, width and branch no.) used the nested factor (plates) as the error term. When significant interactions occurred, data were tested within combination of treatments. [1] At all herbivore combinations; [2] within open plots only. Injured recruits expressed as the proportion of total final density. Treatment abbreviations: F = Full cages; P = Partial cages; O = Open plots. A = Ambient nutrient concentration; M = Medium nutrient addition; H = High nutrient addition.

4.4 Discussion

Overall, my results suggest that at the study site, top-down regulation by herbivory dominated the population development of early stages of these two coral reef seaweeds, and that bottom-up regulation by nutrients was weak. However, the results also suggest that the magnitude of the effects of herbivory and nutrients were variable and depended on the species and type of response measured.

4.4.1 Variability in response between survival and growth, and between species

The different variables considered here are measures of different life-history processes (survival, growth and injury), and, as such, may be expected to respond differently to ecological processes such as nutrient limitation and herbivory. Density, a measure of survival (or inversely, mortality), responded strongly and consistently to herbivore exclusion, but had no detectable response to nutrient manipulations, for both species (Figs. 4.4A and 4.7A). In contrast, the size or growth response to nutrients was species-specific, with no significant response in *Sargassum fissifolium* and an increase in *Lobophora variegata*. The (net) growth response of both species to herbivory was similar in direction but not magnitude: both were reduced by herbivore grazing but growth was more strongly reduced in *S. fissifolium* than in *L. variegata*. Finally, the proportion of injured *S. fissifolium* recruits, primarily a measure of grazing intensity, responded differently to nutrients, depending on the level of herbivory.

These differences in response between species may reflect the different growth forms of the two species. For example, the *S. fissifolium* recruits were relatively large, erect and formed a canopy, whereas *L. variegata* recruits were generally prostrate, smaller, and essentially understorey. Apparently herbivore grazing frequently damaged *S. fissifolium* (Figs. 4.4D and 4.6), thereby reducing growth as well as density. However, few of the remaining *L. variegata* plants showed any signs of grazing damage, so that herbivore grazing may have more often involved consumption of entire plants, affecting density but having less effect on growth (of remaining plants). It is also possible that herbivore reduction of the *S. fissifolium* canopy increased light, and thereby ameliorated any herbivore-induced reduction in size of *L. variegata*. The contrast in nutrient effects between species may also reflect differences in physiology and function between thin-layered, simple prostrate plants (*L. variegata* recruits) and larger, upright leathery macrophytes with more complex tissue organisation and a range of nutrient uptake mechanisms (*S. fissifolium*; e.g. Steneck and Dethier, 1994; Schaffelke, 1999). Thus the impacts of bottom-up and top-down processes cannot be assumed to be uniform, but will vary among species and life-history stages or processes.

4.4.2 Relative magnitude of herbivore and nutrient treatment effects

Notwithstanding this variability, my results indicate that the negative effects of herbivores on the recruitment of the coral reef algae *S. fissifolium* and *L. variegata* overwhelmed any bottom-up enhancement by nutrients. Nutrient effects on growth were very small and found only in *L. variegata* (Figs. 4.4 and 4.7). The relative strength of herbivore effects on macroalgal recruits in this study is consistent with previous work on adult *Sargassum* (McCook, 1996; 1997). To some extent my results will be specific to the species, site and other circumstances, such as distance from land. For example, lower herbivore abundances on inshore reefs may mean that top-down control is less strong in those habitats. However, it is unlikely that nutrient effects will be stronger in other areas, since effects of nutrient additions are likely to be strongest in areas with the least background inputs, such as my study site.

There has been little previous work specifically comparing nutrient limitation and herbivory effects on early stages of macroalgae using factorial experiments, although evidence from temperate systems suggests that their relative importance varies (Lotze et al., 2001), and, unlike my results, may differ between early and adult stages. There is, however, considerable evidence for strong effects of top-down factors on early stages of seaweeds (Lubchenco, 1983; Vadas et al., 1992; Wright and Steinberg, 2001). More generally, previous factorial comparisons in aquatic ecosystems have generally found herbivore reduction causes much larger changes in algal populations than nutrient enrichment, including studies of mature benthic algae on coral reefs (Miller et al., 1999; Thacker et al., 2001; Jompa and McCook, 2002b), in seagrass beds (Heck et al., 2000), and in freshwater periphyton communities (Hillebrand and Kahlert, 2001). However, this pattern is not universal, since some factorial experimental studies have found neither herbivores nor nutrients to have overwhelming control of algal populations (e.g. Rosemond et al., 1993; Smith et al., 2001).

The relative importance of herbivory effects over nutrient limitation has been suggested to be strongest in oligotrophic systems, and reversed in eutrophic systems (Hauxwell et al., 1998; Lotze et al., 2001) or to vary along productivity gradients (van de Koppel et al., 1996). Taken together, the results for both adults (McCook, 1996; 1997) and recruits (present study) support the importance of herbivory effects in oligotrophic systems, but do not suggest increased importance of nutrient limitation in the more eutrophic, inshore system.

Addition of nutrients did not significantly increase growth of *S. fissifolium* recruits (Figs. 4.4B-C), even in the absence of herbivores. This outcome contrasts with results from laboratory experiments, in which nutrient enrichment increased growth of early stages of seaweeds, including species of *Sargassum* from this area (Schaffelke and Klumpp, 1997b; Van Alstyne and Pelletreau, 2000). This contrast probably reflects the differing (physiological and ecological) contexts of the studies, rather than ineffective nutrient treatments, given that *S. fissifolium* tissue nutrients were enriched (Methods), that *L. variegata* showed a growth response to nutrients (Figs. 4.7B-C), and that there may have been a functional response of herbivores to fertilisation (Fig. 4.4D). Thus, it appears that *S. fissifolium* recruits in ambient water conditions on Rib Reef were nutrient sufficient, perhaps because water flow rates ensure sufficient nutrient supply, despite low concentrations (Miller et al., 1999; discussion in McCook, 1999). McCook (1996) showed that adult plants of *Sargassum* transplanted to a similar, nearby reef, were nutrient sufficient. Further, physiological studies usually use isolated specimens in control conditions, whereas in my study, as in nature, recruits were growing within a relatively dense algal mat. Under such conditions, nutrient demand may be less important than intra- or inter-specific competition for other resources, such as light. My results are not consistent with nutrients as the subject of intra-specific competition.

Interestingly, my results for the proportion of injured *S. fissifolium* recruits suggest that the strength of top-down effects increased with the bottom-up availability of nutrient resources to the algae (Fig. 4.4D). Nutrient enriched recruits were apparently more intensively grazed than the unenriched recruits. Although this pattern was not consistent among partial cages, the results from open plots are likely to more accurately represent natural processes, since herbivory appears to have been restricted within partial cages (see Methods). This interaction between herbivory and nutrient availability may indicate a functional response of herbivores to nutrient enriched plants, perhaps due to higher food quality. Miller et al. (1999) found that macroalgae grown under nutrient-rich conditions in a coral reef in Florida were preferred by herbivores and removed at a faster rate than unenriched macroalgae. Such interactions have been suggested in a variety of systems, including invertebrate grazers in temperate marine habitats (Hillebrand et al., 2000), and freshwater lakes (Hillebrand and Kahlert, 2001), as well as arthropods in terrestrial forests (Forkner and Hunter, 2000). These functional responses emphasise the need to examine possible interactions between bottom-up and top-down factors considering specific ecological or life-history processes.

4.4.3 Importance of recruitment, bottom-up and top-down processes during coral reef degradation

The results of this study have important implications in terms of the mechanisms of coral reef degradation, which typically involves overgrowth or replacement of corals by seaweeds. The debate over the relative contributions of over-fishing and eutrophication to algal overgrowth and reef decline (Lapointe, 1997; Hughes et al., 1999), has largely ignored the role of supply-side processes in structuring ecological communities. For example, it is possible that top-down and bottom-up processes act differently on recruits and adults, and that eutrophication could lead to increased recruitment of algae, with profound implications for the abundance of adult populations within a site, and for the ability of seaweeds to colonise and invade new areas, especially after disturbances. However, the present results suggest that, for the two species studied, the relative effects of herbivory and nutrients are similar for recruits and adults (McCook, 1996; 1997; Jompa and McCook, 2002b). This result provides further support for the argument that, where herbivore populations are abundant, increased nutrients alone are unlikely to lead directly to increases in algal abundance, with consequent overgrowth of reefs, because herbivore consumption will increase and absorb any excess algal growth (McCook, 1999). As top-down control by herbivores has consistently strong effects on both adult and early stages of these algae, protection of herbivorous fish populations from over-fishing is vital to preventing algal overgrowth of coral reefs (Hughes, 1994; McCook, 1999; Jompa and McCook, 2002b).

In summary, in this study, early stages of two important coral reef seaweeds were much more strongly influenced by top-down regulation by herbivores than by bottom-up limitation by nutrient supply (resource limitation). Survival and growth of *S. fissifolium* and *L. variegata* and injury to *S. fissifolium*, were strongly influenced by herbivory, whereas nutrients had relatively minor effects. By considering the interactions between nutrient limitation, herbivory and supply-side processes in tropical marine plants, this study is significant in several contexts. It complements previous work on the roles of supply-side processes in other systems and groups, including populations of tropical fish and invertebrates, and temperate marine plants and animals. It complements studies of adult seaweeds, supporting the widespread dominance of herbivory effects over nutrient limitation on algal abundance on coral reefs. However, it is also significant that the absolute and relative strengths of these factors varied among population parameters and between the two species. Thus, as in terrestrial systems, the relative importance of different processes cannot be assumed to be uniform even within a particular ecosystem or habitat. Finally, the results have implications for management, stressing the importance of protecting herbivorous fish populations, in preventing algal overgrowth and coral reef degradation.

Chapter 5

Effects of Nutrient Enhancement on the Reproductive Biomass of a Coral Reef Macroalga

5.1 Introduction

Reproduction and recruitment are critical processes in the dynamics of ecological populations and communities, and fecundity, or reproductive output, is a key aspect of reproduction, one that may exert considerable control over the abundance of species at a site (e.g. for marine algae; Santelices, 1990; Lobban and Harrison, 1997). In many marine ecosystems, and on many coral reefs in particular, there is concern that increased inputs of nutrients, or eutrophication, may lead to increased algal abundance, resulting in phase shifts in which abundant corals are replaced by abundant algae (Morand and Briand, 1996; Lapointe, 1997; Raffaelli et al., 1998; see discussion in McCook, 1999; Hauxwell et al., 2000). For example, on the Great Barrier Reef (GBR), it has been suggested that increased inputs of terrestrial nutrients have led or could lead to increases in abundance and distribution of the large, canopy-forming macroalgae, *Sargassum* (Bell and Elmetri, 1995; Furnas and Brodie, 1996; Schaffelke and Klumpp, 1998a).

However, it is important that these processes (phase shifts and increase algal abundance) be considered not only in the context of ecological interactions such as herbivory (Hughes, 1994; McCook, 1999), but also in the context of the processes of reproduction, such as fecundity, dispersal, and recruitment (Davis et al., 2000). An increase in abundance of algae may involve either or both of two processes: i. Growth of existing algae, resulting in more algal tissue per unit area (provided herbivory levels are low, allowing algal growth to accumulate), due to increased height or density, whether of algae with distinct individuals (e.g. *Sargassum*) or those with turfing growth forms (e.g. algal turfs); or ii. Increases in area occupied by the algae (Fig. 1.1). An increase in area occupied by algae may involve either a. vegetative expansion of existing algal thalli onto new substrate; or b. colonisation by propagules from the plankton, thus involving a numeric increase. In the latter case, increased colonisation may involve either increased fecundity or increased recruitment. In taxa such as *Sargassum*, with distinct individuals and minimal vegetative reattachment, increases in area occupied must involve numeric increases.

Most previous work demonstrating nutrient enhancement of growth in coral reef algae has overlooked the detailed aspects of these population level processes. This work often implicitly assumes that demonstrated increases in algal growth will necessarily lead to increases in area, presumably either through increased reproductive output, or increased viability of propagules (Lapointe, 1997; Schaffelke and Klumpp, 1998a). This assumption, specifically postulated by Ang (1985a), is quite reasonable in principle (Weiner, 1988; De Wreede and Klinger, 1988), but has apparently not been experimentally tested, at least for tropical species. There is experimental evidence, primarily from temperate marine algae, demonstrating important roles for factors such as temperature, photoperiod, and light, in regulating reproductive biomass and fecundity (Lüning and Dieck, 1989; Santelices, 1990; Lobban and Harrison, 1997). However, the relationship between nutrients and algal reproductive development and fecundity is much less clear, and the available evidence suggests it may vary, depending on species, life histories, nutrient levels and supply, etc (Hoffmann et al., 1984; Reed et al., 1996; Coelho et al., 2000). Furthermore it has not been demonstrated that algal growth and reproduction are limited by the same resources (De Wreede and Klinger, 1988).

Given that algal invasions and phase shifts are unlikely to occur without numeric increases in algal populations, and the importance of such invasions during coral reef degradation, there is a need for experimental tests of the relationship between nutrients and algal reproductive biomass and fecundity on coral reefs (Santelices, 1990; Lobban and Harrison, 1997). I present here an initial experimental exploration, examining whether nutrient enhancement affects the reproductive biomass (as a proxy for fecundity or reproductive output) of abundant coral reef seaweed (*Sargassum siliquosum* J. Agardh) in a controlled environment. Although by no means a comprehensive test, the results suggest that enhanced nutrient supply may not lead to increased fecundity.

5.2 Methods

5.2.1 General approach and experimental design

To explore the effects of nutrient enhancement on the reproductive biomass allocation (fecundity) of *S. siliquosum*, I applied experimental nutrient pulses to the algae in outdoor tanks, and tested the effects on the number and biomass of reproductive structures (receptacles). The experimental design involved three levels of nutrients, ambient (control), medium and high, each with five replicates (or tanks), with three fertile adult thalli in each tank. I chose to do the experiment during the reproductive season, to ensure thalli were fertile, and because nutrient pulses occur in the field during this period. However, it is important to recognise that there may be a critical period for nutrient enhancement, and that a comprehensive study would involve nutrient treatments at several different stages of the seasonal growth cycle, a major undertaking beyond the scope of the present study.

5.2.2 Study species, collection and sample preparation

As mentioned in the General Introduction (section 1.2.3), species of *Sargassum* have been implicated in degradation of coral reefs worldwide (Bouchon et al., 1992; Hughes, 1994; Bell and Elmetri, 1995), and both temperate and tropical species appear to have considerable invasive potential (Paula and Eston, 1987; Critchley et al., 1990; Stiger and Payri, 1999a; 1999b). I selected *S. siliquosum* as one of the most abundant algae in the central section of the GBR (pers. obs.); together with other species of *Sargassum*, it forms dense canopies on the reef flats and slopes of inshore reefs of the GBR. Most *Sargassum* populations in this area are highly seasonal, producing abundant reproductive structures (receptacles) during the austral summer. These receptacles are shed during autumn, dispersing propagules. After the reproductive season, *S. siliquosum* thalli die but the holdfast and stems remain for at least several years (Morrissey, 1980; Price, 1989; Martin-Smith, 1993; Vuki and Price, 1994; McCook, 1996; Schaffelke and Klumpp, 1997a; Umar et al., 1998; pers. obs.).

Adult *S. siliquosum* plants were collected in March 2000 from a fringing reef (1-4 m depth) on Goold Island ($18^{o}10'$ 85 S; 146^{o} 10' 05 E), in the inshore, central GBR. This reef is very close to sources of terrestrial nutrients and sediments; further description of the study area can be found in McCook (1996; 2001). At the time of specimen collection, nutrient concentrations at the site (at 2 m depth) ranged between 0.02 – 0.04 µM of NH_4, and 0.05 – 0.07 µM PO_4, although, concentrations vary considerably within short periods of time (McCook, 2001; Devlin et al., 2001).

Fertile female plants of 30 - 40 cm height, with few epiphytes and healthy growing apical tips, were collected, with the attached substrate (carbonate rubble or rocks), and transplanted to the outdoor aquarium at the Australian Institute of Marine Science (AIMS). Initial length and wet weight (blotted dry) of each thallus were measured prior to nutrient manipulations. Algae were kept in running seawater (except during nutrient pulse treatments), in 70 L plastic "nally" bins throughout both transplantation (1 day) and experimental periods (30 days); at the AIMS aquarium, bins were immersed in larger tanks with flowing seawater, to regulate temperature, and aerated to enhance mixing, especially during nutrient additions. Experimental thalli were cleaned regularly of epiphytes with a cloth.

5.2.3 Nutrient enhancement protocols

Nutrient manipulations involved a nutrient pulse protocol comprising addition of nutrients for a 24 h period every 7-11 days for 30 days, using reagent-grade ammonium-chloride and sodium-dihydrogenphosphate (Schaffelke, 1999). Data from other species of *Sargassum* suggest that a one month period is sufficient to induce formation of new reproductive structures (Prince and O'Neal, 1979; Marui et al., 1981). I applied three nutrient concentration treatments: (1) Ambient, untreated controls, using seawater from the AIMS mariculture system (average concentrations ranged between 0.02 – 0.19 µM NH_4 and 0.01 – 0.37 µM PO_4); (2) Medium, with ≈ 5µM of NH_4 and 0.5 µM PO_4; and (3) High, with ≈ 10 µM NH_4 and 1 µM PO_4. These nutrient concentrations are relevant to the range of values recorded on the GBR (Schaffelke and Klumpp, 1997b; Devlin et al., 2001), and were confirmed using the method described in Chapter 4 (section 4.2.4). Seawater (ambient and enriched) was replaced every 4-6 hours during the 24 h pulse. To measure the effectiveness of the nutrient manipulations, I analysed tissue nutrient concentrations in the vegetative and reproductive tissues of *S. siliquosum* at the end of the experiment using the protocol described in Chapter 4 (section 4.2.4).

5.2.4 Response variables and data analysis

At the end of the experiment, each thallus was measured (length), cleaned of epiphytes, rinsed in freshwater, and the receptacles removed, counted, and both vegetative and reproductive (i.e. receptacles) tissues weighed wet and dry (60°C for 48 h). The number and dry biomass of receptacles are used as indices of fecundity, as biomass allocated to reproduction is considered a good descriptor of the relative reproductive output (Bäck et al., 1991). Proportional reproductive allocation or proportional reproductive investment was estimated as the percentage of receptacular dry biomass / total vegetative dry biomass (Mathieson and Guo, 1992). The differences between initial and final length and wet biomass were used as measures of growth during the course of the experiment. The allocation of nutrients to reproductive and vegetative tissues was compared using the ratios of tissue concentrations in the two tissues for each thallus.

Data analyses included one-way ANOVA and SNK tests to test for effects of nutrient enrichment on the number of receptacles, dry biomass of receptacles, dry biomass of vegetative tissue, proportional reproductive biomass allocation and on growth. The ANOVA model included three nutrient levels as fixed factors and five replicates, these being the average of the three thalli in each nally bin. I did not use a nested analysis because thalli within bins were unlikely to be independent, and the effects of variations within bins were of minimal interest. Effects on growth involved four to five replicates per nutrient treatment. Paired t-tests were used to compare the initial and final length and wet biomass within each nutrient treatment. The effects of nutrient enhancement on tissue nutrient concentrations within vegetative and reproductive tissue types, and the proportional allocation of nutrients to the two tissues, were analysed using one-way ANOVAs, with 5 replicates per treatment; post-hoc comparisons used Tukey's test. Tissue nutrients were also compared between the two tissues using paired t-tests. All data were checked for normality graphically, using stem and leaf plots and probability plots; and for homogeneity of variances with Cochran's test, on which bases data were not transformed.

5.3 Results

5.3.1 Test of treatments: tissue nutrient concentrations

Nutrient treatments resulted in clear enhancement of algal tissue nitrogen, but the effects on tissue phosphorus were less clear. Both tissue concentrations (per gram algal tissue) of nitrogen and N : C ratios of both reproductive and vegetative tissues were significantly higher in the nutrient addition treatments than in unenriched controls (Fig. 5.1A; Table 5.1). There were no significant differences in tissue nitrogen between medium and high nutrient treatments for both reproductive and vegetative tissues, suggesting saturation at the medium nutrient treatment. Phosphorus levels (per gram algal tissue) in both reproductive and vegetative tissues were ranked according to the nutrient treatments, but the differences were smaller and not significant, and P : C ratios showed little differences across nutrient treatments (Fig. 5.1B; Table 5.1). Tissue nitrogen and phosphorus concentrations were significantly higher in the reproductive tissue than in vegetative tissue at all levels of nutrient treatment (Fig. 5.1; for N: control:

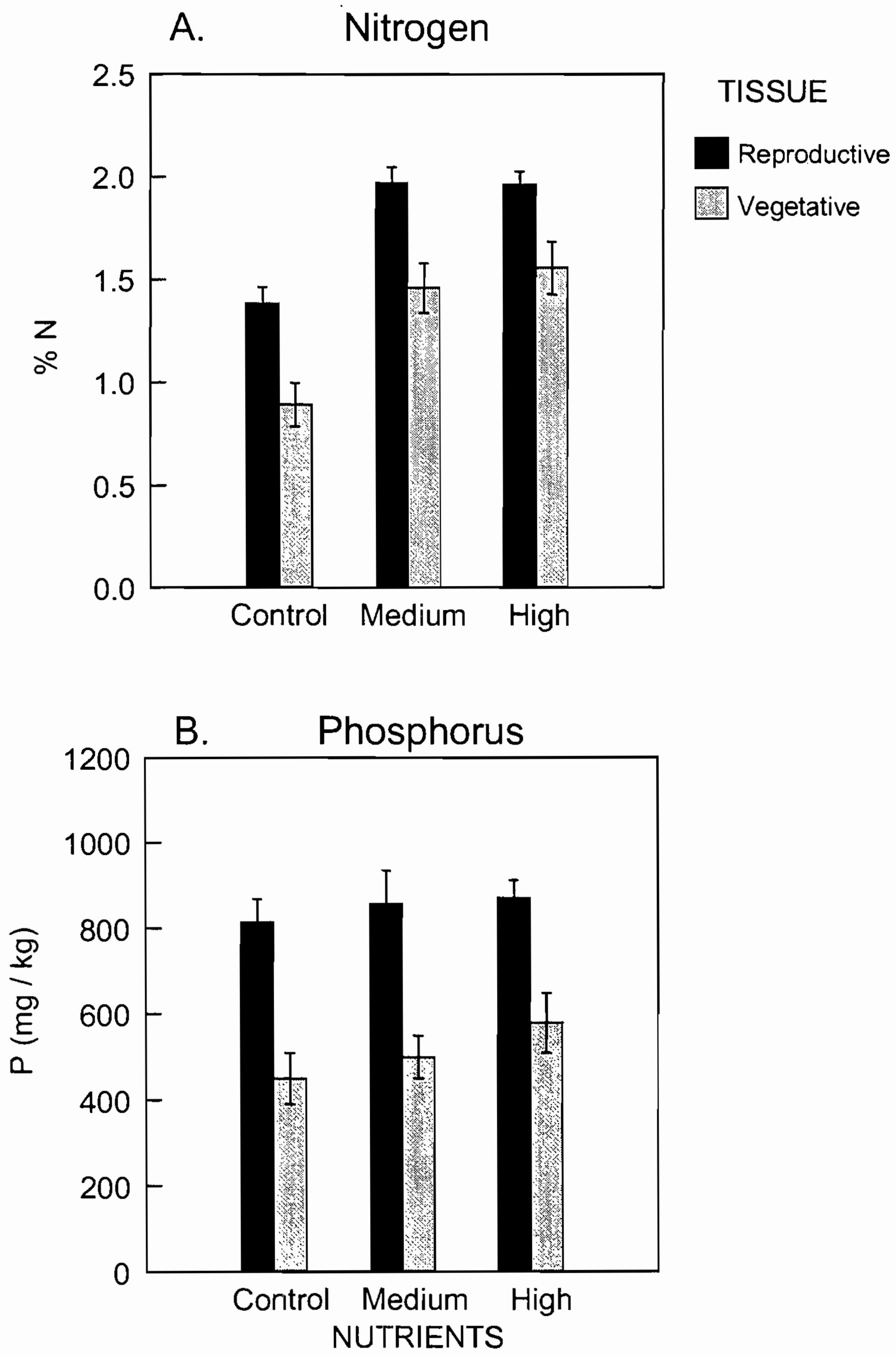


Figure 5.1 Mean tissue nutrient concentrations of nitrogen (A) and phosphorus (B) of reproductive and vegetative tissue of *Sargassum siliquosum* across nutrient treatments (± 1 SE, N = 5).

t = 6.990, df = 4, P = 0.002; medium: t = 3.582, df = 4, P = 0.023; high: t = 2.907, df = 4, P = 0.044; for P: control: t = 6.293, df = 4, P = 0.003; medium: t = 3.415, df = 4, P = 0.027; high: t = 4.427, df = 4, P = 0.011). The proportional allocation of nutrients to the two tissues was not significantly different among nutrient treatments (one way ANOVA, P = 0.19 for N and P = 0.55 for P), although there was a consistent trend to reduced allocation to reproductive tissues in thalli from the enhanced nutrient treatments.

5.3.2 Fecundity: receptacle number and reproductive biomass

Nutrient enrichment reduced the apparent fecundity of *S. siliquosum*. The number and biomass of reproductive structures (receptacles) were significantly lower in treatments where nutrients were added (Fig. 5.2A-B; Table 5.2). Receptacle counts from unenriched control thalli were almost 60 % higher than those of thalli from the medium and high nutrient enrichment treatments (Fig. 5.2A), and reproductive biomass of the control treatment was about 50 % higher than that in the medium and high nutrient enrichment treatments (Fig. 5.2B). There were no significant differences in either measure between medium and high nutrient treatments.

The dry biomass of vegetative tissue in the control treatment was also significantly higher than in the medium and high treatments (Fig 5.2C; Table 5.2). There was no significant difference in vegetative biomass of the medium and high nutrient treatments.

5.3.3 Proportional reproductive biomass allocation (proportional reproductive investment)

Despite the apparent differences in reproductive output per *S. siliquosum* plant, I did not detect a significant effect of nutrient enrichment on the proportional allocation of biomass to reproduction (reproductive dry biomass / vegetative dry biomass; Fig. 5.2D; Table 5.2). Although proportional reproductive investment in the high nutrient treatment was slightly lower than the other two treatments, this difference is unlikely to represent a real effect (type II error) as it was highly non-significant and is not consistent with the patterns seen in the receptacle counts and biomass measures.

5.3.4 Growth: initial vs. final length and total wet biomass

Thallus length did not show significant differences between treatments nor between initial and final measurements at any level of nutrients (control: t = -0.342, df = 4, P = 0.75; medium: t = -1.122, df = 3, P = 0.344; High: t = -0.521, df = 3, P = 0.639;

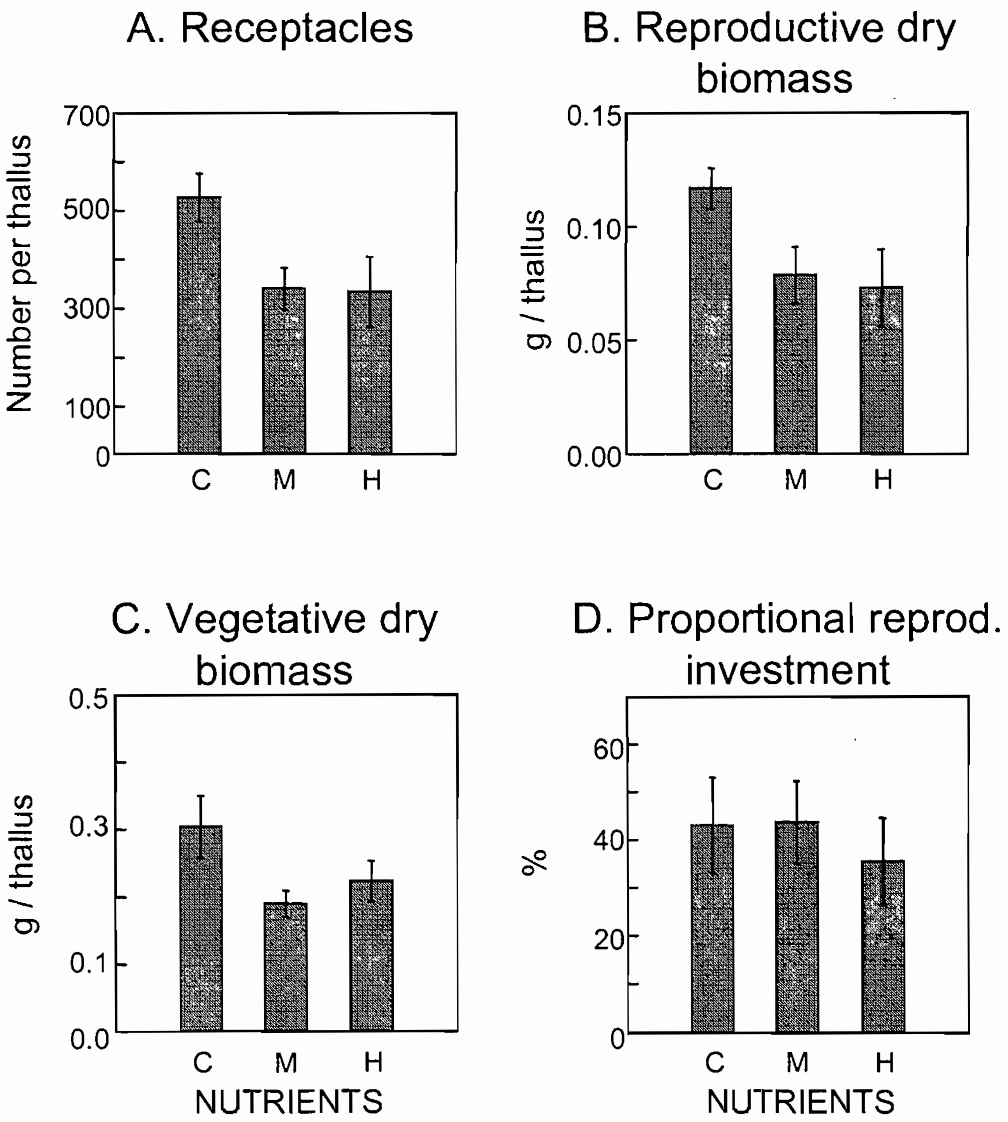


Figure 5.2 Mean number of receptacles (A), reproductive dry biomass (B), vegetative dry biomass (C), and proportional reproductive investment (D) per thallus of *Sargassum siliquosum* across nutrient treatments (C = unenriched control, M = medium nutrient concentration, H = high nutrient concentration; ± 1 SE, N = 5).

Fig. 5.3A), suggesting that growth in terms of thallus length was negligible over the course of the experiment.

Although the length of the algae did not vary, thalli lost significant amounts of tissue during the experiment, through the shedding of secondary branches, leaves, vesicles, and receptacles. This was reflected in the differences in wet biomass, which was significantly reduced by at the beginning than at the end of the experiment, in both the unenriched control (t = 3.27, df = 4, P = 0.031) and at the high nutrient treatments (t = 6.26, df = 3, P = 0.008; Fig. 5.3B); although the difference was not significant at the medium nutrient treatment (t = 1.76, df = 3, P = 0.177). The extent of the differences between the initial and final biomass (growth) varied almost significantly across nutrient treatments: thalli of the high nutrient treatments lost proportionally more biomass than thalli from the control and medium treatments, in part because initial wet weights were higher in the high nutrient treatment (Fig. 5.3B; Table 5.2).

5.4 Discussion

The results of this experiment strongly suggest that nutrient enhancement should not be assumed to lead to increased fecundity and recruitment in benthic macroalgae, as widely assumed. In these experiments, nutrient enrichment apparently reduced the reproductive biomass of mature *Sargassum siliquosum*, in contrast to, and potentially counter-acting, effects on growth rates (Larned, 1998; Schaffelke and Klumpp, 1998a). The number and biomass of reproductive structures (receptacles) were lower in treatments where nutrients were added, and the proportional allocation of biomass to reproductive tissues, whilst not significantly reduced, was clearly not enhanced by nutrient additions. The vegetative biomass was also similarly reduced by nutrient enrichment, suggesting that these nutrient additions were generally detrimental to fertile adult plants (Fig. 5.2). The patterns in length and biomass data are consistent with seasonal patterns in the field, with cessation of thallus growth and initial shedding of distal tissues. Importantly, the length of the thalli did not decrease, indicating that thallus senescence was not far progressed.

Table 5.1 ANOVAs of effects of nutrient enhancement and type of tissue (reproductive or vegetative) on the tissue N and P concentrations and on the N : C and P : C ratios of *Sargassum siliquosum*. C = unenriched control, M = medium nutrient concentration, H = high nutrient concentrations.

		Reproductive tissue				Vegetative tissue			
Source of variation	df	MS	*F*	*P*	Tukey's test	MS	*F*	*P*	Tukey's test
N (%)									
Nutrients	2	0.570	25.87	<0.0001	C < M = H	0.647	11.92	0.0014	C < M ≈ H
Error	12	0.022				0.054			
N : C ratio									
Nutrients	2	0.0004	16.29	0.0004	C < M ≈ H	0.0004	11.31	0.0017	C < M ≈ H
Error	12	0.00003				<0.0001			
P (mg / kg)									
Nutrients	2	4421.4	0.316	0.736	C ≈ M ≈ H	21521.4	1.560	0.250	C ≈ M ≈ H
Error	12	14000.7				13795.6			
P : C ratio									
Nutrients	2	<0.0001	0.096	0.909	C ≈ M ≈ H	<0.0001	0.889	0.436	C ≈ M ≈ H
Error	12	<0.0001				<0.0001			

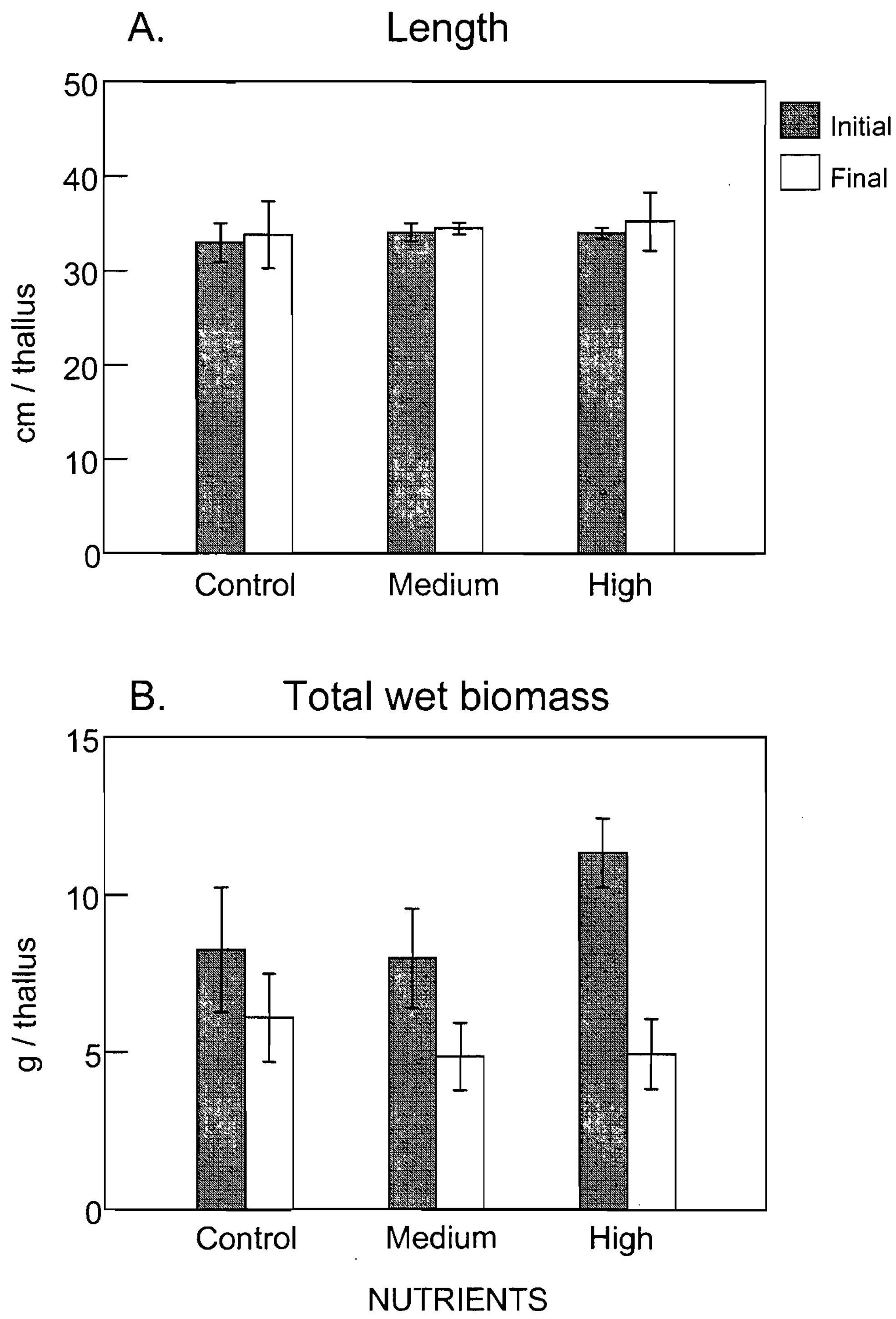


Figure 5.3 Mean length (A) and total wet biomass per thallus (B) of *Sargassum siliquosum* at the beginning (initial) and end of the experiment (final) across nutrient treatments (± 1 SE, N = 4 - 5).

Table 5.2 ANOVAs of effects of nutrient enhancement on the number of receptacles, reproductive and vegetative dry biomass, proportional reproductive investment, and on the difference between initial and final lengths and total wet biomass of *Sargassum siliquosum*. C= unenriched control, M= medium, H= high nutrient concentrations. N.S.= not significant.

Source of variation	df	MS	*F*	*P*	SNK test
Receptacle number					
Nutrients	2	60530.5	5.01	0.026	C>M =H
Error	12	12075.6			
Reproductive dry biomass					
Nutrients	2	0.00286	4.30	0.039	C>M =H
Error	12	0.00066			
Vegetative dry biomass					
Nutrients	2	0.01724	3.89	0.049	C>M ≈H
Error	12	0.00443			
Proportional reproductive investment					
Nutrients	2	0.01043	0.32	0.734	N.S.
Error	12	0.03280			
Difference in length					
Nutrients	2	0.331	0.02	0.985	N.S.
Error	10	21.825			
Difference in total wet biomass					
Nutrients	2	19.489	3.94	0.055	H>C = M
Error	10	4.946			

Although these results contrast with general assumptions about nutrients and fecundity, those assumptions, whilst reasonable, appear to stem from little direct evidence. Ang (1985a), also working with tropical *S. siliquosum*, correlated growth with phosphate concentrations, and postulated a link to fecundity. Hoffmann et al. (1984) found that development of different reproductive stages of a temperate kelp, had variable nutrient requirements, and fertilisation had a relatively narrow optimal range of concentrations; this would not suggest a simple, monotonic relationship between concentrations and fecundity. Also working with temperate kelps, Reed et al. (1996) found contrasting correlations between reproductive allocation and seawater temperature, in two different kelps, and inferred relationships with nutrient availability (based on temperature-nutrient correlations). They suggested that nutrient resources might enhance fecundity in species that reproduce continuously but not in species that that are strictly seasonal. My results for *S. siliquosum*, which is strongly seasonal in reproduction, would be consistent with this suggestion. As previously pointed out (De Wreede and Klinger, 1988), algal growth and reproduction may be limited by different resources. The effects of nutrient increases on algal reproductive biomass and fecundity seem likely to be complex and difficult to generalise.

It is important to recognise that there are limitations to the context of my study, which therefore should not be taken as unequivocal demonstration that nutrients reduced the overall fecundity of this species, but rather as demonstration that nutrient increases may not result in increased fecundity, and that further experimental evidence is required. For example, it is possible that the apparent reduction in reproductive output and biomass in nutrient enhancement treatments reflects either i. a genuine inhibition, or ii. accelerated maturation, with consequent increased tissue losses due to more advanced senescence. The concentrations of nutrients used in this experiment have been widely used in both adults (Schaffelke and Klumpp, 1998b) and early life stages (Schaffelke and Klumpp, 1997b; Chapter 4) in other local species of *Sargassum* and in other fleshy macroalgae (Jompa and McCook, 2002b), generally with neutral or positive effects, but there is evidence for inhibition of *Sargassum* growth at high nutrient levels (McCook et al., 1997; Schaffelke and Klumpp, 1998a). If reproductive processes like fertilisation have optimal nutrient concentrations (Hoffmann et al., 1984) then reductions in reproductive output at higher nutrient levels are not unlikely.

However, given the patterns of biomass losses among treatments, I cannot discount the second interpretation that my nutrient enhancement treatments resulted in earlier onset of propagule release, so that low receptacle counts may be an artifact of more advanced tissue senescence. Nonetheless, this interpretation is not supported by the observation that proportional tissue losses were no different between control and medium nutrient treatments, and even if timing of onset were earlier, this would still not provide evidence of increased reproductive output.

The timing of nutrient enhancement in relation to developmental processes may be important (Hoffmann et al., 1984), so it is also possible that nutrient enhancement at other periods (e.g. during pre-reproductive stages) may have different effects to those in my study. Complete appreciation of nutrient effects may not only require experiments at different times, but may need to integrate the outcome of contrasting effects at different stages, may be dependent on the actual timing or seasonality of actual nutrient events in the field, and are very likely to vary between species (Santelices, 1990).

Similarly, although previous work (Bäck et al., 1991) indicates that receptacle density or biomass provides a good proxy for overall reproductive output, it is important to recognise the potential for nutrient effects on numbers of conceptacles per receptacle, on oogonia per conceptacle, or even on the viability or growth rates of planktonic or settled propagules. Clearly, full consideration of all possible effects, and of timing, was beyond the scope of the present study, and detailed interpretation of process underlying my results will require further experimental evidence on a range of species.

Thus, I interpret these results as providing initial evidence for the potential complexity of nutrient effects on the potential for algal invasions, and as illustrating the need to distinguish between effects on growth, and effects on fecundity and recruitment processes, and consequent invasion potential. In the context of coral reef phase shifts, there is strong evidence that algal abundance, distributions and invasions are less strongly affected by growth rates (and nutrient supply) than by reductions in herbivory, by overfishing or diseases (Hughes, 1994; McCook, 1999; Hughes et al., 1999; Jompa and McCook, 2002b) or to coral disturbances that create new free substrate for algal settlement and colonization (Aronson and Precht, 1997; Williams et al., 2001; Chapter 3). In the specific case of putative invasions by *Sargassum* of inshore reefs on the GBR, available evidence does not indicate that increased nutrient inputs alone can be assumed to cause increased invasions of *Sargassum*. Not only are *Sargassum* distributions strongly influenced by herbivory (McCook, 1996; 1997), but the strong seasonal cycle of growth, reproduction and senescence may mean any nutrient related gain in growth is negated by intrinsic upper limits to biomass per thallus, perhaps due to intraspecific competition or physical constraints, and completely negated during seasonal senescence.

In summary, my results did not provide evidence that increases in nutrients will result in increased fecundity of this highly seasonal, coral reef seaweed, since the number and biomass of reproductive structures decreased with nutrient additions during the reproductive period. The complexity of the processes involved means that these results can only be taken as initial indications, and should not be taken as proof that nutrients inhibit fecundity overall. But they do illustrate the need to distinguish between effects on different life-history processes. Whatever the effects on growth and abundance of pre-existing algae, an increase in the number of propagules that arrive to a site is a crucial step for algal invasions and consequent phase shifts to occur (Davis et al., 2000); growth of individuals does not necessarily result in growth of populations. In the context of coral reef degradation, this provides further demonstration that the documented and serious consequences of eutrophication are unlikely to simply involve increases in algal growth and consequent replacement of coral populations (Ginsburg, 1994; Wilkinson, 2000; McCook et al., 2001b), but are likely to involve complex interactions between processes.

Chapter 6

General Discussion

The aim of the thesis was to investigate the dynamics of, and factors that affect, the recruitment and reproduction of coral reef algae and the potential consequences for populations and community structure and hence for reef degradation. I showed that there was considerable variability in the recruitment process and in the effects of factors on recruitment, and suggest that this variability is very likely to have consequences to the development of adult algal populations and algal invasions on coral reefs. Chapter 2 demonstrated the importance of substrate type to the dynamics of algal recruitment. Healthy live corals inhibited algal recruitment but algae readily recruited onto all other substrate types, suggesting that benthic algal invasions may often require the prior death or stress of the corals. Chapter 3 put Chapter 2 in a specific context of a major event and showed the importance of an ecological disturbance, coral bleaching, as mediator of the dynamics of corals and algae and as a cause for "invasions" of algae on coral reefs. Chapter 4 showed that top-down regulation by herbivory is a critical factor that inhibits the population development of early life history stages. Although nutrients enhanced growth of one species, the contribution was weak. Consequently, herbivory has important implications in preventing the development of algal invasions on coral reefs. Herbivory effects on early life history stages show consistency with results found for adult plants. Chapter 5 gave an example in which the addition of nutrients did not support a positive effect on algal fecundity, and therefore suggests the potential complexity of effects of nutrients on algal reproduction and suggests caution in the interpretations of such results.

6.1 Variation

Taking the results of the individual data chapters together, it is clear that there is considerable variability in the recruitment dynamics and development of early life-history stages across a range of ecological factors and taxa important in reef degradation, and across response variables. Factors that accounted for variability in the recruitment dynamics included availability of substrate and coral disturbances, location and successional stage, reductions in herbivory, differences between taxa and between growth and survival, and to a lesser extent nutrient enhancement. The interactions between these factors also contributed to the observed variability in the outcomes of the recruitment process.

Sargassum spp. and *Lobophora variegata* showed different responses to substrates types, nutrients and herbivory. For instance, *L. variegata* recruits responded to nutrient additions while *S. fissifolium* recruits did not, while herbivory had larger effects on *S. fissifolium* than on *L. variegata*. This variability in responses between taxa may be related to differences in functional morphology, as discussed in Chapter 4 (section 4.4.1). It illustrates that in order to fully understand the complexity and dynamics of phase shifts it is important to consider a range of species with different morphological and anatomical characteristics.

Two key points arise from this variability in outcomes. First, despite the high variability in outcomes of the recruitment process, algae did not recruit on healthy corals and this outcome was not variable across coral taxa, algal species or life history parameters (Chapter 2 and 3). Live corals are clearly distinct from any other substrate tested. Secondly, because algal recruitment is important in determining patterns of adult distributions, the variability in recruitment can be assumed to have considerable implications for changes in adult distributions and consequently for reef degradation, particularly after coral disturbances. For example, the variability in outcomes of bleaching damage and algal colonisation demonstrates the potential for major and variable effects on the recovery of coral populations, with implications for future reef status. Different types of algae can have different effects on different corals (as discussed in Chapter 3).

The variability in numeric and growth responses of the algae (i.e. life-history properties) is important to an understanding of algal dynamics during phase shifts because these properties measure different things. Density refers to survival or mortality and is a property of a population, and size refers to growth increases and is a property of an individual. Importantly, an increase in growth of individuals is often taken to imply an increase in the abundance of the population, but this assertion requires examination. However, an increase in densities (i.e. survival) may imply an increase in the population without necessarily relying in increases in growth of the individuals. The distinctions between growth and numeric responses are important to the understanding of reef degradation and phase shifts, because these properties responded differently to environmental factors. These distinctions suggest a necessity to measure a range of variables appropriate to the process being studied. Growth may not necessarily be the most appropriate parameter to be measured with regard to algal invasions and phase shifts.

An important outcome of this project is that it supports the crucial role that herbivory plays in controlling the potential development of algal invasions on coral reefs (Hay, 1985; Steneck, 1994; McCook, 1996; Hughes et al., 1999). The effects of herbivory overwhelmed the contribution by nutrient enhancement to the development of populations of early stages (Chapter 4). Furthermore, the addition of nutrients did not enhance algal fecundity (Chapter 5). These results are significant contributions to the current debate about the causes of algal blooms in coral reefs in that they demonstrate the potential effects of top-down factors like herbivory, while demonstrating a weak contribution by nutrients. These results complement studies of adult seaweeds supporting the widespread dominance of top-down over bottom-up effects on algal abundance on coral reefs. Moreover, these results support the argument that where herbivore populations are abundant, nutrient eutrophication alone is unlikely to lead directly to increases in algal abundance, because herbivore consumption will increase and absorb any excess algal growth (Chapter 4).

6.2 Mechanisms of coral replacement by algae

As mentioned in the General Introduction, coral reef phase shifts result from the replacement of corals by competing algae. Conceptually, the replacement of corals by algae may occur by two main mechanisms (Table 6.1).

Table 6.1 Mechanisms of coral replacement by algae.

	Settlement of propagules from plankton	Vegetative overgrowth
Healthy corals	Unlikely	Rare
Disturbed corals (stressed or dead)	Important	Slow - Rapid

Algae can replace corals through settlement and growth of propagules from the plankton or by competitive vegetative overgrowth from adjacent algal thalli. These mechanisms can take place on healthy coral tissue or on disturbed corals (injured, stressed, or dead). However, both mechanisms are more likely to occur with disturbed corals compared to healthy corals. This framework does not attempt to discount other mechanisms of replacement, for example, fragmentation of adult thalli and subsequent attachment on healthy or dead corals.

The mechanism of replacement through algal settlement from the plankton onto healthy coral tissue seems to be rare for a range of algal groups and forms (Chapter 2 and 3). Healthy corals clearly inhibited the recruitment of algae but algae readily recruited onto moribund or dead corals. Algae never settled on healthy corals. The second mechanism, replacement by vegetative overgrowth, is directly related to competitive processes and has been documented for fleshy macroalgae (including *L. variegata*) and filamentous algal taxa, both on nearby islands of the GBR (Jompa and McCook, 2002a; 2002b) and in the Caribbean (Hughes, 1994). In a recent review on coral–algal competition, we suggest that competition may be widespread but a highly variable process in coral reefs (McCook et al., 2001a).

The potential importance of coral disturbances and subsequent algal settlement and recruitment or vegetative overgrowth in a phase shifts is highlighted in Chapter 3. The 1998 coral bleaching event precipitated an ecological shift from live corals to benthic algae (Wilkinson, 2000; McClanahan et al., 2001), where all dead corals studied were rapidly colonised by diverse algal assemblages while healthy corals remained healthy. Algal recruitment was not the initial cause of coral decline, rather the consequence, although it may have contributed to the failure of corals to recover after disturbances. Algal settlement and colonisation is an almost universal consequence of coral tissue death, or even injury or stress, as discussed in Chapter 3.

This mechanistic view of the process of phase shifts provides a framework for the study of coral replacement by algae. For example, it appears that rather than settlement of algal propagules directly from the plankton, the replacement of healthy corals by algae is more likely to involve either lateral, vegetative overgrowth by competing algae or coral disturbance and subsequent algal colonisation and vegetative overgrowth. It also illustrates that there are a limited number of mechanisms by which this replacement can occur.

6.3 Implications for reef degradation

Understanding the processes that modify the supply of propagules and dynamics of algal recruitment to benthic communities has important implications for the management of coral reef degradation and algal blooms. For instance, herbivory played a crucial role in controlling algal recruitment and potential algal blooms on reefs with abundant fish populations. For this reason, reefs with abundant herbivore populations are less likely to experience blooms of fleshy macroalgae following increases in nutrients. If herbivores are removed, however, considerable evidence suggests that algal blooms may occur (Chapter 4). If supply of nutrient increases in coral reefs where herbivore populations are abundant, it is likely that algal growth may be promoted but biomass accumulation may be modified by the herbivores that consume the excess algal production. However, if nutrient supply increases in reefs where herbivore populations are scarce, macroalgal recruits will have the potential to develop into algal blooms (provided there is a supply of algal propagules to that reef). The latter scenario will be more likely to occur on inshore reefs or reef flats where herbivory seems to be lower compared to midshelf and offshore reefs or reef crests (see discussion in Chapter 4 and references therein). The magnitude of response of algal recruits to increases in nutrient supply or reductions in herbivory will depend upon the species, nutritional ecology of the algae, nutrient backgrounds, herbivore composition, etc. These results therefore have implications for management of reef degradation by indicating that the protection of herbivore populations is fundamental to minimising algal overgrowth and coral reef degradation (Chapter 4).

The different responses of growth and survival of early stages (Chapter 2 and 4) and the suggestion of a non-positive effect of nutrients on the reproductive output (and therefore on numeric response, Chapter 5) raises concern about the appropriate life-history parameters that should be measured when studying phase shifts and algal invasions. Responses in algal growth (increase in size) have been generally related to phase shifts and to increases in the population sizes of invasive algae. However, as noted before, since growth is a property of an individual, it is risky to extrapolate effects of an individual to a population level. Most work on algal phase shifts has focussed on changes in algal growth but not at changes in numeric response (Fig. 1.1). Density responses may more accurately represent effects on the population level, especially for *Sargassum* spp., which have seasonal growth, as described in Chapter 5. This distinction may have implications for measurement of algal variables during phase shifts since growth, density, and increases in area occupied provides information about the dynamics of different levels of organisation (e.g. individuals, populations, or communities). Since algal recruitment is fundamental to algal invasions, and because recruitment requires suitable substrate, the increase in area occupied is also a parameter critical for understand the dynamics of corals and algae.

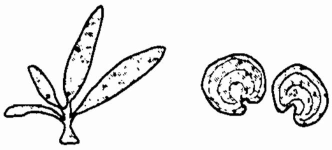
The relative importance of eutrophication (bottom-up) and over-fishing of herbivores (top-down) as direct causes of macroalgal blooms have recently received considerable attention (see Chapter 4 and references therein). Both of these perspectives suggest that decreases in coral abundance are caused by increases in algal abundance (due to increased algal competitiveness). However, disturbances such as bleaching may result in similar relative changes in abundance of coral and algae but with reversed causality: the decline in coral abundance is the cause of increased algal abundance. Such distinctions may have significant implications in management of phase shifts, in particular if human impacts limit the recovery of reefs from natural disturbances, rather than or as well as directly causing coral mortality. My results illustrate therefore the significance of broadening the bottom-up and top-down approaches to include the roles of coral disturbances as potential causes of algal blooms in coral reefs (Done, 1992; Hughes, 1994; Williams et al., 2001; Knowlton and Jackson, 2001; as discussed in Chapter 3).

The dynamics of recruitment are critical to the development of algal colonisation and invasions on coral reefs. For example, low algal recruitment onto reefs may imply that those reefs are less likely to be invaded by macroalgae than reefs with higher supply of propagules, particularly if herbivore populations are scarce. Thus, a better knowledge of the processes that modify the supply side and dynamics of algal recruitment has important implications for management. Exploring the variability in mechanisms and responses by which algal supply side and recruitment processes interact with coral disturbances, substrate characteristics and prior occupants, herbivores, and nutrients is a valuable step in understanding the roles of algae during reef degradation.

6.4 Conclusions

- Benthic algae did not recruit on healthy live coral tissue.
- Benthic algae universally colonised dead coral.
- Herbivory played a major role in regulating algal recruitment.
- The contribution of nutrients to the development of populations of early stages and in the facilitation of fecundity of macroalgae was weak. This contrasts with the overwhelming negative effect of herbivory on population development.
- There is considerable variability in algal recruitment at different spatial and temporal scales, and across ecological factors related to reef degradation (i.e. coral disturbances and herbivory). This variability may have consequences on developing adult algal populations.

- The variability between life-history properties (growth and density) has implications for understanding the mechanisms of phase shifts. Growth is a property of an individual but density is a measure of increase at a population level.



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