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Influences of benthic algae on coral settlement and post-settlement survival: implications for the recovery of disturbed and degraded reefs

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ABSTRACT

Benthic algae generally dominate degraded and disturbed coral reefs, however our understanding of how algae influence coral recruitment, a critical process for the recovery of these reefs, is limited. Surveys to compare benthic biota close to versus distant from coral recruits on inshore reefs of the Great Barrier Reef identified several key groups of algae that are frequently associated with, and thus potentially favour coral recruitment. In particular, filamentous algal turfs dominated the substrata surrounding coral recruits and crustose coralline algae and the brown alga *Lobophora variegata* were also abundant and therefore may promote coral recruitment. In contrast, soft corals and even hard corals were less frequently found adjacent to coral recruits, suggesting that they are likely to have negative impacts on coral recruitment.

Subsequently, I experimentally investigated the effects of two filamentous algal turfs established on dead coral surfaces, and sediments, which are often trapped by algal turfs, on settlement of the coral *Acropora millepora*. Adding sediment reduced settlement but the effects of different algal turfs varied, a newly established (<6 week old) and relatively ungrazed turf reducing settlement, and a well established turf (up to 2.5 years) and grazed turf only reducing settlement when combined with sediments. This suggests that algal turfs can delay the recovery of coral populations on disturbed reefs, in particular in high sediment environments and with low grazing regimes.

Next, I investigated the potential for water-borne chemical influences from benthic algae to affect coral settlement, comparing settlement in seawater influenced by an alga identified as likely to promote and others identified as likely to hinder coral recruitment in surveys of coral recruit-algae associations. The fleshy alga *Lobophora variegata*

enhanced coral settlement, whereas the green filamentous alga *Chlorodesmis fastigiata* (Turtle weed) delayed coral settlement, and another brown alga *Padina sp.* (Funnel weed) apparently had no effect on coral settlement. Furthermore, these waterborne chemical influences were demonstrated to affect settlement of the coral *Acropora millepora* on the crustose coralline alga *Hydrolithon reinboldii*, which is known to induce the settlement of several *Acropora spp.* corals. The demonstration of waterborne effects suggests that some benthic algae can influence coral settlement before coral larvae reach the reef substrata and even where the immediate settlement location is free of algal cover.

Finally, I investigated early survival and growth up to four months after settlement of *Acropora millepora* recruits in reef environments dominated by fleshy algae (*Sargassum spp*. and *Padina spp.*), which had developed from algal turf assemblages solely as a result of reduced grazing. Surprisingly, I found recruits survived and grew more in reef environments dominated by the fleshy algae at a time when seawater temperatures were abnormally high, thus contradicting the paradigm that fleshy algae generally hinder coral recruitment.

My research suggests that, at least on inshore reefs of the Great Barrier Reef, corals may have no alternative but to recruit in habitats dominated by algae. Furthermore, the outcome of algal influence on coral recruitment, and consequently reef recovery from disturbance, may differ as a result of environmental stresses (sedimentation, elevated seawater temperatures), and the specific algae and coral life-stage (e.g. settlement, early survival) involved in coral-algal interactions.

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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.

Chico Liam Birrell

Chapter 1. General Introduction

1.1. The need for greater understanding of the impact of algae on coral reef replenishment processes

The increasing rate of degradation of coral reefs globally (Wilkinson 1993, 2000, 2002) highlights the need for increased understanding of factors affecting reef recovery processes, particularly of those that affect coral recruitment. Degradation of coral reefs generally arises from human-related activities, for example from increased sedimentation and water turbidity, inorganic pollution, increased nutrient inputs and the over-exploitation of fisheries, that typically result in increasing abundance of algae and even “phase shifts” from coral to algal dominated communities (Hughes 1994a, Brown 1997, Wilkinson 1999, 2002, Hughes et al. 2003). While it is commonly acknowledged that macroalgae (herein also referred to as benthic algae i.e. all algae but phytoplankton) play an important role in the functioning of coral reef ecosystems (see section 1.2), very few studies have evaluated the roles of specific algal groups (other than for crustose coralline algae (Morse et al. 1988, 1996) on coral recruitment. Given predictions that less than a third of the world’s coral reefs may escape devastation within the next few decades (Wilkinson 1993, Bryant et al. 1998, Hoegh-Guldberg 1999), the longer-term resilience of coral reefs will largely depend on coral recruitment as a major replenishment process. Thus it is critical that we understand how macroalgae, generally the dominant component of benthic communities on degraded reefs, affect replenishment processes.

The need to understand the role of macroalgae on coral replenishment processes is generally thought to be particularly acute on coastal and inshore reefs close to highly populated areas, which are most at risk from human-related activities (Bryant et al.

1998, Wachenfeld et al. 1998, 2003). However, repeated mass-bleaching events globally in the past decade on even relatively pristine and remote reefs (Wilkinson 2000, 2002) indicate that all coral reefs are susceptible to degradation regardless of their present condition. Moreover, such widespread degradation from coral bleaching is believed to relate to global climate change and increased sea surface temperatures, and is predicted to become more frequent in the next few decades (Goreau and Hayes 1994, Hoegh-Guldberg 1999, Strong et al. 2000, Hughes et al. 2003).

Replenishment of coral cover following disturbance events occurs primarily through regrowth of partially dead colonies or as a result of colonisation of the reef substrata by new coral recruits (Done 1992, Connell et al. 1997). Coral recovery is likely to be faster from acute disturbances, where the source of disturbance is only temporary (e.g. cyclones, lava flows), than from longer-term, chronic disturbances (e.g. pollution, sedimentation) that may be accompanied by overall degradation of the populations supplying new recruits (Connell 1997, Connell et al. 1997, Hughes and Connell 1999). If coral recruitment fails over a number of years, then disturbed coral populations can become locally extinct within a few generations, leading to long-term declines in coral cover (Hughes 1989, 1996, Hughes and Tanner 2000). Given that replenishment of coral populations can fail as a result of interruptions or reductions in a number of different processes, including adult fecundity, larval supply, coral settlement, and survival of coral recruits, each of these, in turn, is critical to reef recovery from degradation and disturbance (Harrison and Wallace 1990, Caley et al. 1996, Hughes and Tanner 2000). Therefore, understanding how benthic algae impact replenishment processes at each of these levels is fundamental to predicting and managing coral reef recovery from disturbance.

1.2. The fundamental roles of benthic algae on pristine, disturbed and degraded reefs

The importance of the ecological roles of benthic algae to the functioning of coral reef ecosystems (Berner 1990, Hay 1997, Adey 1998) is often overshadowed by the fact that algal dominance is generally an indicator of a disturbed or degraded coral reef (Done 1992, Goreau 1992, Hughes 1994a, McCook 1999). Algae turfs and calcified algae are the major contributors to primary production and nitrogen fixation on reefs, and also make important contributions to reef building through calcification and cementation of the reef matrix (Littler and Littler 1984, Hatcher 1990, Carpenter et al. 1991, Macintyre 1997, Adey 1998). Macroalgae as well as phytoplankton are at the base of food webs in coral reef environments (Hatcher 1983, 1990, Karlson 1999 and reference therein). Furthermore, macroalgae, having evolved a diverse range of defences against herbivores, have simultaneously provided habitats and become food sources for motile mesograzers as well as for juvenile reef invertebrates and fish, which also gain protection and refuge from predators by associating with defended hosts (Hay 1997).

In contrast, by dominating degraded and disturbed coral reefs and competing with corals, macroalgae can contribute to the demise of coral populations, with serious consequences for the economic and ecological values of reefs (Done 1992, Hughes 1994a, McCook 1999). The rapid colonisation of dead corals and substrata temporarily cleared of other benthic biota following disturbance events is the major mechanism by which macroalgae dominate coral reefs (Price 1975, Connell et al. 1997, Airoldi 1998, 2000, McCook 2001, Diaz-Pulido and McCook 2002). Any disturbance event causing coral mortality, regardless of the specific cause(s), appears to facilitate spatial dominance of macroalgae (reviewed in McCook 1999). Once established, macroalgae assemblages may hinder the recovery/replenishment of coral populations following a disturbance event (e.g. McCook 1999, Hughes and Tanner 2000), even killing coral surfaces through competitive interactions (reviewed in McCook et al. 2001, Jompa and McCook 2002a, 2002b, 2003a, 2003b). Thus, macroalgae have the capacity to restrict the distribution of coral communities on large spatial and temporal scales following disturbances (Miller 1998).

Measures of reef degradation that consider only the spatial dominance of benthic algae are simplistic, because the biomass per unit area, dominant functional forms of macroalgae and even the taxonomic composition of algal assemblages can differ as a result of grazing pressures, physical disturbance regimes and nutrient levels (Littler and Littler 1984, Lewis 1986, Steneck and Dethier 1994, McCook 1999, Cheroske et al. 2000). Authors disagree on the relative roles of eutrophication (bottom-up regulation) and herbivory (top-down control) in facilitating dominance by fleshy (corticated) macroalgae or increased biomass of benthic algae per unit area of substrata, termed "phase shifts" (Hughes 1994a, 1994b, Hodgson 1994, Ogden 1994, Lapointe 1997, 1999, Hughes et al. 1999a). However, it is likely that both bottom-up and top-down processes determine algal dominance (e.g. Littler and Littler 1984), and it is unlikely that high algal biomass per unit area or a "phase shift" develops unless herbivory is unusually or artificially low (McCook 1999). Physical disturbance (e.g. wave action or rubble abrasion) can also remove algal biomass and maintain benthic algae as turfs or epilithic algal assemblages (Cheroske et al. 2000). Thus, degraded and disturbed reefs that maintain functional herbivore populations or are in high energy or frequently disturbed environments are likely to be dominated by epilithic or turf algal communities (e.g. McClanahan et al. 2001). In contrast, reefs with reduced herbivore populations (e.g. overfished) can undergo community "phase-shifts" becoming dominated by fleshy macroalgae or high algal biomass (e.g. Done 1992, Hughes 1994a). Thus the algae communities established following a disturbance will vary with factors affecting either the physical environment or other components of the community, and each may influence coral replenishment processes differently.

1.3. The potential impacts of benthic algae on coral recruitment and the recovery of degraded and disturbed reefs

Given that degraded and disturbed coral reefs require coral recruitment to recover, but are dominated by benthic algae, effects of benthic algae on coral recruitment play a critical role in the replenishment of coral populations and reef recovery. Although it is known that coral recruitment failed on algae dominated reefs in the Caribbean, it is unclear whether reduced larval supply (including coral fecundity), reduced larval settlement or reduced survival of recruits ultimately caused recruitment failure (Hughes et al. 1987, Hughes 1989, 1996, Hughes and Tanner 2000). The lack of knowledge of macroalgal impacts on coral recruitment arises at least partly because coral reef ecologists rarely study macroalgae, knowledge of macroalgal distributions is limited, and resources for the identification of macroalgae are scarce (Hay 1997, McCook and Price 1997). Thus, it is not surprising that knowledge of algal influence on coral recruitment, in particular on degraded and disturbed reefs is limited.

The mechanisms by which macroalgae can affect coral recruits or larvae include overgrowth, shading, abrasion, chemical (including allelopathy), space pre-emption or recruitment barriers, and epithelial sloughing interactions, although experimental evidence of these mechanisms is scarce (McCook et al. 2001). In most cases, it is macroalgal influences on the benthic environment that affect coral recruitment. For example, benthic algae can restrict coral recruitment by determining the availability of benthic space and access to the substrata (e.g. Hughes 1996, Connell et al. 1997, McCook et al. 2001). Secondly, benthic algae can influence light conditions by means of shade in the benthic environment, which may have species-specific impacts on coral settlement and recruit survival (e.g. Mundy and Babcock 1998, Baird and Hughes 2000). Thirdly, benthic algae can alter the surrounding chemical environment (e.g. Amsler 1992, Walters et al. 1996, McConnaughey et al. 2000), which could have a range of effects on coral recruitment as reported for other invertebrates (reviewed in Pawlik 1992, Steinberg et al. 2001, 2002, Steinberg and de Nys 2002). Finally, benthic algae can influence water flow regimes and particle suspension or deposition (e.g. Eckman et al. 1989, Duggins et al. 1990, Carpenter and Williams 1993, Vogel 1994, Steneck 1997, Purcell 2000), which in turn can potentially hinder coral recruitment (e.g. Rogers 1990, Hodgson 1990, Babcock and Davies 1991, Abelson and Denny 1997, Gilmour 1999). However, with the exception of the role of macroalgae in determining benthic space for coral recruitment, none of these potential influences on coral recruitment have been investigated directly in experimental manipulations using macroalgae.

Most studies of macroalgal impacts on coral settlement have focused on crustose coralline algae or other calcareous red algae (e.g. Morse et al. 1988, Morse and Morse 1991, Morse et al. 1994, 1996, Heyward and Negri 1999, Raimondi and Morse 2000, Negri et al. 2001), and potentially none have considered chemical influences from other macroalgae. In contrast, most studies of macroalgal impacts on recruit survival focus on fleshy macroalgae and, to a lesser extent, filamentous algae (e.g. Birkeland 1977, Bak and Engel 1979, Sammarco and Carleton 1981, Hughes et al. 1987, Hughes 1989, 1996). However, studies of the impacts of fleshy macroalgae on recruit survival are principally natural experiments, and recruits detected *in situ* tend to be at least 5mm in diameter (e.g. Bak and Engel 1979, Babcock 1991, Hughes et al. 1987), thus at least 6 months old (Harrison and Wallace 1990, Babcock et al. 2003). Therefore, there is a clear need to advance knowledge of algal influences on coral larvae and recruits because present knowledge under-represents the complexity of this area.

1.4. Specific objectives

The research presented in this thesis investigates potential effects of benthic algae on coral recruitment, which is critical to the recovery of coral populations on degraded and disturbed coral reefs. To increase understanding of algal influences on coral recruitment, I identify benthic algae likely to affect coral recruitment, and explore the impacts of these algae on either coral settlement or the post-settlement survival of coral recruits. The specific aims of my research were:

1.4.1. To identify benthic algae that are likely to influence coral recruitment on degraded and disturbed coral reefs (Chapter 2).

Comparisons of *in situ* patterns of benthic biota close to coral recruits versus those distant to recruits (representing the general or background community of each reef) on degraded, disturbed and relatively pristine reefs, provide valuable insight into: a) the benthic algae most likely to affect coral recruitment; and b) the potential influences of benthic algae on coral recruitment that may be most relevant to reef recovery from disturbance and degradation. Patterns revealed in these field studies were used to identify important questions regarding the impact of algae on coral recruitment on degraded reefs, which became the basis for manipulative experiments in the following chapters.

1.4.2. To explore the effects of algal turfs, alone and in combination with sediments, on the settlement of coral larvae (Chapter 3).

In this chapter, I used manipulative studies to determine the effects of algal turfs and sediments on coral settlement and provide important insights into the recovery potential of disturbed and degraded reefs, particularly in inshore areas and high sediment environments.

1.4.3. To investigate potential waterborne chemical influences of benthic macroalgae on the settlement of coral larvae (Chapter 4).

In this chapter, I used seawater that previously contained macroalgae to investigate waterborne chemical influences that could affect the settlement of coral larvae on a crustose coralline alga known to induce coral settlement. This study indicated that macroalgae can influence coral settlement before larvae reach the reef substrata, even where the immediate settlement location is free of algal cover, and elucidates previously overlooked impacts on coral recruitment on algae dominated reefs.

1.4.4. To investigate the effects of fleshy macroalgae dominance on the early survival and growth of coral recruits (Chapter 5).

In this chapter, I investigated the impact of a fleshy macroalgae bloom, experimentally produced through a large-scale caging experiment that excluded grazers, on survival and growth of coral recruits up to four months after settlement. This study provided new insight into the importance of local circumstances, features of algae and the size of coral recruits in determining the success of coral recruitment on algae dominated reefs.

Chapter 2. Large-scale patterns of associations between coral recruits and benthic algae on inshore reefs of the Great Barrier Reef.

2.1. Introduction

The successful recruitment of corals is critical to the recovery of degraded and disturbed coral reefs, as well as the long-term persistence of coral communities (Connell et al. 1997, Hughes and Tanner 2000). However, benthic biota established on a reef influence the distribution and success of coral recruitment by influencing either coral settlement (e.g. Morse et al. 1988, Pawlik 1992, Maida et al. 1995a, 1995b, Heyward and Negri 1999, Koh and Sweatman 2000) or the survival of coral recruits (e.g. Bak and Engel 1979, Aceret et al. 1995, Hughes 1989, 1996). Given the heterogeneity of reef environments, reef biodiversity and biotic composition on reefs (Wells 1956, Done 1983, McCook et al. 1997, Bellwood and Hughes 2001, Veron 2001), the benthic communities that influence coral recruitment are likely to differ considerably in local composition. Therefore, to manage and understand coral population dynamics, and the recovery potential of coral populations following disturbance, it is important to know how and which benthic biota influence coral recruitment.

In order to understand the influences of benthic biota on coral recruitment, it is important to first establish which biota are likely to have quantitatively significant, ecological effects in the real world. For example, unless a particular taxon co-occurs with coral recruits sufficiently frequently (at relevant scales) in the field, any experimentally demonstrated *potential* influences may be ecologically irrelevant. Thus, there is a need for large-scale surveys specifically focussed on exploring patterns of association between coral recruits and different benthic biota, to provide a quantitative, empirical basis for more mechanistic, experimental studies. One useful first approach to this question is to compare the relative abundance of the major benthic biota in close proximity to coral recruits with their abundance in the overall “background” community. Thus, within a particular area or habitat, if a taxon which is relatively common overall, is rarely found in close proximity to coral recruits, it *may* be that that taxon has some negative impact on success of coral recruitment, either because coral larvae are unable to or avoid settling near that taxon, or because the taxon reduces post-settlement survival. Similarly, taxa which are found more commonly in close proximity to recruits than in the broader, background community, *may* be beneficial to the settlement or post settlement survival. Importantly, such empirical evidence would not only establish the ecological context of interactions already studied experimentally, but may identify important interactions not previously recognised.

In such surveys, there would be particular value in exploring any associations between coral recruits and different types of benthic algae, given the cover of algae on coral reefs generally (Berner 1990, McCook and Price 1996, Adey 1998), but especially because benthic algae dominate degraded and disturbed coral reefs (Price 1975, Done 1992, Hughes 1994a, McCook 1999, Diaz-Pullido and McCook 2002), and thus are the benthic biota most likely to influence the coral recruitment necessary for recovery of degraded and disturbed reefs (Done 1992, Hughes 1994a, McCook 1999). However, different algae are likely to have very different effects on coral recruitment, as the outcomes of coral-algal interactions can depend more on features of the algae than of the corals involved (review McCook et al. 2001). Thus it is important that such surveys resolve benthic algal types in some detail, ideally both taxonomically and in terms of functional form groups (Littler 1980, Littler and Littler 1980, Steneck and Dethier 1994, McCook and Price 1997, McCook et al. 2001).

The purpose of this study is to describe the benthic biota associated with coral recruits on inshore reefs of the Great Barrier Reef, with particular emphasis on benthic algae, and in doing so identify biota that are likely to significantly influence coral recruitment. Given current concerns about the impacts of terrestrial runoff on reef recovery dynamics (Wachenfeld et al. 1998, 2003, Furnas 2003, Wolanski et al. 2003), the survey design incorporated comparisons between reefs subject to terrestrial run-off from a developed catchment and from a relatively undeveloped catchment.

2.2. Methods

2.2.1.Survey Approach and Sampling Design

To identify patterns in benthic associations that characterise successful coral recruitment, I compared the abundance of all algal and benthic invertebrate groups close to (<20 cm) versus distant from coral juveniles or in background communities on inshore reefs. Fieldwork and access to survey sites in this study was made possible courtesy of a multi-disciplinary effort to compare water quality and reef status between reefs of two regions (CRC Reef Task 2.2: www.reef.crc.org.au), which inevitably constrained both the design, and replication within each factor, of my study. Within each region, accessible survey sites covered a range of reefs, site exposures to weather conditions and depths, and comparisons were made for two genera of corals. The overall survey design thus incorporated six factors: 1) *distance* from coral recruits (four levels: less than 5 cm, 5-10 cm, 10- 20 cm, and randomly placed quadrats see Figure 2.1); 2) coral *genera* (two levels: *Acropora* and *Favites*); 3) *depth* (two levels: 1 m and

5 m); 4) *exposure* to predominant winds and waves (two levels: exposed and sheltered); 5) *Reef* (four levels; the four islands in each region); and 6) *region* (two levels: Wet Tropics and *Princess Charlotte Bay*, Figure 2.2). Interpretative consequences of the constraints on my study are less conclusive information about factors within the design and more representation of general overall or regional patterns, as opposed to identification of localised trends from more replicates within factors.

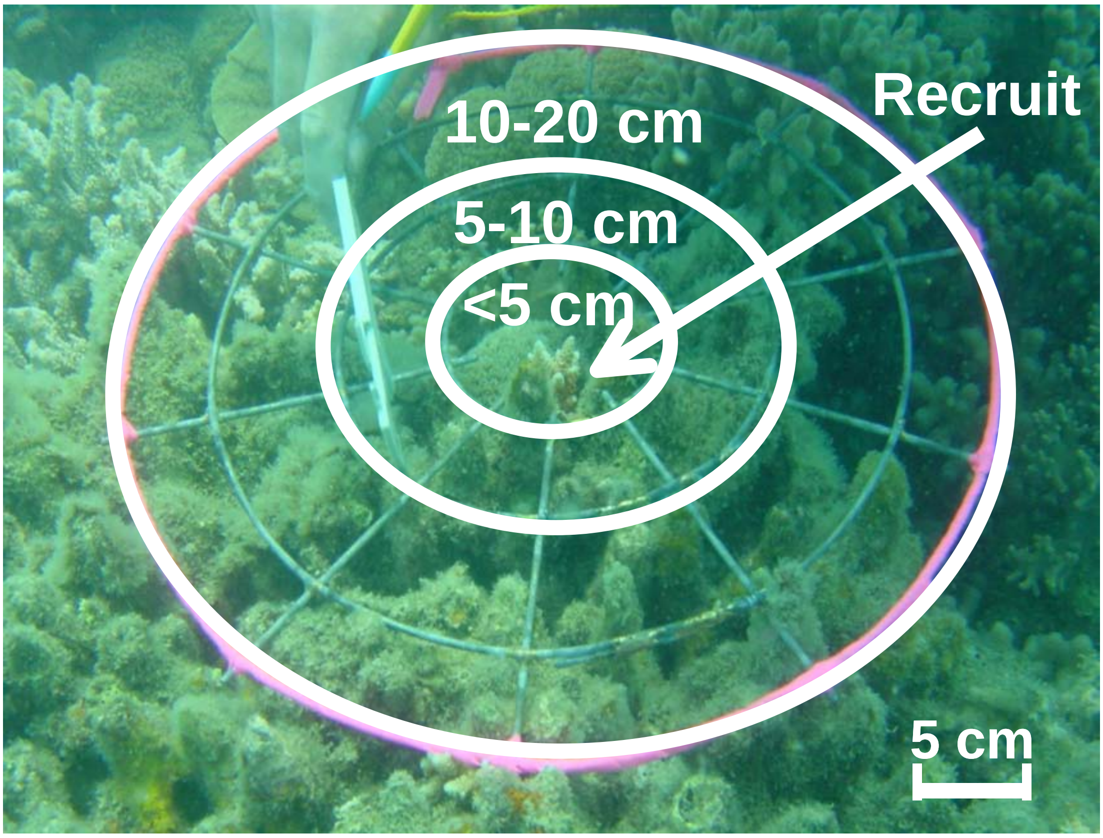

Figure 2.1. A circular sampling-device used to describe the benthic biota close to coral recruits. The percent cover of benthic biota was described within 5 cm of a coral recruit, between 5-10 cm and between 10-20 cm from a coral recruit, and, finally in 1 m × 1 m randomly laid quadrats. The device was centred on coral recruits of maximum diameter 4 cm, here an *Acropora sp*. recruit. In this image the substrata surrounding the coral recruit is dominated by filamentous algae turf.

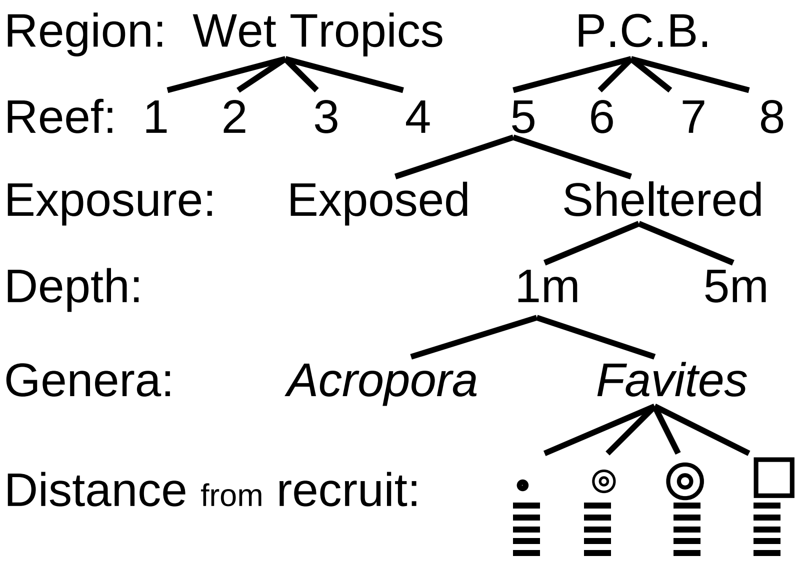

Figure 2.2. Sampling design for the survey using a circular sampling device (•<5 cm, ⊙ 5-10 cm and ⊙ 10-20 cm from recruits, Figure 2.1) and of benthic biota in background communities using a 1 m × 1 m quadrat (□). Benthic biota were described surrounding five replicate coral recruits of each genus and in five quadrats along a 1 m × 50 m transect parallel to the reef crest, used to standardise search patterns at each site on reefs in the Wet Tropics region and the Princess Charlotte Bay region (P.C.B.).

2.2.2. Survey Sites and Regional Comparison

The regional comparison involved comparison of reefs adjacent to the Wet Tropics region, with relatively high terrestrial run-off from a catchment “developed” for intensive agriculture and highly populated, and reefs in the Princess Charlotte Bay region, which are subject to terrestrial run-off from a comparatively “undeveloped” and unpopulated catchment (Figure 2.3). In the Wet Tropics region, surveys were undertaken on fringing reefs surrounding Fitzroy Island (16°56’S, 145°59’E), High Island (17°09’S, 146° E), Normanby Island (17°13’S, 146°05’E) and Russell Island (17°12’S, 146°04’E), all of which are uninhabited continental islands, which are mostly

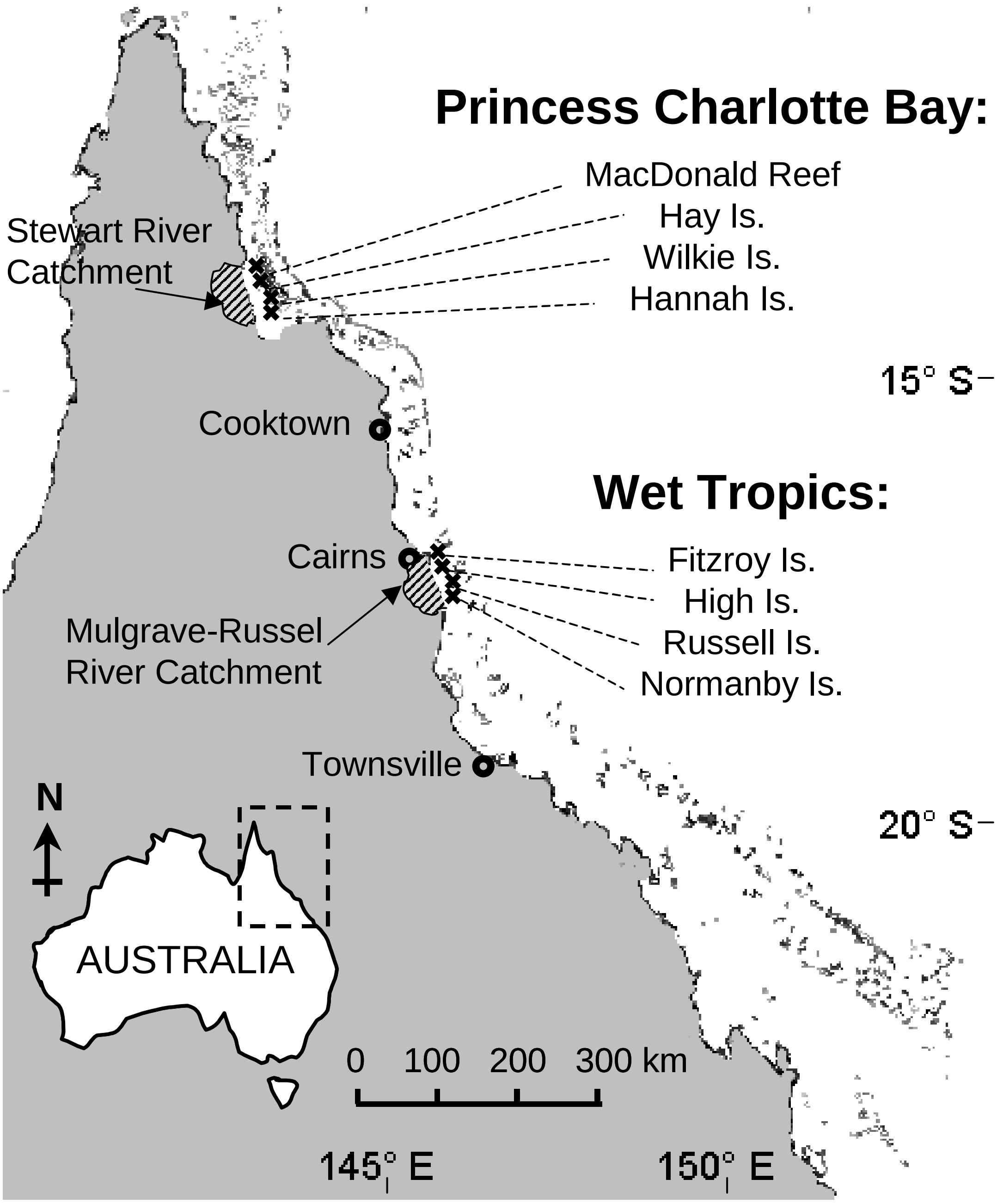

Figure 2.3. Map of the Great Barrier Reef and Queensland coastline showing survey reefs (×) adjacent to the Wet Tropics catchment, with high levels of terrestrial run-off and catchment development, and in the Princess Charlotte Bay area, with lower terrestrial run-off from a relatively undeveloped catchment.

forested. These islands are all located approximately 10 nautical miles offshore. Terrestrial run-off to reefs surveyed in the Wet Tropics region is most likely to originate from the Mulgrave-Russell river. The average annual discharge from the Mulgrave-Russell river is 4.67 km^3, and is estimated to contain 0.14×10^6 tonnes of fine sediment, a total of 1441 tonnes of nitrogen, and a total of 116 tonnes of phosphorous (Furnas

2003). Hard coral cover was generally low (<15 %) on reefs in the Wet Tropics region, which in general displayed signs of widespread disturbance (e.g. bleaching, crown-of-thorns starfish outbreaks) and were dominated by algal turfs. In the Princess Charlotte Bay region surveys were undertaken on fringing reefs surrounding Wilkie Island (13°46’S, 143°38’E), Hannah Island (13°51’S, 143°43’E), Hay Island (13°40’S, 143°41’E) and MacDonald reef (13°39’S, 143°37’E), all located in the Claremont Islands group. The Claremont Islands are unpopulated coral cays, dominated by mangroves and most likely to be influenced by run-off from the Stewart River catchment, although run-off from the Normanby river may also affect these islands. The average annual run-off from the Stewart River catchment is 1.21 km^3 and is estimated to contain 0.05×10^6 tonnes of fine sediment, with a total nitrogen export of 479 tonnes and a total phosphorous export of 158 tonnes (Furnas 2003). Hard coral was generally high (over 75%) at all sites in the Princess Charlotte Bay region, where signs of recent reef disturbance were minimal. At each reef, surveys were done at a shallow site (1m) on the reef crest and deeper site (5m) on the reef slope, and in areas either exposed to or sheltered from dominant wind or wave directions.

2.2.3. Sampling Methods

To compare background benthic composition at each site with that close to coral recruits, I used a circular sampling-device to estimate the percent cover of biota at a range of distances from coral recruits (<5 cm, 5-10 cm and 10-20 cm, Figure 2.2). The circular sampling-device was centred on the first five coral recruits (<4 cm diameter) found along a 1 m × 50 m transect laid parallel to the reef crest at each study site and used only as an aid to standardise search patterns for recruits. Background communities were described at each site as percent cover of biota in five 1 m × 1 m quadrats (with 10 x 10 strings) randomly placed along the same transects. The size of these quadrats was selected to ensure sampling was representative of the overall community, and that the scale of habitat heterogeneity did not obscure the overall community composition. This has the disadvantage that comparisons of overall communities with those close to recruits was confounded by the differences in quadrat sizes; however, the only alternative would have been to take a large number of small quadrats, which was not logistically feasible. Where possible, algae were identified to genus or species level, *in situ* and from sample specimens. Filamentous algal turfs and crustose coralline algae can only be reliably identified to functional groups. Benthic biota other than algae were identified in as much detail as possible in the field, and subsequently grouped in general categories (e.g. hard coral, soft coral, sponge, zoanthid) for analysis. All observations were made in October of 2000 prior to annual increases in algal biomass (November to April).

2.2.4. Data and interpretation

Patterns of association are presented at three levels of detail. Firstly, the overall patterns are explored in terms of the simple frequency with which different broad categories of biota occurred in the 1 m quadrats and at any of the distances within the circular sampling-device (i.e. “close to”, or within 20 cm of the recruit). Frequencies were derived from the percent cover data, and included all five quadrats and all five recruits at all sites for each coral genus, then were calibrated to frequencies per one hundred observations. Secondly, overall percent cover of broad benthic categories within the circular sampling device was compared with that in the 1 m quadrats. Overall percent cover within the circular sampling device was calculated as the sum of area weighted averages of the percent cover data in each of the three distance ranges (i.e. <5 cm, 5-10 cm and 10-20 cm), and was calculated for five recruits in each genus surveyed at each site. Overall percent cover for biota in background communities was calculated from the five quadrats at each site. Thirdly, detailed patterns were explored for key algal groups, hard corals and soft corals, comparing percent cover between each distance range within the circular sampling device (i.e. <5 cm, 5-10 cm and 10-20 cm) and the quadrats, and between regions, within sites (reefs, exposure, and depth).

The patterns are interpreted graphically, rather than statistically for four reasons. Firstly, to emphasise the exploratory nature of the study. Secondly, because of the complexity of the design. Thirdly, because of non-independence of the data within different sampling distances from the same recruits (i.e. <5 cm, 5-10 cm and 10-20 cm). Finally as a result of problems of scale in comparing data from a 1 m quadrat with the circular sampling device (e.g. larger sampling units bias against detection of small biota/patches). In this sense, I emphasise that interpretation of the patterns is intrinsically limited by these constraints, and by the correlational nature of the results, thus although the results may provide useful indicators of possible causal associations, they do not demonstrate causality. This is because to demonstrate causality appropriate experimental studies are necessary. Similar limitations apply to the interpretation of the regional comparison, which may provide useful indicators of the effects of terrestrial run-off, but is intrinsically confounded by numerous other differences between the study regions (e.g. latitude).

2.3. Results

2.3.1. Trends for benthic biota groups.

2.3.1.1. Frequency of presence trends

Macroalgae were observed close to coral recruits and in background communities at all the surveyed sites, and in general more frequently than other groups of biota both close to recruits and in background communities (Figure 2.4). Hard corals and soft corals were observed less frequently close to coral recruits than in the background communities that were surveyed. Trends for other groups of biota were either inconsistent or the frequency of these groups was too low (less than 20% of observations) to differentiate between substrata surveyed close to recruits versus in background communities.

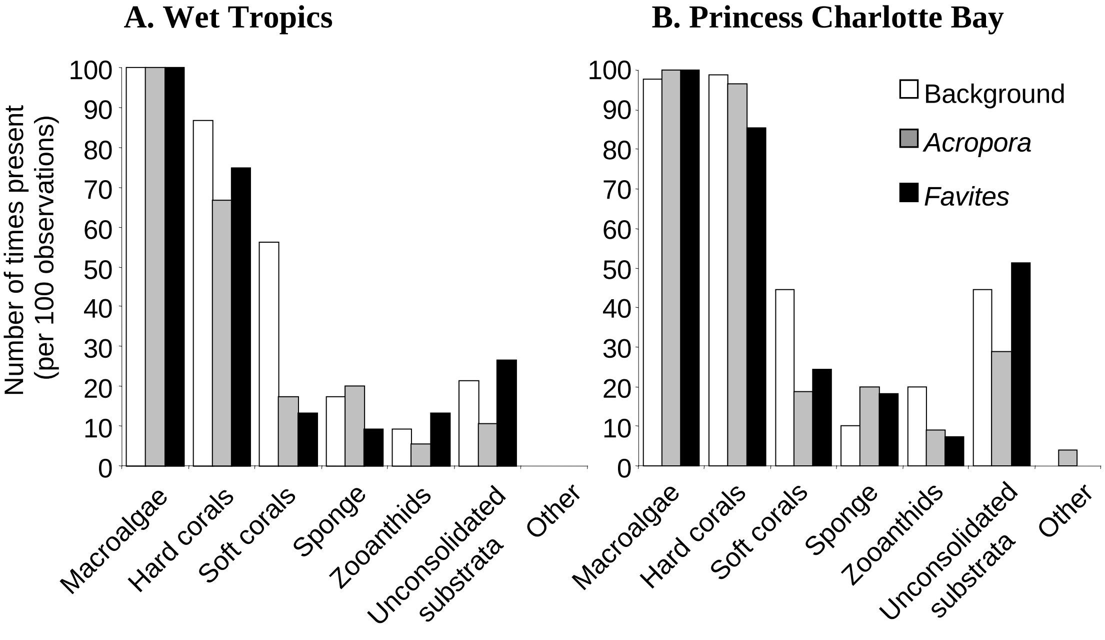

Figure 2.4. The frequency of major benthic biota categories observed in the vicinity (<20 cm) of *Acropora* and *Favites* coral recruits and in background communities on reefs in the Wet Tropics region (A) and the Princess Charlotte Bay region (B).

On reefs in the wet tropics region hard corals were present close to 67% of *Acropora* recruits and 75% of *Favites* recruits, versus in 87% of background communities surveyed. Soft corals were observed three times less frequently close to *Acropora* and *Favites* recruits (17% and 13% of observations respectively) than in background communities (56% of observations), and were generally less frequent than hard corals. On reefs in the Princess Charlotte Bay region hard corals were observed in all background communities (99%), and close to 96% of *Acropora* recruits and 87% of *Favites* recruits. Soft corals were half as frequent close to *Acropora* and *Favites* recruits (19% and 24% of observations respectively) than in background communities (44% of observations), and in general were less than half as frequent as hard corals.

2.3.1.2. Abundance trends

Macroalgae were generally more abundant close to coral recruits than in background communities, and dominated the substrata both close to recruits and in the background communities surveyed in both regions. Other groups of biota were generally less abundant close to recruits than in background communities (Figure 2.5). On reefs in the Wet Tropics region macroalgae were more than thirty-times as abundant as any other group of biota, thus dominated substrata close to recruits (approximately 90% cover) and in background communities (80% cover, Figure 2.5A). The remaining substrata close to recruits were mostly occupied by hard corals (5-8%), which were half as abundant close to recruits versus the background communities surveyed (14%). Soft corals were less than four times as abundant close to recruits (<1% cover) relative to the background communities surveyed (4.5% cover). On reefs in the Princess Charlotte Bay region, algae also dominated the substrata close to recruits (approximately 70% and 65% for *Acropora* and *Favites* recruits respectively), and in background communities (50%). Close to recruits hard corals were half as abundant (approximately 30%) as macroalgae, and other groups of biota were less than ten times less abundant as macroalgae (Figure 2.5B). Hard corals were also dominant in the background communities (43%) surveyed in the Princess Charlotte Bay region. Finally, soft corals were less than half as abundant close to recruits (<2.5% cover) relative to the background communities surveyed (5%).

More detailed interpretation of spatial patterns was possible for hard corals, soft corals, and some algal categories (filamentous algae, crustose coralline algae and *Lobophora variegata*, described below) as a result of sufficient data to separate factors in the experimental design graphically (Figure 2.6). The abundance of hard corals was generally lowest within 5 cm of coral recruits and tended to be greater further from recruits, in particular on reefs in the Princess Charlotte Bay region, where the average background cover of hard corals was relatively high (at some sites over 75% cover, Figure 2.6A). The abundance of soft corals decreased closer to coral recruits, and soft corals tended not to be observed within 10 cm of recruits, in particular at sheltered sites where abundance of soft corals was relatively high in the background communities surveyed (occasionally over 40% cover, Figure 2.6B).

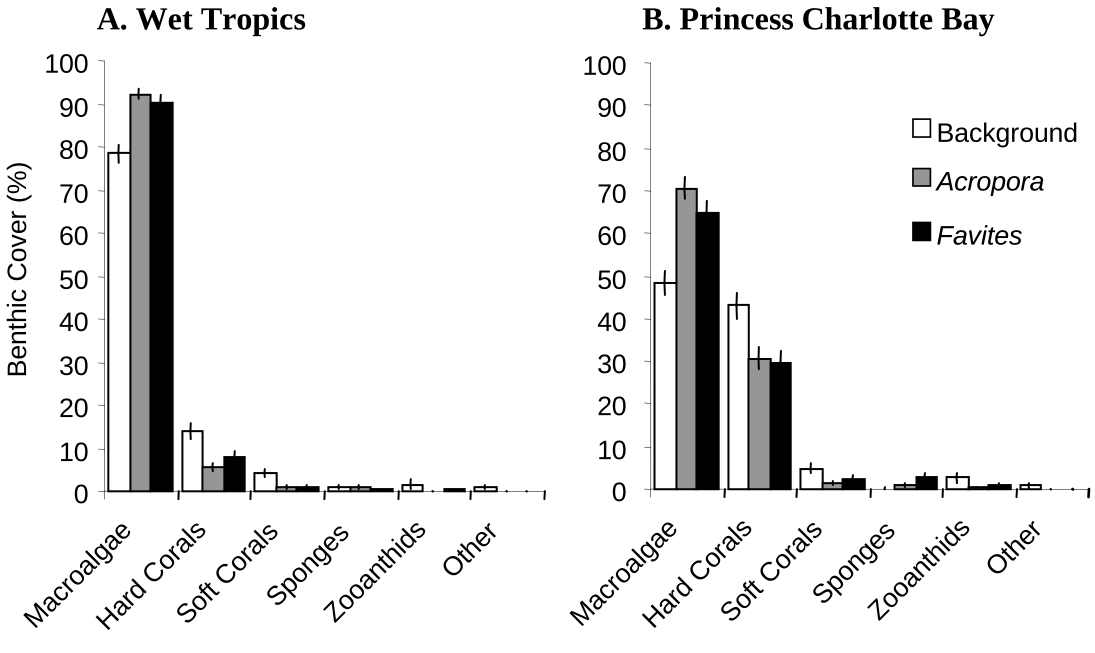

Figure 2.5. The percent benthic cover (±1 SE) of major groupings of benthic biota observed in the vicinity (<20 cm) of *Acropora* and *Favites* coral recruits and in background communities on reefs in the Wet Tropics region (A) and the Princess Charlotte Bay region (B).

2.3.2. Trends for algal categories within the macroalgae group

Twenty-seven categories of algae (23 identified genera and 4 categories) were identified on the substrata close to (<20 cm) coral recruits and in the background communities surveyed. However, the algal categories that were most frequently observed and that covered most substrata were filamentous turfs, crustose coralline algae and the alga *Lobophora variegata* in particular on the substrata close to coral recruits (Figures 2.6, 2.7 and 2.8). As a result of low frequency and low abundance interpretation of trends for other algal categories, referred to as “minor” algal categories, was less reliable.

2.3.2.1. Filamentous algal turfs.

Filamentous algal turfs were the primary algal category observed close to coral recruits, representing 87% and 77% of all benthic algae close to recruits on reefs in the Wet Tropics (WT) and Princess Charlotte Bay (PCB) regions respectively. Filamentous algae were present close to all coral recruits and in all the background communities surveyed on reefs in the Wet Tropics Region, and present close to over 95% of recruits and in 90% of the background communities surveyed on in the Princess Charlotte Bay region (Figure 2.7 A and B). Filamentous algae were over 50% more abundant in the Wet Tropics region relative to the Princess Charlotte Bay region, but in both regions were more abundant close to recruits (WT 75-80% cover, PCB 40-50%) when compared to background communities (WT 65%, PCB 30%, Figure 2.8). No consistent spatial trends in the abundance of filamentous algal turfs were observed within 20 cm of coral recruits (Figure 2.6 C).

2.3.2.2. Crustose algae.

Crustose coralline algae (CCA) were more frequently present close to the coral recruits (WT approximately 80% of observations, PCB 60-70% of observations) versus in the background communities (WT 76% of observations, PCB 14% of observations) surveyed in both regions (Figure 2.7 A and B). Nonetheless CCA were approximately ten times less abundant than filamentous algae turfs both close to recruits and in background communities surveyed (Figures 2.7 and 2.8). The spatial trends in CCA abundance indicate CCA were most abundant within 5cm of coral recruits (at times above 40%), and were progressively less abundant at greater distances from recruits (generally below 20% and 10% within 5-10cm and 10-20cm from recruits respectively, Figure 2.6.D.). Other crustose algae (i.e. non-coralline) were also positively associated with coral recruits (less than 10% of observations), however crustose algae of the genera *Peysonnellia* were negatively associated with recruits on reefs in the Wet Tropics region (Figure 2.7.A and B, Figure 2.8).

2.3.2.3. The brown alga *Lobophora variegata*.

The brown alga *Lobophora variegata* was present more frequently, and covered more substrate close to coral recruits relative to the background communities surveyed (Figure 2.7). On reefs in the Wet Tropics region *L. variegata* was present more than three times as frequently close to recruits (55% of the *Acropora* recruits, 50% of the *Favites* recruits) than in the background communities surveyed (15%). On reefs in the Princess Charlotte Bay region *L. variegata* was similarly present close to recruits (54% of *Acropora* recruits, 41% of *Favites* recruits) and observed less frequently (32% of observations) in the background communities surveyed. The abundance *L. variegata* was generally lowest in the background communities surveyed (less than 20% cover) when compared to substrata close to coral recruits (at times over 30% cover within 20 cm of recruits). However, the abundance of *L. variegata* also tended to be low within 5 cm of coral recruits when compared to the percent cover of *L. variegata* within 5-20 cm from recruits (Figure 2.6 E).

Figure 2.6. The average percent benthic cover of (A) hard corals, (B) soft corals, (C) filamentous algal turf, (D) crustose coralline algae and (E) the brown alga *Lobophora variegata* at less than 5 cm, 5-10 cm, 10-20 cm from described in randomly placed 1 m × 1 m quadrats). Data is separated into individual graphs according to genera of coral recruits (described with the circular sampling-device, Figure 2.1) and in background communities (recruits (*Acropora* or *Favid*), reef *exposure* to wave action (exposed and sheltered) and *depth* (1m and 5m below datum). Each graph contains data for four reefs in the Wet Tropics region (grey -o-), and four reefs in the Princess Charlotte Bay region (P.C.B., black -•-), which are subject to terrestrial run-off from a developed catchment and undeveloped catchment respectively. The percent cover data in each graph is calibrated to exclude unconsolidated substrates from estimates and data points represent five observations (± 1 SE) from each study site.

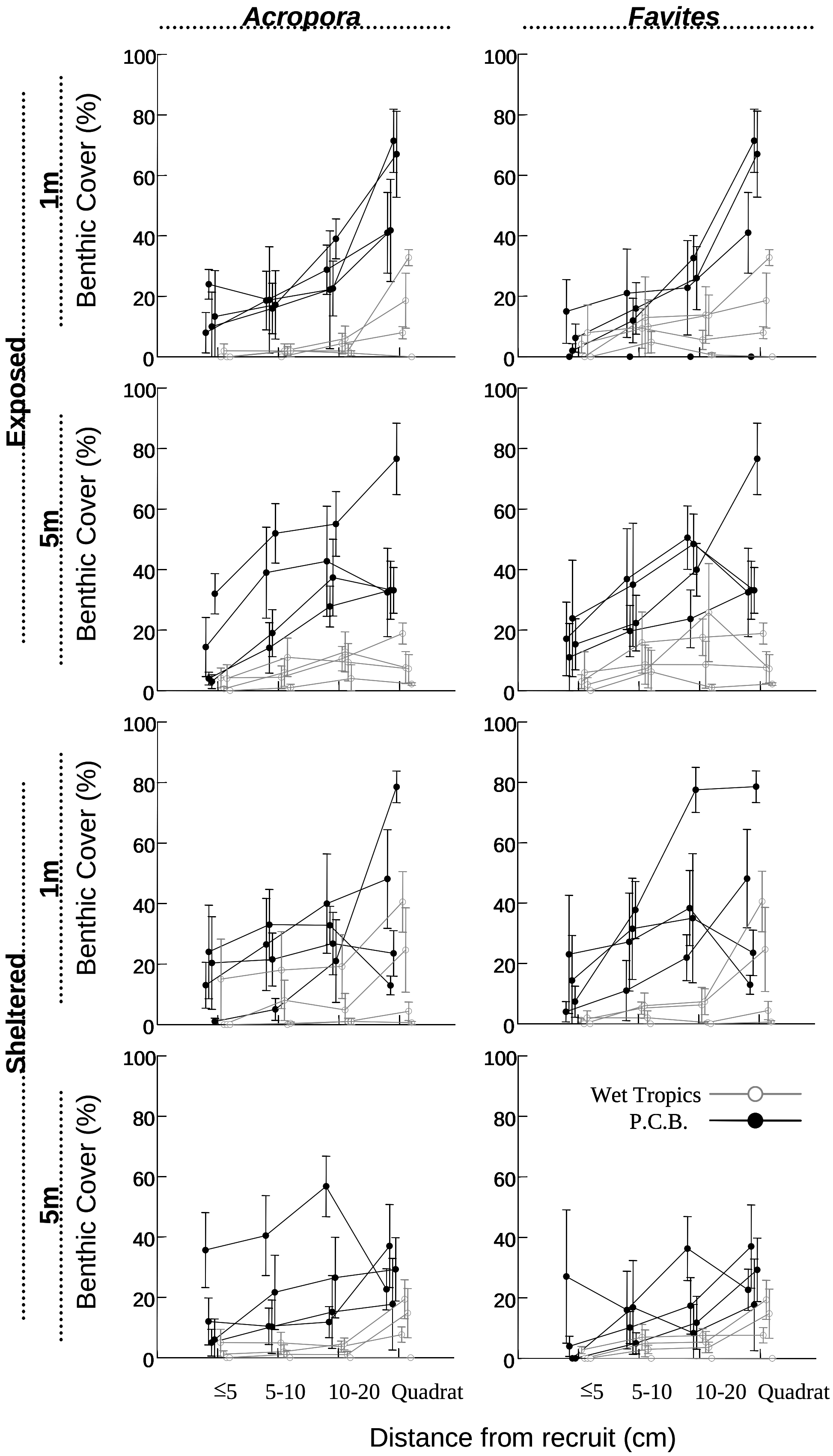

Figure 2.6.A. Hard Corals (*Scleractinia*, general figure caption on page 37).

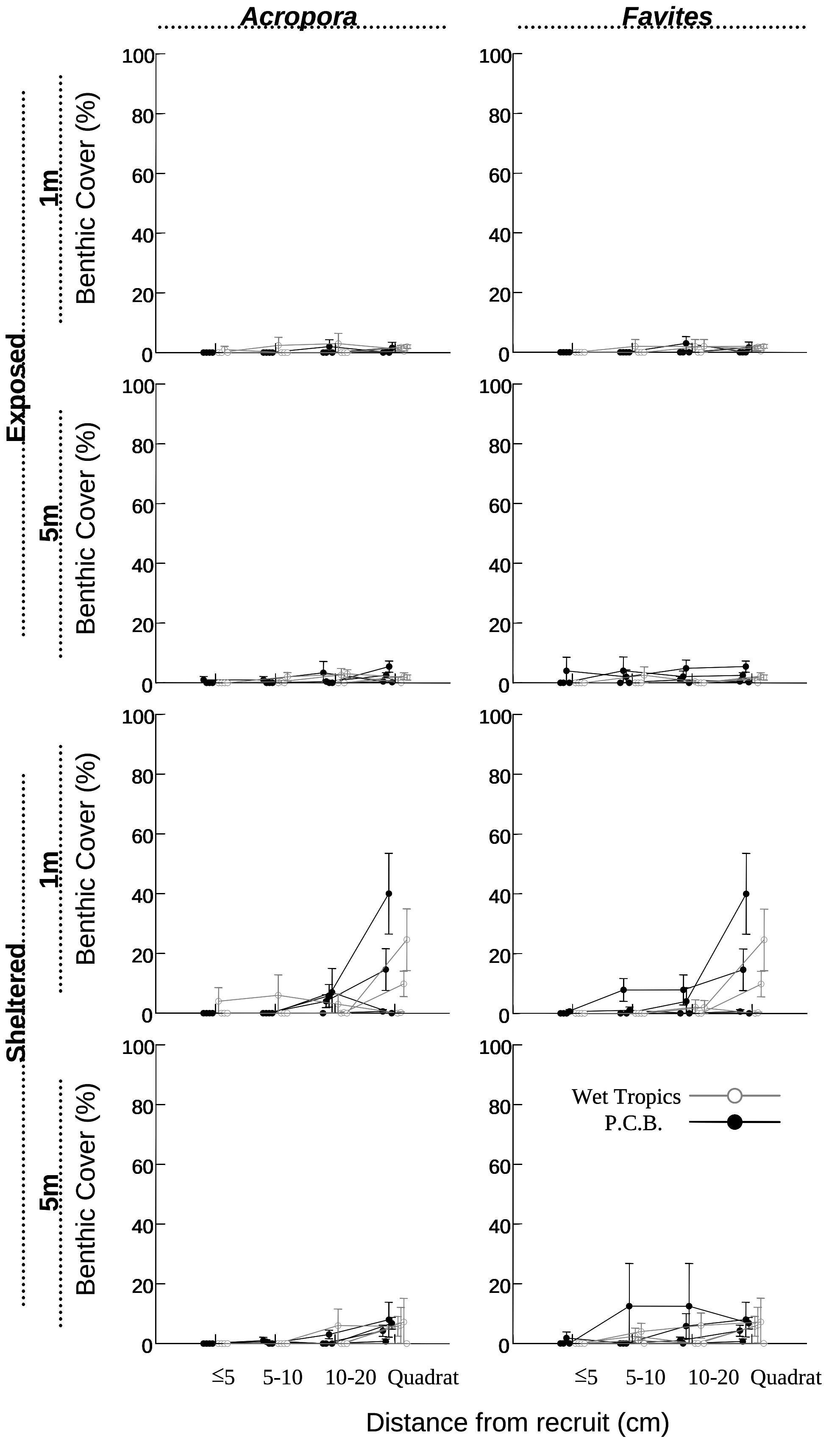

Figure2.6.B. Soft Corals (*Alcyonacea*, general figure caption on page 37).

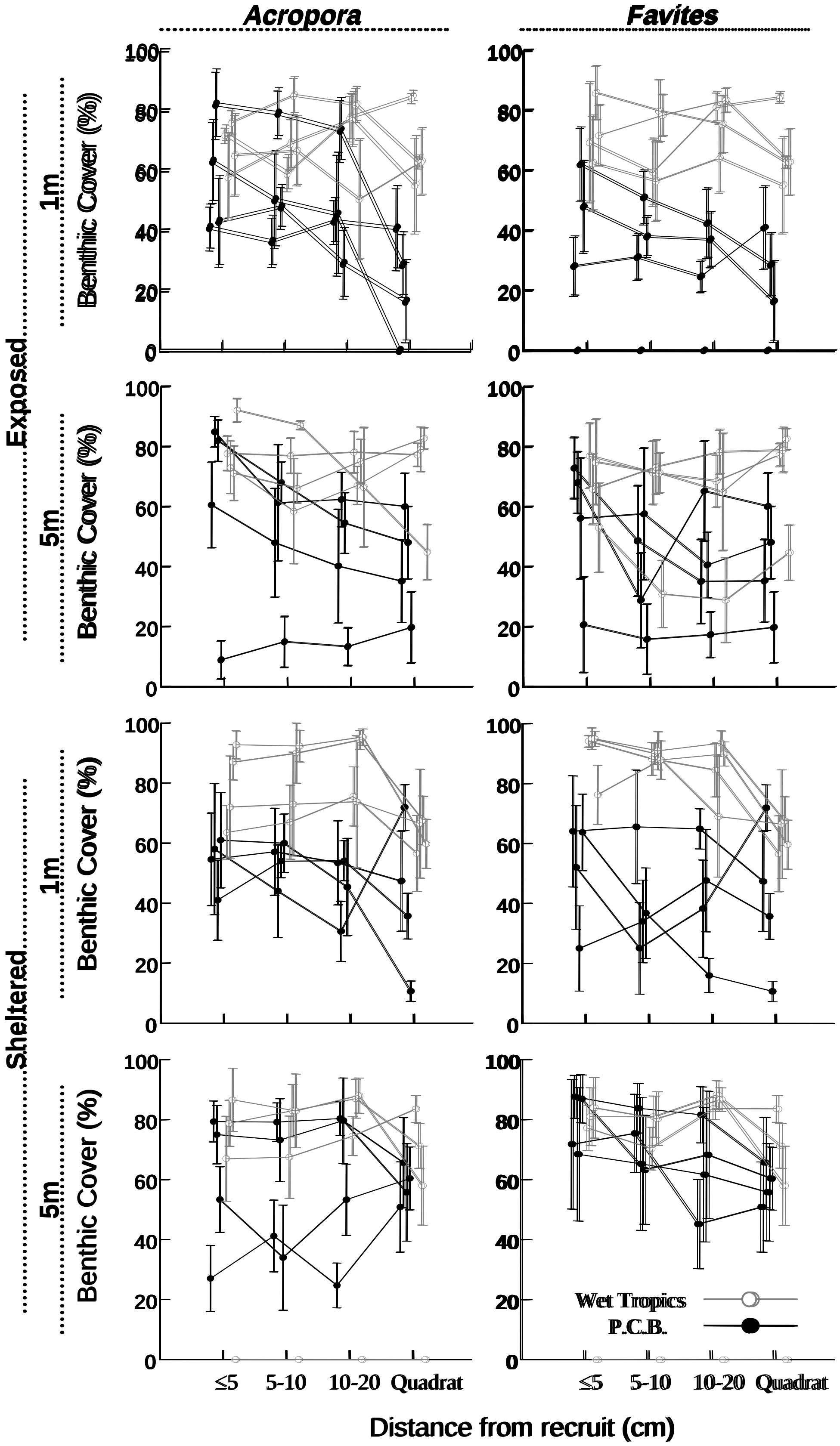

Figure 2.6.C. Filamentous algal turfs (general figure caption on page 37).

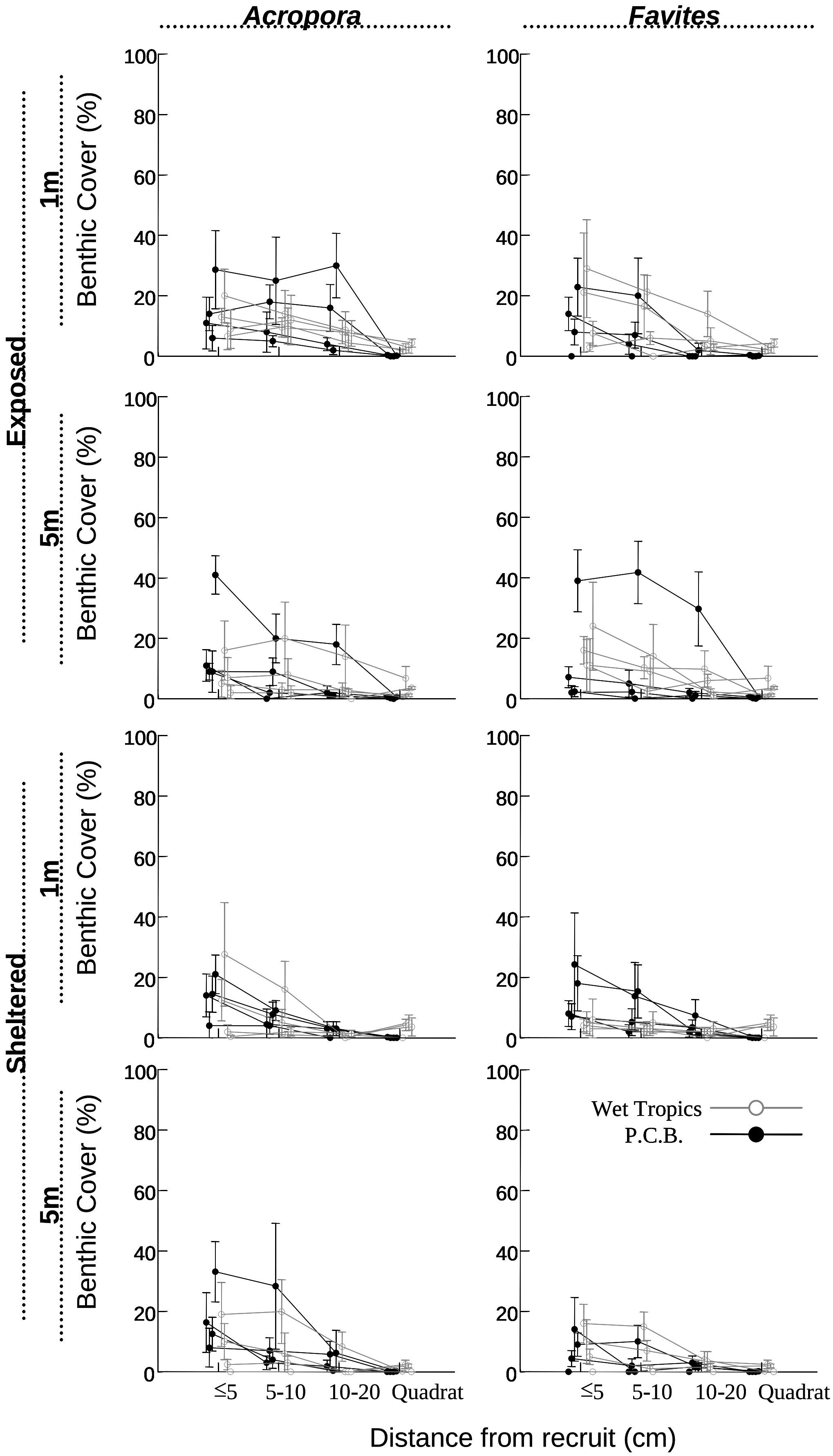

Figure 2.6.D. Crustose coralline algae (CCA, general figure caption on page 37).

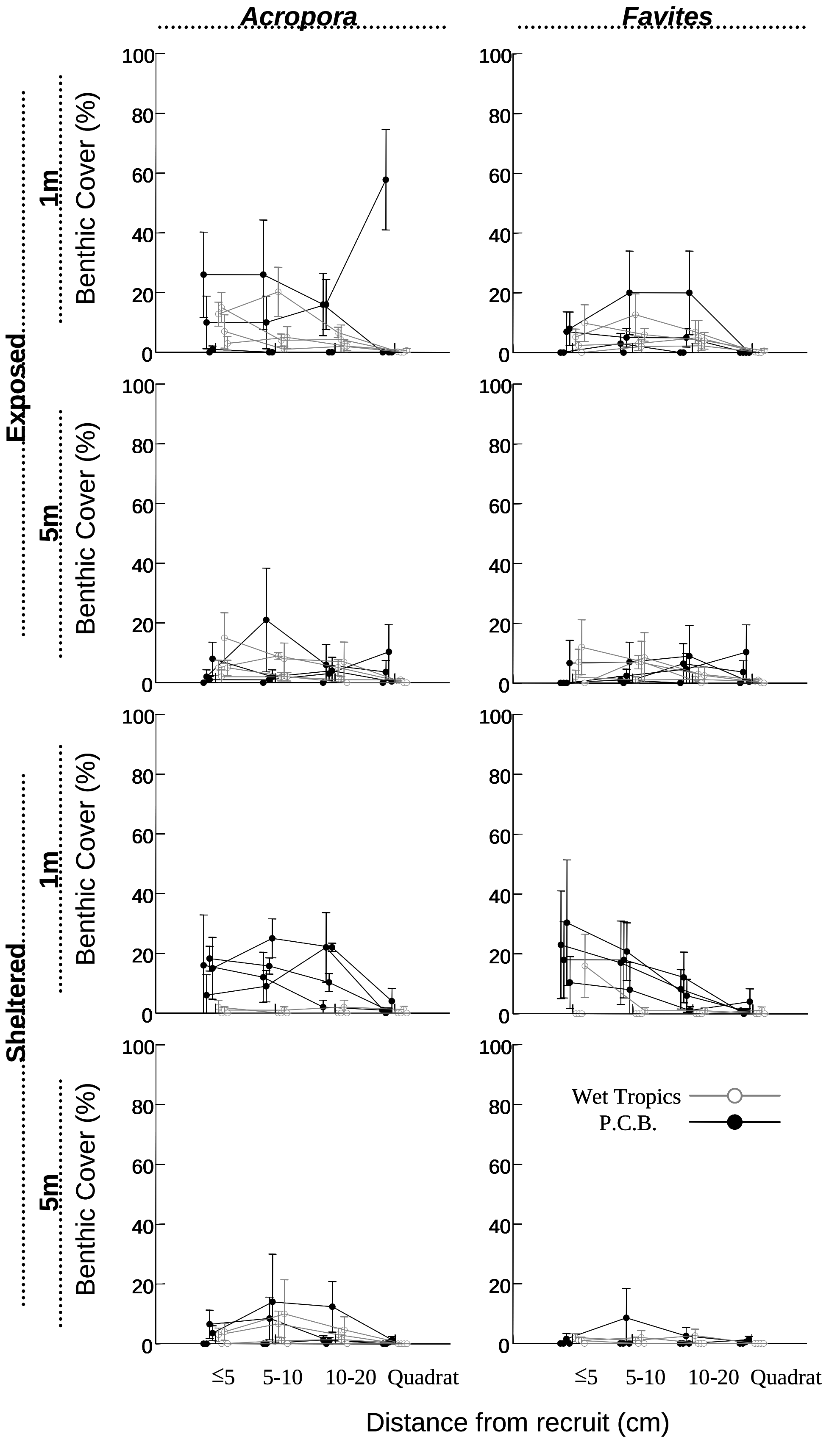

Figure 2.6.E *Lobophora variegata*, a corticated foliose brown alga (general figure caption on page 37).

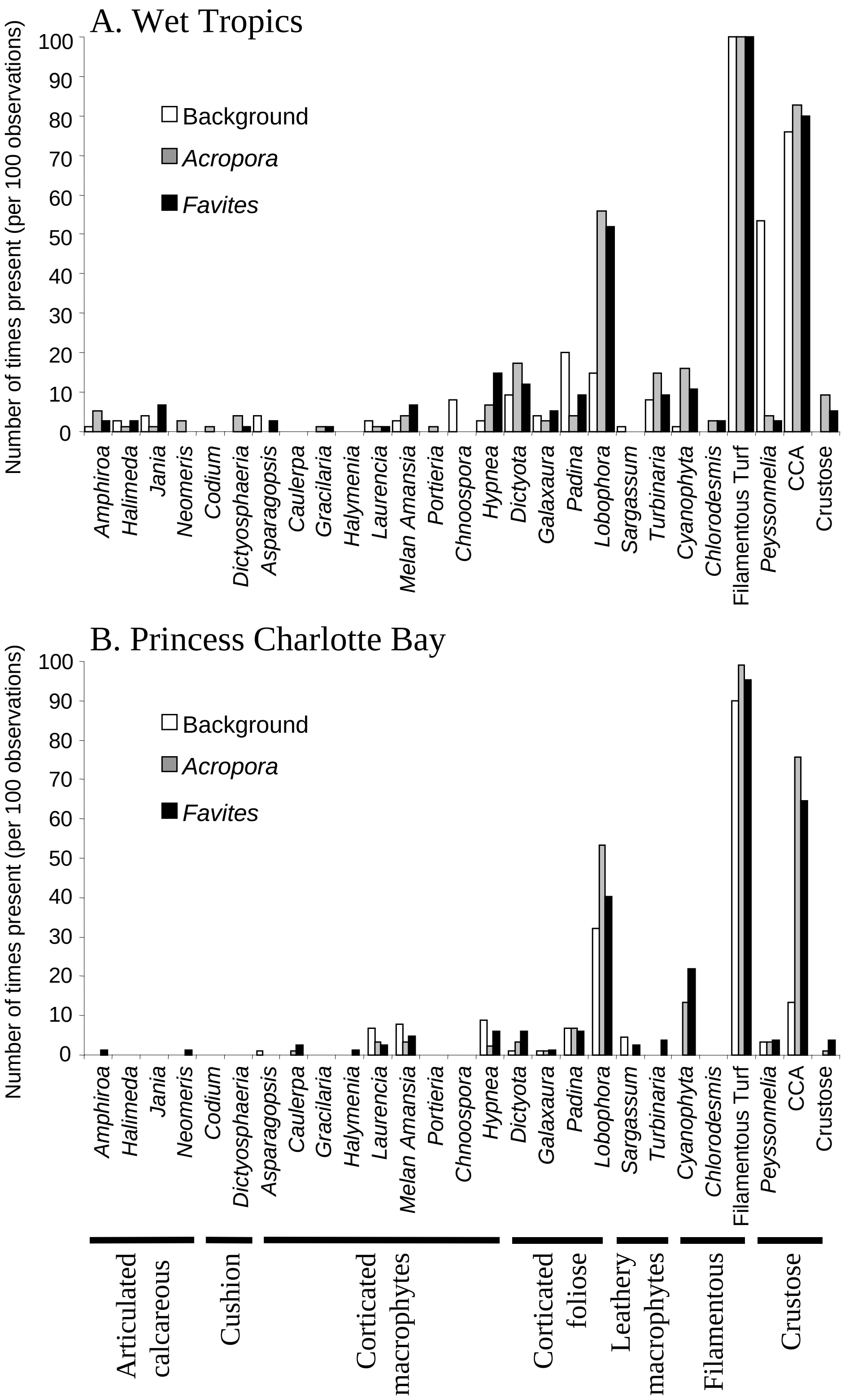

Figure 2.7. The frequency of algal genera and groups (Filamentous turfs, crustose coralline algae (CCA), crustose algae and cyanophyta) observed in the vicinity (<20 cm) of *Acropora* and *Favites* coral recruits, and in background communities, on reefs in the Wet Tropics region (A) and the Princess Charlotte Bay region (B). Algal functional groups (e.g. crustose, filamentous) correspond to those of Steneck and Dethier (1994) and McCook et al. (2001).

2.3.2.4. Potential trends for “minor” algal categories.

Other algae were usually recorded close to recruits (<20 cm) or in background communities in less than 20% of observations, which provided insufficient data to reliably identify spatial trends of abundance. However, potentially positive associations were identified from frequencies of observation for algae of the genera *Amphiroa*, *Dictyota* and *Turbinaria,* and for Cyanophyta. Similarly, potential negative associations were identified for algae of the genera *Padina, Laurencia and Chnoospera* (Figure 2.7 A and B).

2.3.3. Regional comparison of algae close to coral recruits

Besides the trends in percent cover and frequency of presence described above, more algal categories were observed close to coral recruits and in background communities on reefs in the Wet Tropics region than on reefs in the Princess Charlotte Bay region (Figure 2.7). In the Wet Tropics region 23 categories of algae were observed close to coral recruits, and 18 categories of algae were observed in the background communities surveyed. In contrast, in the Princess Charlotte Bay region 18 categories of algae were observed close to coral recruits, and 12 categories of algae were observed in the background communities that were surveyed. In particular algae of the genera *Halimeda*, *Jania*, *Neomeris, Codium*, *Dictyosphaeria*, *Asparagopsis, Gracilaria, Portieria*, *Chnoospera* and *Chlorodesmis* were observed close to recruits on reefs in the Wet Tropics region, but not on reefs in the Princess Charlotte Bay region.

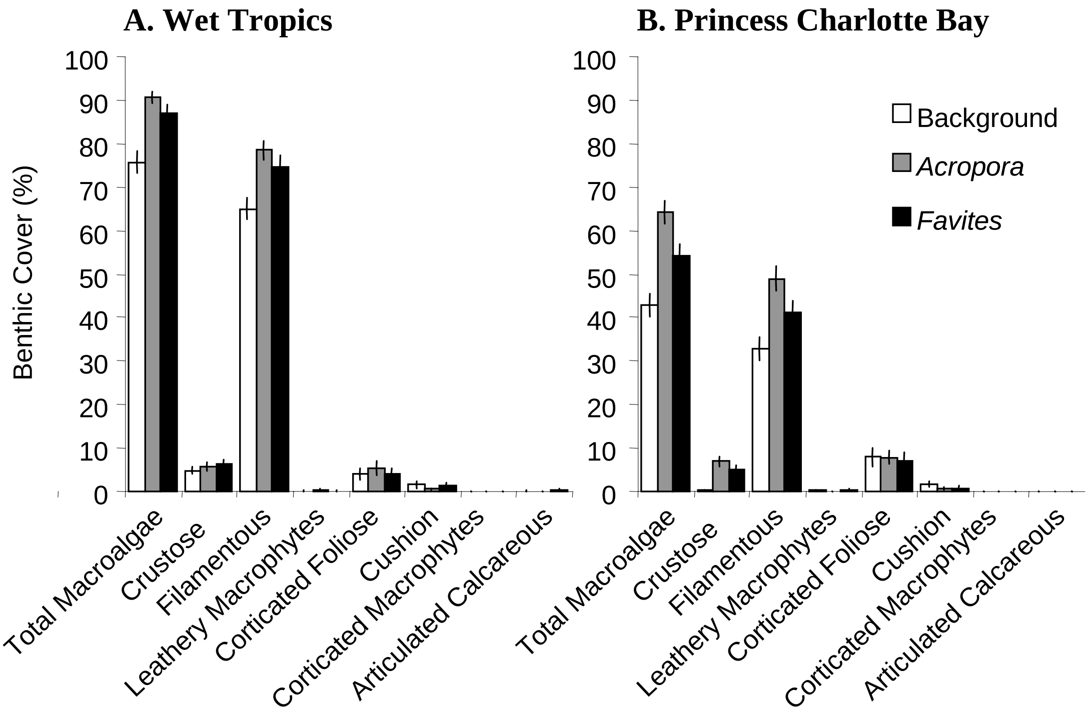

Figure 2.8. The percent benthic cover (±1 SE) of algal functional groups in the vicinity (<20 cm) of *Acropora* and *Favites* coral recruits, and in background communities on reefs in the Wet Tropics region (A) and the Princess Charlotte Bay region (B). Algal functional groups (e.g. crustose, filamentous) correspond to those of Steneck and Dethier (1994) and McCook et al. (2001). Note that the corticated foliose functional group is dominated by the brown alga *Lobophora variegata*.

2.4. Discussion

This study found that macroalgae were more frequently present and covered more substrata close to coral recruits (<20 cm) than in the background communities that were surveyed. Correspondingly, in this study benthic biota other than macroalgae (e.g. hard corals and soft corals) were observed less frequently and covered less of the substrata close to coral recruits compared to in the background communities that were surveyed. The main algal categories surrounding coral recruits were filamentous algal turfs, crustose coralline algae and the brown alga *Lobophora variegata*, all of which were more frequently present and more abundant close to *Acropora* and *Favites* recruits than in the background communities surveyed. A range of other “minor” algal categories were not observed with sufficient frequency or abundance to reliably interpret trends of association with coral recruits. Nonetheless, data for these minor algal categories provide indications that trends of algal association with coral recruits vary considerably across taxa, ranging from positive to negative associations of various strengths.

2.4.1. Potential associations of main algae

The more frequent presence and greater abundance of filamentous algal turfs, crustose coralline algae and the brown alga *L. variegata* close to coral recruits versus the background communities surveyed, suggests that coral recruitment can be more successful in microhabitats with these algae compared to microhabitats with other benthic biota. To some extent this pattern is likely to reflect the strong inhibition of settlement by hard and soft corals, and the higher abundance of turfs and other algae when corals are less abundant. Coral larvae are unlikely to settle on surfaces of live coral as they would be eaten. Thus settling in "empty" spaces away from live corals might increase the probability of observing algae close to coral recruits. However, patterns of coral recruit-algae association were consistent when data were re-analysed as proportions of space without hard or soft corals, suggesting that the patterns are not simply explained by the absence of corals, but do indicate real interactions between the coral recruits and algal assemblages. There is a lack of relevant experimental evidence on possible causal relationships between coral recruits and algae (Chapter 1). Nonetheless, none of the alternative hypotheses seem more likely: ie. that the presence of coral recruits influenced the presence of algae, that the relative availability of space influenced the presence of both coral recruits and algae sufficiently to cause the observed patterns, or that my results were a sheer coincidence.

Filamentous algal turfs are widely assumed to be detrimental to corals, nonetheless the variability of algal turfs (e.g. height, density, taxonomic composition) is often overlooked, even though several studies have investigated interactions between corals and filamentous algal turfs (McCook et al. 2001). There is a lack of evidence that algal turfs affect coral settlement. However, in a two year study Tanner (1995) observed no recruitment on substrata at Heron Island cleared of all benthic algae other than turfing forms at 6 to 8 week intervals. Furthermore, there is evidence that filamentous algae turfs can compete with coral recruits, established corals and crustose coralline algae (Bak and Engel 1979, Littler and Littler 1997a, 1997b, Steneck 1997, Smith et al. 2001, McCook 2001, McCook et al. 2001, Jompa and McCook 2003a, 2003b). Thus filamentous algal turfs can reduce coral recruit survival, however coral recruits can also overgrow filamentous algal turfs (Littler and Littler 1997). Furthermore, it appears likely that other benthic biota such as soft corals (Aceret et al. 1995, Maida et al. 1995a, 1995b) and hard corals (Lang and Chornesky 1990, Koh and Sweatman 2000) can hinder coral recruitment more than filamentous algal turfs. Thus, although filamentous algal turfs may not favour coral recruitment, coral recruitment may be more successful close to filamentous algal turfs than close to other biota.

The positive association of coral recruits with crustose coralline algae (CCA) is consistent with previous reports that several species of crustose coralline algae can induce coral settlement (Morse et al. 1988, 1994, 1996, Heyward and Negri 1999). However, recruits in this study (<4 cm diameter) are potentially observed one year or more after settlement, thus the observed recruits also survived successfully close to CCA. CCA can also compete with (e.g. overgrow) and kill coral recruits (Bak and Engel 1979, personal observation), nonetheless observing more coral recruits close to CCA than many other biota may also indicate CCA are less deleterious to recruits than other benthic biota. Some CCA slough epithelial tissue, which prevents biota from establishing on the CCA (e.g. Littler and Littler 1999). Thus, coral recruits close to

CCA that slough epithelial tissue would be likely to compete primarily with the CCA for space, instead of other, potentially more competitive biota, that could not establish on the CCA. Thus, the chances for coral recruit survival would be increased as a result of fewer competitive interactions.

It is surprising that the brown alga *Lobophora variegata* was observed more frequently, and in greater abundance close to coral recruits relative to background communities, particularly as *L. variegata* can overgrow and kill established corals and coral recruits (Hughes et al. 1987, Hughes 1994a, Jompa and McCook 2002a, 2002b). However, the outcome of competition between corals and *L. variegata* can turn in favour of corals if herbivores graze on *L. variegata* (Jompa and McCook 2002a, 2002b). Thus it is possible that the observed coral recruits survived successfully close to *L. variegata* as a result of coral-algal interactions mediated by herbivores. An alternative suggestion is that the alga *L. variegata* has positive impacts on coral recruitment that have previously not been explored (Chapter 4).

2.4.2. Potential trends of minor algal categories

2.4.2.1. Potential positive associations.

A small number of coral recruits were observed close to (<20 cm) *Amphiroa spp., Dictyota spp., Turbinaria spp.*, and Cyanophyta (blue green algae), which, given that these algal categories were less frequent in background communities, could suggest interactions that favour coral recruitment. This is most likely for algae of the genus *Amphiroa*, which are articulated or non-geniculate coralline algae, in particular as some *Amphiroa spp.* have been shown to induce coral settlement (Heyward and Negri 1999). It is surprising that *Dictyota spp.* were observed close to coral recruits, because many algae of this genus can produce secondary metabolites that may inhibit the settlement of invertebrates (Schmitt et al. 1995, Walters et al. 1996, Steinberg et al. 2001). Furthermore, *Dictyota spp.* were among several algae that overgrew corals and dominated degraded Jamaican reefs, upon which coral recruitment failed throughout recent decades (Hughes et al. 1987, Goreau 1992, Steneck 1994, Hughes and Tanner 2000, McCook et al. 2001). Observing more *Turbinaria spp.* close to coral recruits than in background communities was also surprising, given that established *Turbinaria spp.* can abrade corals (Tanner 1995), can rub settlement panels clean of coral recruits (Gleason 1996), and that the abundance of *Turbinaria* has been inversely correlated with coral abundance (Crossland 1981, Sheppard 1988). However, in this study *Turbinaria spp.* were often observed in diminutive forms amidst algal turfs (e.g. grazed or damaged by wave action), or as isolated individuals and not as a dominant algae in large stands more likely to affect corals, as described by other authors. The Cyanophyta or Blue Green algae recorded had a filamentous morphology and thus may affect coral recruitment in similar ways to filamentous algal turfs (discussed above) as a result of similar features (see Steneck and Dethier 1994).

2.4.2.2. Potential negative associations

The benthic algae that were observed less frequently close to coral recruits than in the background communities (*Padina spp.*, *Laurencia spp.*, *Peyssonnelia spp.*, and *Chnoospera spp.*) can all have deleterious effects on coral recruitment as a result of competitive interactions (reviewed in McCook et al. 2001). Many algae of the genus *Laurencia* have allelopathic properties, and over 570 chemical compounds have been described from *Laurencia spp.* (Munro et al. 1999, cited in Paul et al. 2001), including compounds that can inhibit the settlement of marine invertebrates (Walters et al. 1996, Steinberg et al. 2001). Thus, it is likely that many *Laurencia spp.* have deleterious effects on coral recruitment, in particular as several studies list *Laurencia spp.* among algal assemblages linked with the demise of coral populations (e.g. Crossland 1981, Steneck 1994, McCook et al. 2001). Algae of the genus *Padina* were among dominant algae on degraded reefs in Jamaica, where coral recruits where overgrown and killed by benthic algae, largely contributing to the demise of coral populations (Hughes et al. 1987, Hughes 1994a, Hughes and Tanner 2000). Furthermore, allelopathic influences from *Padina australis* reduced larval settlement of the Bryozoan *Brugula neretina* (Walters et al. 1996), thus some *Padina spp.* may have similar affects on coral settlement. In contrast, some *Peyssonnelia spp.* can induce coral settlement (Morse et al. 1996, Heyward and Negri 1999), which would be expected to result in greater frequency of coral recruits near *Peyssonnelia spp*. However, *Peyssonnelia spp.* like other crustose algae are also capable of overgrowing and killing corals recruits (Bak and Engel 1979, James et al. 1988, Tanner 1995, review McCook et al. 2001). Thus by reducing coral settlement or the survival of coral recruits these algal categories may be negatively associated with coral recruits.

2.4.3. Negative associations of benthic biota other than algae

My study provides an indication that few corals recruit successfully when close to other hard corals and soft corals, based on a large-scale survey. Many soft corals can exude secondary metabolites that have deleterious effects on the survival of hard corals (Aceret et al. 1995), and can inhibit coral settlement (Maida et al. 1995a, 1995b). Some hard corals can also hinder coral settlement by means of allelopathic interactions (Koh and Sweatman 2000). However, the secretion of mucus by corals also inhibits settlement of fouling organisms (e.g. Diaz-Pullido and McCook 2002). Furthermore, mechanisms of competition prevalent amongst hard corals (e.g. overgrowth, overtopping, and stinging) are likely to reduce the success of coral recruitment close to established colonies (Lang and Chornesky 1990, Baird and Hughes 2000). In general experimental studies test hypothesis based on *in situ* observations, nonetheless large-scale surveys that focus on coral recruits and can verify the relevance of tested hypothesis, like this study, are scarce (but see Bak and Engel 1979).

2.4.4. Regional comparison: Potential effects of terrestrial runoff.

In this study benthic algae were more frequent and abundant close to coral recruits (<20 cm) on reefs in the Wet Tropics region than on reefs in the Princess Charlotte Bay region. Algal taxonomic richness was also greater on the reefs surveyed in the Wet Tropics region when compared to the Princess Charlotte Bay region. These results are consistent with reports that benthic algae become more abundant and potentially more diverse on degraded reefs (e.g. Goreau 1992, Done 1992, Hughes 1994a, McCook 1999). Nonetheless, because of confounding issues inherent in any large-scale comparison, such as this study, differences in the algal communities close to the coral recruits and in background communities surveyed cannot unambiguously be attributed to differences in land-use. Examples of confounding factors include regional variation in supply of coral larvae (Hughes et al. 1999b, 2002) and latitudinal or regional differences in benthic algae composition (McCook et al. 1997, McCook and Price 1997). Furthermore, the disturbance history of the reefs in the Wet Tropics region included crown-of-thorns starfish outbreaks in the 1990s (Engelhardt et al. 1997) and extensive bleaching in 1998 (Berkelmans and Oliver 1999), whereas the reefs in the Princess Charlotte Bay region were relatively undisturbed and not bleached in 1998 (Fabricius et al. pers. com., pers. observ.). Thus, algae colonisation of dead coral substrata following crown-of-thorns disturbance and the 1998 bleaching is likely to have resulted in greater benthic cover of algae, in particular filamentous algal turfs, on reefs in the Wet Tropics region (Price 1975, McClanahan 2000, McClanahan et al. 2001, Diaz-Pulido and McCook 2002). However, bleaching and other disturbances are unlikely to have resulted in the consistently greater presence of filamentous algae turfs close to recruits when compared to the background communities surveyed. Thus despite separating data from the two regions in this study, I emphasise that regional differences in coral recruit-algae associations should be interpreted cautiously. In contrast, consistent patterns in coral recruit-algae associations are reliable.

2.4.5. Conclusions

In conclusion this survey has indicated macroalgae were always present and more abundant close to (<20 cm) coral recruits when compared to background communities, which suggests that coral recruitment is widely influenced by macroalgae on inshore reefs of the GBR. In particular filamentous algal turfs were dominant close to coral recruits, however crustose coralline algae and the brown alga *Lobophora variegata* were also present at significant levels close to coral recruits. Thus, these three algal categories may favour coral recruitment, or have less deleterious effects on coral recruitment relative to other biota. Although causality cannot be determined unambiguously, this survey has provided hypotheses to be tested experimentally in subsequent chapters of this thesis (e.g. do filamentous algal turfs hinder coral recruitment?; does *L. variegata* favour coral recruitment?). It is important to recognize that, as the surveys took place at a single season, the patterns identified may in part depend on the time of year. However, filamentous algal turfs, crustose coralline algae, and the predominant form of *Lobophora variegata* found in these surveys (encrusting form) are not likely to show major changes in abundance with season. Thus it is unlikely that the patterns identified are strongly dependent on the season. A range of less frequent (minor) macroalgae that potentially hindered (*Padina spp., Laurencia spp., Peyssonnelia spp.,* and *Chnoospera spp.*) or favoured (*Amphiroa spp., Dictyota spp., Turbinaria spp.,* and Cyanophyta) coral recruitment were also identified. Hard corals and soft corals were less frequent and less abundant close to coral recruits compared to background communities, thus this survey is potentially a large-scale verification that these biota can hinder coral recruitment, at least on inshore reefs of the Great Barrier Reef. Finally, coral recruits were observed in habitats with a greater algal abundance and taxonomic composition on reefs in the Wet Tropics region versus the Princess Charlotte Bay region, which suggests that terrestrial run-off from the developed catchment may have community level effects that can hinder coral recruitment.

Chapter 3. Effects of algal turfs and sediment on the larval settlement of the hard coral, *Acropora millepora*.

3.1. Introduction

The process of larval settlement, a critical stage in the successful recruitment of corals, is readily influenced by benthic inhabitants on reefs (Harrison and Wallace 1990, Caley et al. 1996). Since algae are one of the dominant members of the benthic community, they are likely to be a major determinant of the settlement success of coral larvae. Turf algae, in particular, were found to be present in greater abundance close to coral recruits than would be predicted based on patterns of abundance on substrata distant from coral recruits (Chapter 2), suggesting that they may play an important role in the settlement of coral larvae. However, there are few studies that investigate the effects of benthic algae on coral settlement (McCook et al. 2001).

Turf algae rapidly colonise the surfaces of dead corals and dominate most degraded and disturbed coral reefs, particularly when herbivores maintain low biomass of large and upright macroalgae through cropping (McCook 1999). Such dominance can persist for several years (Price 1975, Diaz-Pulido and McCook 2002). For example, algal turfs have comprised up to 90% of benthic cover across large areas of the Australian Great Barrier Reef, particularly the inshore regions, after disturbances by mass-bleaching events and regional outbreaks of crown-of-thorns starfish (McCook and Price 1996, McCook et al. 1997, Sweatman et al. 2000, 2001). Similarly, algal turfs dominated reefs in Kenya on the East coast of Africa, following the 1998 mass-bleaching event

(McClanahan et al. 2001). The increasing frequency and geographic extent of mass-bleaching events, crown-of-thorns starfish outbreaks and terrestrial run-off impacts (Goreau 1992, Berkelmans and Oliver 1999, Hoegh-Guldberg 1999, McCook 1999, McClanahan 2000, McClannahan et al. 2001, Wilkinson 2000, Sweatman et al. 2000, 2001) suggest that algal turfs are likely to increasingly dominate substrata onto which coral larvae have to settle on degraded reefs.

In addition to characteristically high percentage cover of macroalgae, degraded reefs throughout the Caribbean, Pacific and Indian Oceans tend to be close to coastlines where human activities such as agriculture, deforestation, coastal development, construction, mining, drilling and dredging have caused increased inputs of sediments to reef waters (Brown and Howard 1985, Rogers 1990, Goreau 1992, Brown 1997, Bryant et al. 1998, Wilkinson 2000, 2002). Experimental work has shown that even low levels of suspended sediment reduced the fertilisation of coral gametes as well as survival and settlement of coral larvae (Gilmour 1999). Sediments deposited on the reef substratum have also inhibited the settlement of coral larvae and smothered newly settled juveniles (Babcock and Davies 1991). Therefore turbid waters and deposited sediments can reduce coral settlement and hinder recovery of degraded reefs.

Benthic algae assemblages, and algal turfs in particular, tend to accumulate sediments (Eckman et al. 1989, Steneck 1997, Airoldi 1998, Purcell 2000). Thus, there is also the potential for algal turfs and sediments to act in combination to hinder coral settlement, an aspect of particular concern on degraded inshore reefs subject to high inputs of sediments. There are a number of mechanisms that would promote a synergistic interaction between algal turfs and sediment impacts on coral settlement. Firstly, algal assemblages reduce the flow of water in the boundary layer, enhancing sediment deposition and reducing flows that could resuspend the sediment (Eckman et al. 1989, Carpenter and Williams 1993, Vogel 1994). Secondly, algae assemblages can physically trap sediment and prevent resuspension (Purcell 2000). Sediment accumulation in algal turfs has been shown to enhance the ability of these assemblages to smother and overgrow other benthic biota, such as crustose coralline algae (Steneck 1997), which would be like the impacts predicted for coral recruits. Given that algal turfs are often associated with sediments on degraded reefs, it is important to understand the potentially synergistic impacts of both algal turfs and sediments on coral settlement.

The purpose of this study was to explore the effects of algal turfs, and algal turfs combined with sediments, on the settlement of coral larvae. In particular, I tested if the presence of algal turfs and/or sediments on dead coral substrata can reduce larval settlement of the hard coral, *Acropora millepora* (Ehrenberg), which provides insight into the potential for algal turfs to limit the recovery of disturbed and degraded reefs, in particular in inshore and high sediment environments.

3.2. Materials and Methods

3.2.1. Experimental design and Approach

To test the hypothesis that algal turfs hinder coral settlement and that sediments accumulated in algal turfs enhance this effect, I manipulated the presence of algal turfs and sediments on dead coral substrata, and compared the number of corals that settled in six different treatments. To explore potential variability in the impact of the turfs on coral settlement, I used two different algal turf assemblages, each with and without the addition of sediment. Thus, the experimental design included three factors: *algal turf* *presence* (two levels: with and without; fixed factor), *sediment presence* (two levels: with and without; fixed factor) and *substrate origin* (two levels: Turf 1 and Turf 2). To replicate within each combination of these treatments, I used three *tanks* (nested factor) and inside each tank placed six settlement surfaces (replicates; Figure 3.1).

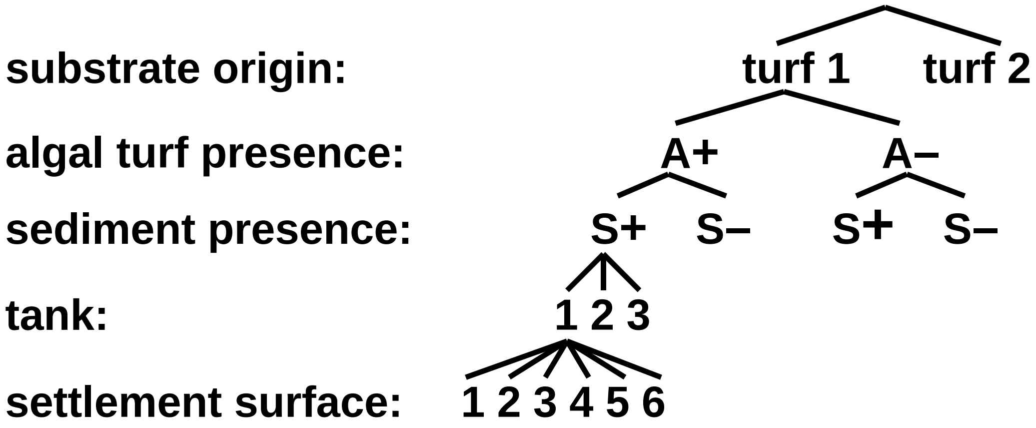

Figure 3.1. Experimental design for settlement experiments using larvae of the hard coral *Acropora millepora* to test the hypothesis that algal turfs hinder coral settlement and that sediments accumulated in algal turfs enhance this effect.

3.2.2. Settlement of larvae on experimental substrates

3.2.2.1. Experimental settlement surfaces and sediment treatments

Experimental settlement surfaces consisted of 5 cm × 5 cm pieces of dead, tabulate *Acropora* colonies that had well-established algal turf assemblages. For treatments without algal turfs, I carefully removed algal turfs with a brush. Sediment addition treatments involved the addition to each tank of 50 cm^3 of sediment, which was allowed to settle on the coral settlement surfaces. I obtained the sediment by filtering (15 µm) seawater from the reef crest in front of the Orpheus Island Research Station (18°46’ S, 146°50’ E).

3.2.2.2. Source of settlement surfaces with two different algal turfs

The first turf assemblage ("Turf 1") was established *de novo* on settlement surfaces that had been cut from a dead colony of tabular *Acropora* coral, cleaned with a high-pressure water hose, exposed to sunlight for one week, and then re-immersed for six weeks, to allow algal turfs to recolonise. The settlement surfaces were suspended from buoys one metre below the sea surface and 100 m offshore from the reef crest at Orpheus Island (18°46’S, 146°50’E), where herbivore abundance was low (pers. obs.).

The second turf assemblage (“Turf 2”) was a well-established community on an *in situ* dead colony of tabular *Acropora*, which was collected from shallow waters (1-3 m depth) on the North-East (exposed) corner of Orpheus Island (18° 37.0’ S, 146° 29.4’ E) and cut into settlement surfaces. Orpheus Island reefs were extensively bleached in 1998, resulting in the death of up to 90% of *Acropora* corals (Berkelmans and Oliver 1999, Marshall and Baird 2000), which were subsequently colonised by algal turfs (Diaz-Pulido and McCook 2002), suggesting the assemblages in this experiment were approximately 2.5 years old.

3.2.2.3. Study site and aquarium set-up

For all experimental work, I used the outdoor aquarium facilities at the Orpheus Island Research Station. To set up the experiments, I put tanks (9 litre volume opaque plastic rectangular bucket) in a shaded outdoor raceway, supplied each tank continuously with 25-30 litres per hour of filtered seawater (15 μm), and maintained temperatures at 28-30°C by circulating seawater around the outsides of tanks. So as not to lose coral larvae, overflow from each tank occurred through a hole covered by plankton mesh. To cause larvae to settle on the upper surfaces of substrates, I reduced the light levels in tanks by covering the aquarium set-up with 70% shade cloth and placed experimental substrates on the bottom of each tank (see Mundy and Babcock 1998).

3.2.2.4. Supply and settlement of coral larvae

I raised larvae for the settling experiments from the coral *Acropora millepora* (Ehrenberg), a common coral on Orpheus Island reefs that is easily maintained in aquaria and spawns predictably (Willis et al. 1985). During the mass coral spawning in December 2001, I followed procedures detailed in Willis et al. (1997) to spawn the corals, fertilise the gametes and raise the larvae. To standardise larval supply, I added 5000 (±500) competent larvae to each tank and allowed these to settle for four days. To confirm corals had settled and metamorphosed before making observations, I looked at randomly selected settlement surfaces using a dissecting microscope. So that recruits and algal turfs remained alive throughout observations, experimental settlement surfaces were submerged in seawater at all times.

3.2.3. Data collection and analysis

To measure coral settlement, I counted the number of metamorphosed coral larvae (hereafter referred to as *recruits*) on each experimental settlement surface. I used a dissecting microscope with a 1 cm × 1 cm grid placed over the experimental settlement surfaces to search for coral recruits methodically and mapped the location of each recruit. Qualitative differences between Turf 1 and Turf 2 in substrate structure and turf assemblages were noted whilst counting the recruits.

The mean number of coral recruits in each treatment combination was compared using a nested ANOVA, followed by post-hoc Student-Newman-Keuls (SNK) comparisons.

However, the initial differences between the two turf assemblages were so marked, resulting in a significant 3-way interaction, that I decided *a posteriori* not to make statistical comparisons of the number of corals settled on the different algal turf substrates (Turf 1 and Turf 2). Thus, two detailed analyses were performed, corresponding to the two levels of the factor, *substrate origin*. Data were investigated graphically for homogeneity of variance (Cochran's C test), outliers, and independence and normality of residuals. To satisfy statistical assumptions, data were logarithmically transformed ($\log_{10}\alpha$=number of recruits per experimental substrate + 0.01).

3.3. Results

3.3.1. Qualitative differences between Turf 1 and Turf 2

The two algal turf assemblages used in experimental studies of the impact of algal turfs and sediments on the settlement of coral larvae differed considerably. Differences were primarily attributable to the time-scale, the grazing regime and the predominant hydrodynamic conditions under which each algal turf developed, Turf 2 assemblages being more characteristic of a high wave energy, heavily grazed environment (Table 3.1). The average height of algae was greater for algal Turf 1 (5-8mm) than for Turf 2 (less than 3mm), which was more even in height because of grazing. Turf 1 algal assemblages were less dense and covered a smaller percentage of the settlement surfaces (85%) compared to Turf 2 algal assemblages (93%). More crustose coralline algae existed beneath the Turf 1 algal mat compared to the Turf 2 algal mat (6.5% and 2.0% respectively). The topography of the settlement surface used to grow the Turf 1 algal assemblage was irregular, as a result of the branching morphology of the dead coral. In contrast, the dead coral substrate upon which the Turf 2 algal assemblage grew was even, solid and without a branching morphology. There were potentially other differences between the settlement surfaces, such as differences in bacterial communities and species composition of the algae, but describing these was logistically beyond the scope of this study.

Table 3.1. Qualitative features of algal turf assemblages (Turfs 1 and 2) used in experimental treatments.

	Algal Turf 1	**Algal Turf 2**
Preparation of settlement surfaces	Cleared, algal turfs allowed to recolonise	Not cleared, turfs well-established
Time of turf development	5-6 weeks	Potentially 2.5 years
Grazing pressures during development	Low	High
Wave exposure	Sheltered	Exposed
Height of turf	5 to 8mm	Less than 3mm
Topography of settlement surfaces	Uneven	Even
Benthic cover of: a) CCA	6.5% (±2.6% SE)	2.0% (±1.3% SE)
b) Filamentous	85.3% (±3.4% SE)	93% (±2.4 SE)
c) unoccupied coral skeleton	1.9% (±0.9% SE)	1.0% (±1.0% SE)
Preparation/algal colonisation of dead coral substrates	Cleared substrate recolonised by algal turfs	Collected with algal turf established *in situ*

3.3.2. Impacts of the two algal turfs on coral settlement

There were considerable differences in the effects of the two algal turf assemblages on coral settlement, as evidenced by the significant three-way interaction between substrate origin, algal presence and sediment presence (Table 3.2). In particular, the effect of algal turf on larval settlement differed depending on whether or not sediment had been added to the experimental treatment. Therefore, given the differences in the turf assemblages described above (3.4.1), it was considered more appropriate to analyse the impacts of sediment and algal presence separately for the two algal turf assemblages, However, effects on settlement cannot be attributed solely to qualitative features of the algae.

Table 3.2. Results of analysis of variance tests comparing the effects of algal turf assemblages (A) and sediment (S) on larval settlement of the coral *Acropora millepora*. Results of a 3-way ANOVA, which includes two levels of algal turfs (Turf 1 and Turf 2) as the third factor, origin (O), are shown, as well as the results of two 2-way ANOVA's which analyse the impact of algae and sediment separately for each type of algal turf. Only the significant 3-way interaction term is shown for the 3-factor ANOVA to demonstrate the need to analyse the two types of algal turfs separately. Data are logarithmically transformed ($x' = \log_{10}$(number of recruits+0.01)). Cochran's critical C $_{p<0.05}$ = 0.3029. Note for *Turf 1*: *P* values are not included for the factors Algae and Sediment as a result of the significant A×S interaction; SNK test results are reported in the text.

Analysis	**Source of variation**	**MS**	**df**	***F*-ratio**	***P***
Turf 1 and *Turf 2*	O × A × S	13.834	1	5.503	0.032
	Tank (O × A × S)	2.514	16	3.395	<0.001
	Residual	0.741	123		
Turf 1	Algae (A)	6.693	1	4.438	------
	Sediment (S)	16.034	1	10.632	------
	A × S	11.801	1	7.825	0.023
	Tank (A × S)	1.508	8	2.077	0.052
	residual	0.726	60		
	Cochran's C	0.2051			
Turf 2	Algae (A)	0.111	1	0.032	0.863
	Sediment (S)	19.510	1	5.543	0.046
	A × S	3.329	1	0.946	0.359
	Tank (A × S)	3.520	8	4.844	<0.01
	Residual	0.727	60		
	Cochran's C	0.2315			

3.3.3. Effects of algal Turf 1 on coral settlement

The presence of either ungrazed, newly established algal turfs (SNK, p<0.05) or sediments (SNK, p<0.05) reduced coral settlement to extremely low levels, most often to zero. Overall, mean larval settlement was low (<1 larva per plate) in all treatments where algae or sediments were present, either alone or in combination (i.e. A+S+, A+S-, A-S+), reflecting plates with no settlement in each of these treatments (Figure 3.2). In the absence of both algae and sediments, mean settlement was five to fifty times greater (i.e. 3.6 larvae per plate ± 1.0 SE). There was some variation in the number of recruits between tanks within treatment combinations, although this nested factor was not statistically significant (Figure 3.1, Table 3.2).

3.3.4. Effects of algal Turf 2 on coral settlement

The presence of grazed, older turf assemblages (Turf 2) had little impact on settlement of coral larvae (p=0.863, Table 3.2, Figure 3.2). However, the addition of sediment uniformly reduced larval settlement (p=0.046, Table 3.2) and this impact was consistent regardless of whether the turf assemblage was present or absent (p=0.359, Table 3.2). The lack of significant interaction between sediments and grazed, older algal assemblages may reflect high within treatment variability due to the low numbers of larvae settling and considerable variability in settlement between tanks within treatments (p<0.01, Table 3.2). Interestingly, coral settlement tended to be lower in the presence of algae and was uniformly zero in the presence of both sediments and algae, suggesting a possible synergistic inhibition of settlement by the two factors. The highest number of corals that settled was again observed in one of the tanks where both sediments and algae were absent (A-S-, 6.3 recruits ± 2.3 SE).

Importantly, the significance of the variability between tanks within treatments was strongly dependent on the zero variance in the treatment with both sediments and algae present (A+S+: no settlement in any tank). When this treatment was excluded, variability between tanks within treatments was not statistically significant (two-tailed F test, P>0.05).

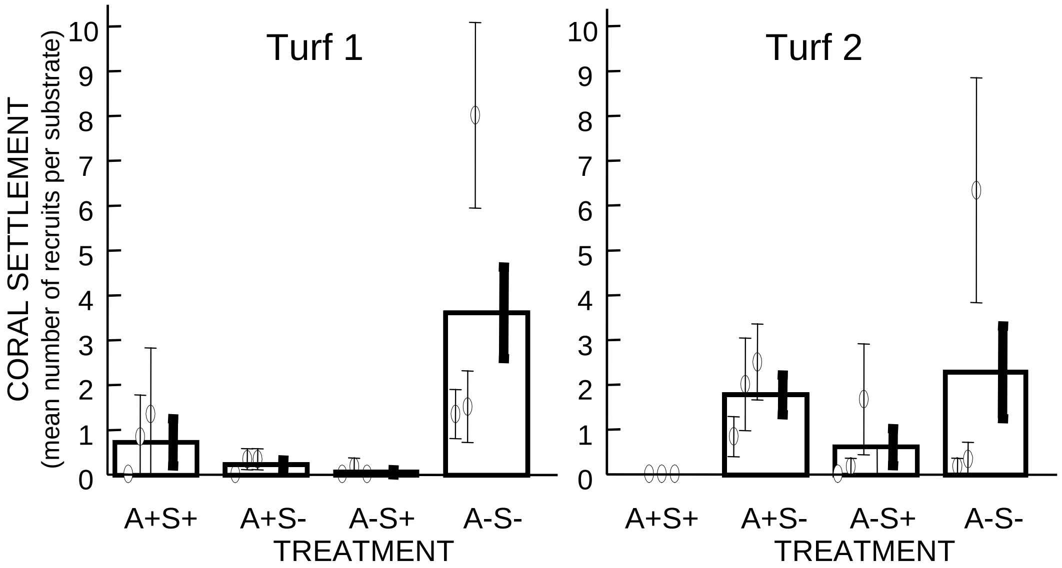

Figure 3.2. Average number of settled *A. millepora* larvae (± 1 SE) on experimental settlement surfaces with two different algal turfs: a) Turf 1 and b) Turf 2. Experimental treatments were 1) with both algal turfs and sediment (A+S+), 2) with algal turfs and without sediment (A+S-), 3) without algal turf and with sediment (A-S+), and 4) with neither algal turf or sediment (A-S-). Bars in graphs represent averages (± 1 SE) for each treatment, and dot graphs to the left of each bar represent averages (± 1 SE) for three tanks nested within each treatment. No coral larvae settled in the A+S+ treatment of Turf 2. Presence of sediment reduced coral settlement, but the effects of algal turfs varied, in one case reducing settlement (Turf 1; SNK $p<0.05$) in the other only reducing settlement when combined with sediments (Turf 2; Table 3.2).

3.4. Discussion

The results of this study provide several useful contributions to the understanding of larval settlement processes that are critical to the recovery of reefs from degradation and disturbance. Firstly, they provide experimental evidence that indicates some algal turfs reduce coral settlement in their own right. When coral settlement surfaces colonised by ungrazed, newly established (<6 week old) algal turfs were presented (Turf 1 treatment), coral larvae settled almost exclusively on surfaces that were cleaned of algal turfs and without sediments. The reduced settlement in the presence of sediment is consistent with previous studies that have investigated the effects of sediments on coral settlement (e.g. Babcock and Davies 1991). In contrast, grazed, well-established algal turfs (Turf 2 treatment) had relatively little, and non-significant, effects on coral settlement. However, the presence of sediments combined with these latter grazed turf assemblages completely inhibited coral settlement, suggesting that even algal turfs that might not normally inhibit coral settlement may do so on inshore reefs where sediment regimes are likely to be high.

The results of this study suggest that coral recovery can be delayed on reefs dominated by algal turfs, particularly those stressed by high sedimentation, through reduction and even inhibition of coral settlement. This is particularly concerning for inshore reef areas worldwide, which are vulnerable to terrestrial run-off and high sediment inputs from developed catchments (Rogers 1990, Goreau 1992, Richmond 1993, Brown 1997, Bryant et al. 1998, Wilkinson 2000, 2002, Wachenfeld et al. 1998, 2003). My results could at least partly explain the much lower recruitment found on reefs influenced by terrestrial run-off from a developed catchment area (Wet Tropics or Cairns to Innisfail region) compared to a relatively undeveloped catchment area (Princess Charlotte Bay region) (Chapter 2, Fabricius et al. pers. comm.). It is noteworthy that at the time of the surveys, the reefs in the Cairns to Innisfail region (developed catchment) were dominated by algal turfs following high coral mortality during crown-of-thorns starfish outbreaks during the mid to late 1990s (Engelhardt et al. 1997) and the mass-bleaching event of 1998 (Berkelmans and Oliver 1999, Sweatman et al. 2000, 2001). Therefore results of my experimental study are consistent with results of the large-scale field surveys, which showed impeded recovery on reefs stressed by sediments and dominated by algal turfs after crown-of-thorns starfish and mass-bleaching disturbance.

The likely role of algal turfs in hindering the recovery of coral populations between successive disturbance events, would also contribute to the long-term degradation of reefs. Algal turf assemblages have been observed to dominate bleached coral surfaces for at least two and a half years (Diaz-Pulido and McCook 2002). Similarly, algal turfs can dominate corals killed by crown-of-thorns starfish outbreaks for over a year and a half (Price 1975). In both of these examples, algal turfs were observed to dominate dead coral surfaces for time scales that potentially span two or more coral spawning seasons, thus could contribute to reduced coral recovery also for at least 2-3 years. Nonetheless, low densities of reproductive corals is likely to result in low larval supply and also hinder coral recovery. Furthermore, as many as 3-4 mass-bleaching events per decade have been predicted in the near future (Hoegh-Guldberg 1999), and given that algal turfs are likely to dominate bleached reefs (McClanahan et al. 2001, Diaz-Pulido and McCook 2002) they could play an important role in reducing reef resilience to bleaching potentially resulting in the long-term degradation of coral reefs. However, besides mass-bleaching, other disturbance events such as cyclones and crown-of-thorns starfish outbreaks, can alternate and potentially disturb reefs every two to three years, even if only on localised spatial scales (Connell 1997, Hughes and Connell 1999).

This study also provides evidence that benthic algal assemblages that may not be competitively superior to established corals, can still have negative impacts on coral populations by affecting coral settlement. Algal turf assemblages generally do not out-compete mature corals but instead colonise dead coral surfaces (Price 1975, McCook 2001, Diaz-Pulido and McCook 2002, Jompa and McCook 2003a, 2003b). Just as many studies have shown that small corals are more vulnerable to competition than larger established corals (Hughes and Jackson 1985, Hughes 1989, 1996), coral larvae are also likely to differ in their vulnerability to competition compared to recently settled recruits. Thus our conceptual framework for understanding the role of coral-algal competition in the degradation of coral reefs must recognize that competition varies with different life history stages of corals and has the potential to generate very different outcomes.

Differences in the average number of recruits on substrates from the same treatment, suggests that heterogeneity of biological or physical features, other than the overall presence or absence of algal turfs and sediments, also affected coral settlement. For example, bacteria and other benthic biota (e.g. foraminiferans, polychaetes, crustose red algae) associated with the substrates and algal turf assemblages can affect coral settlement (Morse et al. 1988, Johnson et al. 1991, Johnson et al. 1997, Negri et al. 2001, Baird et al. 2003). Differences in the taxonomic composition of the algae in the turfs could also have caused variable coral settlement. In particular, many algae have chemical influences on the settlement of invertebrate larvae (Steinberg et al. 2001, Steinberg and de Nys 2002), and although little is known about the chemical effects of algae on coral settlement, Jompa and McCook (2003a, 2003b) suggested that allelopathy by a filamentous alga killed established *Porites* corals. Morphological features of the algal turf assemblages such as height and density, can also determine the effects of algal turfs on other organisms, and thus may also have contributed to the differences between turfs (Steneck and Dethier 1994, McCook et al. 2001). Finally, the physical heterogeneity of substrates can also affect coral settlement (Harrison and Wallace 1990). Thus algal turfs, in particular when combined with sediments can reduce coral settlement, however more specific features of algal turfs are also likely to influence their impact on coral settlement.

3.4.1. Conclusion

In conclusion, sediment reduced coral settlement, but the effects of different algal turfs varied, a newly established (<6 week old) algal turf (Turf 1 treatment) reducing settlement, and a well established and grazed algal turf (Turf 2 treatment) only reducing settlement when combined with sediments. Therefore this study indicates that coral settlement can be hindered on reefs dominated by algal turfs after disturbance, slowing coral recruitment and the recovery of these reefs. However, recovery of disturbed reefs, is more likely to be hindered and at times inhibited, if reefs dominated by algal turfs, even those that might not normally inhibit coral settlement, are also stressed by sediment deposition.

Chapter 4. Allelochemical effects of macroalgae on larval settlement of the coral *Acropora millepora.*

4.1. Introduction

The settlement of larvae is a critical but vulnerable stage in the early life history of corals, linking the dispersal and supply of planktonic larvae to the survival and growth of benthic juveniles. The outcome of settlement will depend on how coral larvae respond to and are impacted by influences from the physical environment and benthic biota (Harrison and Wallace 1990, Maida et al. 1995a, 1995b, Abelson and Denny 1997, Mundy and Babcock 1998, Raimondi and Morse 2000). Since macroalgae invariably dominate degraded and disturbed coral reefs, they potentially exert a controlling influence on coral settlement and consequently on the recovery of these reefs (Done 1992, Hughes 1994a, Connell 1997, McCook 1999). In addition to the physical pre-emption of space and changes to the character of settlement surfaces through processes like the trapping of sediments (Chapter 3), algae also largely determine the chemical environment confronting larvae during the settlement process (Jensen 1977, Amsler et al. 1992, McCook et al. 2001). However, the potential for algae to affect settlement of coral larvae through allelochemical processes has not been previously investigated.

Mounting evidence indicates that a diversity of algae can influence the settlement of marine invertebrates via chemical processes (reviewed in Pawlik 1992, Morse 1991, 1992, Hadfield and Paul 2001, Steinberg et al. 2001, 2002, Steinberg and de Nys 2002).

Macroalgae chemically alter the settlement environment by influencing the alkalinity:acidity ratio of seawater (McConnaughey et al. 2000) and by altering nutrient concentrations (e.g. Carpenter et al. 1991) in seawater as a result of photosynthesis, respiration and calcification. Further impacts on the chemical environment can result from algal release of primary and secondary metabolites and shedded plant material such as fruit bodies (e.g. Jensen 1977, Amsler et al. 1992, Steinberg and de Nys 2002). These chemical influences may affect invertebrate larvae, most of which are chemotactic, or display movement orientated by chemical gradients, which in turn determines larval habitat selection and settlement (Pawlik 1992)

The chemical effects of algae on invertebrate larvae can range from lethal antifouling compounds to settlement cues and inducers. Walters et al. (1996), investigated allelopathic effect of twelve macroalgae, common on coral reefs, on a fouling polychaete (*Hydroides elegans*) and bryozoan (*Bugula neritina*), and demonstrated that chemical influences from different algae can be toxic to larvae (e.g. *Dictyota spp.* and a *Laurencia sp.*), inhibit larval settlement (e.g. *Padina sp.*, *Halimeda sp.*), stimulate larval settlement (e.g. *Hypnea sp.*, *Ulva sp*.), or have no effect on larval settlement (e.g. *Sargassum spp*.). However, the responses of *H. elegans* and *B. neritina* larvae to chemical influences from each alga differed in response to some alga, for example chemical compounds from the alga *Padina australis* stimulated settlement of *H. elegans* and inhibited settlement of *B. neritina.* Schmitt et al. (1995) found extracts containing terpenoids collected from the surface of the brown alga *Dictyota menstrualis* also inhibited settlement of *B. neritina*, thus were likely to maintain alga *D. menstrualis* relatively unfouled in the field. Williamson et al. (2000) found the echinoid *Holopneustus purpurascens* metamorphosed and to a lesser extent settled, in response to a floridoside-isethionic acid complex isolated from the red alga *Delisea pulchra*, also present in several other red algae, but not green or brown algae. Thus a range of algal chemical influences on the settlement of invertebrates other than corals have been demonstrated.

Several calcareous red algae have been shown to induce coral settlement (Morse et al. 1988, 1996, Heyward and Negri 1999), however, as with many other invertebrates, these studies have primarily identified surface-bound effects of algae on invertebrate larvae (see Pawlik 1992). For example Morse et al. (1988, 1994, 1996) suggest water-insoluble polysaccharides present in the cell walls of several crustose coralline algae induce the settlement of *Agaricia spp*. corals in the Caribbean and *Acropora spp*. corals in the Pacific. Steinberg and de Nys (2002) reviewed chemical mediation of colonisation of algal surfaces, and in line with earlier work (Rittschoff 1990, Steinberg et al. 2001), suggested inducers of larval settlement are most likely to be primary metabolites (e.g. polysaccharides, amino-acids, peptides), because these are typically present in higher concentrations than secondary metabolites and readily leak or are exuded from algae into seawater. Thus, Steinberg and de Nys (2002) highlight the potential for water-soluble influences from algae to signal sites for invertebrate settlement. For example, larvae of the specialist herbivore *Alderia modesta* (Opisthobranchia: Ascoglossa) settled and metamorphosed in response to both water-soluble and surface-associated carbohydrates of the alga *Vaucheria longicaulis* (Krug and Manzi 1999). This raises the question of whether waterborne chemical cues from algae can affect coral settlement.

The settlement of coral larvae is particularly likely to be hindered by secondary metabolites released from benthic biota. Maida et al. (1995a, 1995b) provided evidence that the soft corals *Sinularia flexibilis* and *Sarcophytum glaucum* produce water-soluble chemicals, which reduced coral settlement in down-current areas. The toxins that potentially inhibited coral settlement were diterpenes, which have been derived from soft corals (*Sinularia flexibilis* and *Lobophytum hedleyi*) and shown to have toxic effects on established colonies of the hard corals *Acropora formosa* and *Porites cylindrica* (Aceret et al. 1995). Many macroalgae also produce secondary metabolites that are active against epibiota (Clare 1996, de Nys and Steinberg 1999). For example brown algae of family Dictyotaceae, which includes common coral reef genera such as *Dictyota*, *Padina* and *Lobophora*, are known to produce a variety of toxic substances including terpenoids, tannins, hydrocarbons and sulphur-containing compounds (McEnroe et al. 1977, Wright et al. 1990, Schmitt et al. 1995, Targett 2001). Nonetheless, the possibility that macroalgal release of such chemicals to the water column may affect coral settlement has not been previously investigated.

In this study I explored the possibility that benthic macroalgae affect coral settlement through water-soluble chemicals. I specifically investigated how seawater influenced by three macroalgae, *Lobophora variegata, Padina sp. and Chlorodesmis fastigiata*, which are common and widespread especially on degraded reefs, affects the pre-settlement responses and the settlement of larvae from the coral *Acropora millepora* (Ehrenberg).

4.2. Materials and Methods

4.2.1. Experimental Design and Approach

To investigate potential water-soluble chemical effects of algae on coral settlement, I raised larvae of the coral, *Acropora millepora,* using aquarium facilities at Lizard Island Research Station during November 2002. Larvae were raised according to established procedures (Babcock and Heyward 1986, Willis et al. 1997) and presented with live surfaces of the crustose coralline algae, *Hydrolithon reinboldii,* for settlement. The experimental design involved a single factor, seawater treatment, which had five levels: 1-3) seawater collected from tanks holding one of the macroalgae, *Lobophora variegata*, *Chlorodesmis fastigiata*, or *Padina sp*., selected because they can be common on degraded reefs, 4) seawater collected from a tank holding pieces of reef substrata (substratum control), and 5) seawater collected from the water column (seawater control). Each level of treatment was replicated in ten petri dishes, with each petri dish containing a piece of *Hydrolython reinboldii* (Figure 4.1).

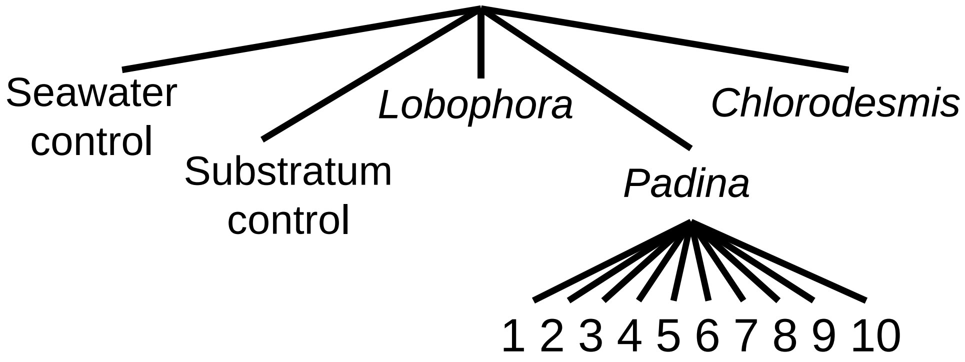

Figure 4.1. Experimental design for settlement experiments using larvae of the hard coral *Acropora millepora* to compare coral settlement on a crustose coralline alga (*Hydrolithon reinboldii*) in seawater which previously contained macroalgae (*Lobophora variegata*, *Padina sp*. and *Chlorodesmis fastigiata*) to control seawaters (seawater influenced by *substrata* and unconditioned *seawater*). Ten replicates were used for each level of seawater treatment.

4.2.2. Experimental Treatments and Procedures

To create the different seawater treatments, I placed live, whole algae of the taxa *Lobophora variegata* (Lamouroux), *Chlorodesmis fastigiata* (C. Agardh) and *Padina sp.* in tanks of still seawater. For each treatment, I conditioned six litres of seawater for 90 minutes with 250 g of each algae (± 25 g wet weight). Algae were collected within 24 hours of experiments from fringing reefs surrounding Lizard Island (14° 41‘S, 145° 28‘ E) on the Australian Great Barrier Reef. To avoid the release of stress activated compounds into seawater treatments, I collected algae attached to pieces of substrata and discarded any damaged specimens. Because algae remained attached to portions of reef substrata, a treatment was required to control for potential influences from biofilms or other microbiota associated with the substrata. To create the substrata control, 100g of reef substrata (± 10 g; wet weight) were placed in six litres of seawater for 90 minutes. To control for the potential presence of waterborne chemicals in seawater used in the experimental treatments, six litres of seawater were left to stand for 90 minutes (seawater control).

Assays to test for potential effects of waterborne chemicals on larval settlement consisted of replicated plastic petri dishes, each containing 40 ml of the appropriate seawater treatment, a live fragment of *Hydrolithon reinboldii* and 20 competent coral larvae. To assess larval development and competence to settle, random sub-samples of larvae were observed in seawater using a dissecting microscope at daily intervals after fertilisation. Colonies of *Hydrolithon reinboldii* were collected from fringing reefs surrounding Lizard Island within 24 hours of the experiment and fragmented into pieces of equal surface area (1.0 cm^2 ± 0.1 cm^2) with equal volumes of attached substratum (0.5 cm^3 ± 0.05 cm^3). To place twenty larvae in each replicate petri dish, I counted larvae as I added them, using a glass pipette. Replicates where maintained at a constant room temperature of 26° C and moderate levels of natural light.

4.2.3. Data and Analysis

As the primary response variable, I recorded the number of coral larvae settled (metamorphosed) on *H. reinboldii* surfaces after 48 hours, which I expressed as a percentage of the twenty larvae added to each replicate. I made these observations using a stereo dissection microscope and accounted for all twenty larvae originally placed in each petri-dish. These observations confirmed that larvae that did settle, settled on the live *H. reinboldii* surfaces and not the petri-dish or substratum attached to *H. reinboldii*. The data analysis of treatment effects on coral settlement involved a one-way analysis of variance (ANOVA) followed by post-hoc Student-Newman-Keuls (SNK) tests.

As secondary response variables, I used three measures of larval behaviour: 1) *substratum testing*, for activities in which larvae touched surfaces with their aboral end repeatedly and occasionally attached, but without metamorphosis; 2) *swimming*, for visibly motile larvae; and 3) *stressed*, for larvae observed to be motionless or floating at the water surface, a category which also included dead larvae (Harrison and Wallace 1990, Raimondi and Morse 2000). I recorded the percentage of larvae expressing each category of behaviour when initially added to each petri dish, and at 2, 10 and 24 hours later. A magnifying glass was used to observe the larvae to avoid moving the petri dishes and disturbing settled or unsettled larvae.

The data for the three measures of behaviour are presented graphically, but only substratum testing, the variable most relevant to settlement, was analysed statistically, since the three measures are not independent (observations are from the same 20 larvae in each petri dish). This analysis of treatment effects involved a one-way analysis of variance (ANOVA) followed by post-hoc Student-Newman-Keuls (SNK) tests, at each of 4 times (time=0, 2, 10 and 24 hours after adding larvae to treatments) using Bonferroni's correction ($\alpha''=0.05/4$) to limit experiment-wise error rates; repeated measures analysis was not used because repeated measures were not independent.

To satisfy the assumptions of statistical significance tests, I tested homogeneity of variance (Cochran’s C test) for all data and inspected the normality of residuals visually and with Kurtosis and Skewness tests available in Systat 8.0^{TM}. To satisfy homogeneity of variance, I arc-sin transformed *substrata testing* data, as recommended for percentage data (Underwood 1997).

4.3. Results

4.3.1. Effects of water-soluble influences on coral settlement

Mean settlement of *Acropora millepora* larvae was approximately two-fold greater in seawater that had been collected from tanks containing the algae *Lobophora variegata* for 90 minutes (76 % ±4.6 % SE), than in the unconditioned seawater control (37 % ±4.6 % SE) (Figure 4.2, SNK p<0.001). Larval settlement in seawater collected from tanks holding the other two algal species, *Chlorodesmis fastigiata* (46 % ±4.6 % SE) and *Padina sp*. (39 % ±6.7 % SE), did not differ significantly when compared between these two treatments or to either of the two controls (SNK p>0.05). Similarly, larval settlement in the seawater (37 % ±4.6 % SE) and substrate control (55 % ±6.0 % SE) treatments did not differ significantly (SNK p>0.05).

Table 4.1. Results of analysis of variance tests comparing the effects of waterborne influences of macroalgae on larval settlement of *Acropora millepora* among the macroalgal treatments (*L. variegata*, *C. fastigiata*, *Padina sp.*) and controls (*substratum* and *seawater control*). Cochran's C test indicates the homogeneity of variance (C critical value = 0.307). Data are not transformed. ~ indicates significantly different groupings based on SNK tests.

Source of variation	df	Mean square	*F*-ratio	*P*	Conclusion / SNK
Treatment	4	101.47	8.434	<0.001	*L. variegata* ~ other treatments (SNK p<0.001)
Error	45	12.031			
Cochran's C = 0.295					

4.3.2. Effects of water soluble influences on larvae behaviour

In the *Chlorodesmis fastigiata* treatment, almost no *Acropora millepora* larvae were observed to display substrata testing behaviour at time 0 (2.5% ± 1.3% SE), whereas significantly more (SNK p<0.01, Table 4.2) larvae tested substrata in all other treatments (Figure 4.3A). Within 2 hours, the mean percentage of larvae testing substrata in this treatment increased by over twenty-fold (to 71% ±3.8% SE) and subsequently remained approximately constant (65-70%) for the first 24 hours. However, even though consistently fewer larvae (by 10-15%) were observed to test substrata after 2, 10 and 24 hours in the *C. fastigiata* treatment versus other treatments the only statistically significant differences were between the *C. fastigiata* and *L. variegata* treatments at 2 (SNK p=0.012), 10 (SNK p<0.001) and 24 hours (SNK p=0.024).

In contrast to the *C. fastigiata* treatment, nearly all (99% ± 0.7% SE) and significantly more (SNK p<0.01) *Acropora millepora* larvae were testing substrata at time 0 in the *Lobophora variegata* treatment, and more larvae tended to test substrata throughout later observations when compared to other treatments. Within 2 hours the percentage of larvae testing substratum in the *Lobophora variegata* treatment decreased by approximately 10% but still tended to remain higher than in other treatments thereafter. Similarly to the behaviour trends in the *Chlordesmis fastigiata* treatment, the percentage of larvae testing substrata in the *Lobophora variegata* treatment changed little in subsequent observations (10 and 24 hours, Figure 4.3A).

In the *Padina sp.* treatment, the average percentage of *Acropora millepora* larvae observed testing substrata was initially 83.5% (±1.7% SE), and throughout the later observations tended to change less than 5% (Figure 4.3A). In the substratum control treatment, the average percentage of *Acropora millepora* larvae observed testing substrata was initially 87.5% (±1.7% SE), and within 2 hours decreased by approximately 5-10% remaining at approximately 80% throughout the later observations. Initially the average number of larvae testing substrata in the seawater controls (84.5% ±1.2% SE) did not differ significantly to the substratum controls, and did not become different despite fluctuating between 75-90% in later observations.

Table 4.2. Results of analysis of variance tests comparing the effects of waterborne influences of macroalgae on the *substrate testing* response by larvae of the coral *Acropora millepora* among the macroalgal treatments (*L. variegata*, *C. fastigiata*, *Padina sp*.) and controls (*substratum* and *seawater control*). Data is arc-sin transformed (x'=arcsin√proportion of larvae showing response). Tests compare observations made at time = 0, 2, 10, and 24 hours after larvae were added to treatments. Cochran's C test indicates the homogeneity of variance (C critical value = 0.4241) for all data. To reduce experimental error rates, probability values were corrected using the Bonferroni method (α''=0.05/4). ~ indicates significantly different groupings based on SNK tests.

Compared observation	Source of variation	df	Mean square	*F*-ratio	*P*	Conclusion / SNK
Immediate (0 hours)	Treatment	4	3.032	247.36	**<0.001**	*L. variegata* ~ *Padina sp.* & controls ~ *C. fastigiata* (SNK p<0.001)
	Error	45	0.012			
	Cochran's C =	0.3709				
2 hours	Treatment	4	0.154	4.740	**0.012**	*Alternative hypothesis not identified*
	Error	45	0.033			
	Cochran's C =	0.4211				
10 hours	Treatment	4	0.212	6.875	**<0.001**	*Alternative hypothesis not identified*
	Error	45	0.031			
	Cochran's C =	0.2516				
24 hours	Treatment	4	0.135	4.158	**0.024**	*Alternative hypothesis not identified*
	Error	45	0.032			
	Cochran's C =	0.3765				

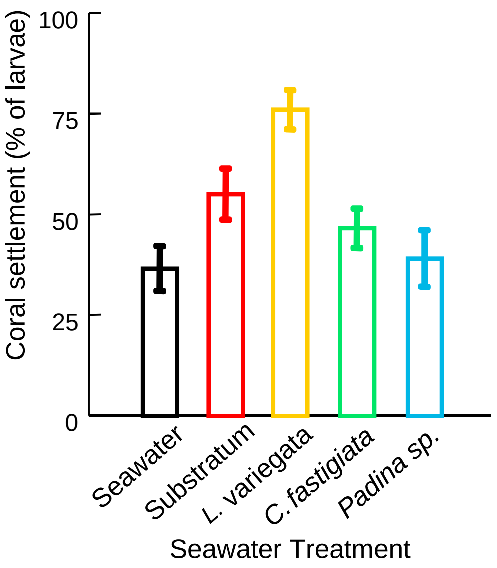

Figure 4.2. The mean percentage (± 1 SE) of coral larvae settled on live surfaces of the crustose coralline algae *Hydrolithon reinboldii* after 48 hours in macroalgal treatments (*L. variegata*, *C. fastigiata*, *Padina sp.*) and controls (*substratum* and *seawater control*). Means for each treatment are calculated from ten replicates, which each contained twenty coral larvae. Significantly more larvae settled in the *L. variegata* treatment (ANOVA: p < 0.001, df = 4, F = 8.434, SNK p<0.001).

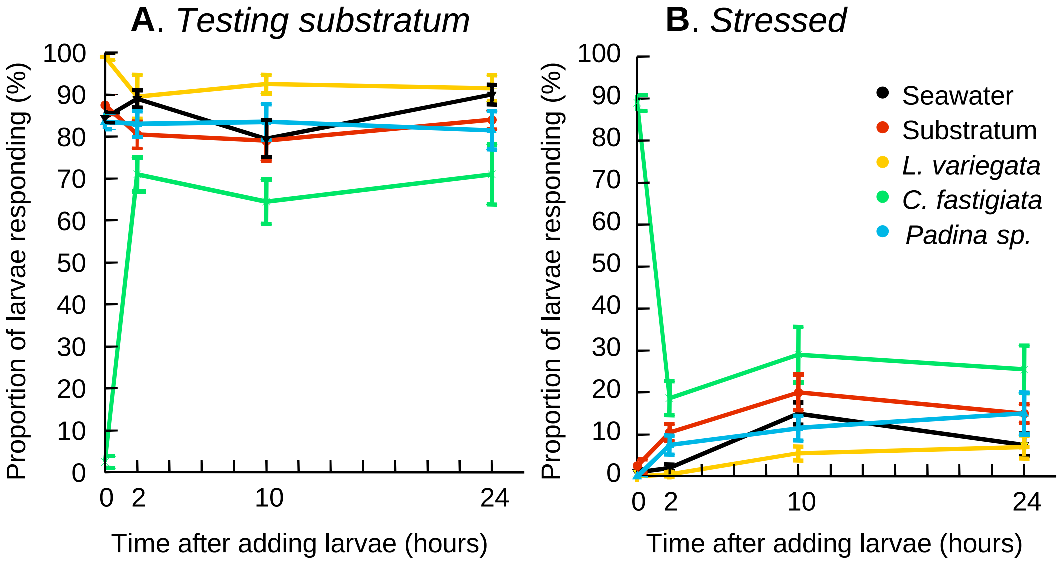

Figure 4.3. The mean percentage (± 1 SE) of larvae displaying the behavioural responses defined as A. *testing substratum* and B. *stressed* in macroalgal treatments (*L. variegata*, *C. fastigiata*, *Padina sp.*) and controls (*substratum* and *seawater control*). Observations were made at time = 0, 2, 10 and 24 hours after adding larvae to treatments. Means for each treatment are calculated from ten replicates, which each contained twenty coral larvae. The response of larvae in *C. fastigiata* treatments is unlikely to promote settlement in the vicinity of this macroalgae.

Initial observations also indicated that nearly all larvae (89% ±1.8% SE) in the *Chlorodesmis fastigiata* treatment were *stressed* (Figure 4.3B). Although the percentage of *stressed* larvae in the *Chlorodesmis fastigiata* treatment decreased 3-4 fold within 2 hours, at least 10% more larvae appeared stressed in the *C. fastigiata* treatment compared to other treatments throughout the experiment. In contrast to in the *C. fastigiata* treatment, less than 5% of larvae in other treatments appeared to be *stressed* initially; instead larvae were either *testing substrata* or *swimming*. Slight increases in the average percentage of stressed larvae were observed in later observations, although generally less than 20% of larvae appeared to be stressed in treatments other than the *C. fastigiata* treatment.

4.4. Discussion

The results of this study are significant to coral recruitment and recovery on degraded reefs for four main reasons. Firstly, they demonstrate for the first time that some algae can influence coral settlement by means of water-soluble chemical influences. This highlights an overlooked mechanism of coral-algae interaction with serious implications for coral recruitment on disturbed or degraded reefs, which are dominated by benthic algae. Secondly, the results demonstrate that waterborne influences of algae had species-specific effects on the settlement and behaviour of *Acropora millepora* larvae. The foliose brown alga *Lobophora variegata* (Lamouroux) enhanced coral settlement by approximately 40 % relative to control treatments. In contrast, the filamentous green alga *Chlorodesmis fastigiata* (C. Agardh - "Turtle weed") delayed settlement responses of larvae, which suggests *C. fastigiata* may hinder coral settlement. *Padina sp.*, a foliose brown alga closely related to *Lobophora variegata,* had no apparent effect on coral settlement. Thirdly, the demonstration of waterborne effects on coral settlement suggests that macroalgae can potentially affect coral settlement before larvae reach the reef substrata, and even where the immediate area of substrata that larvae can settle on is free of algal cover. Fourthly, the results demonstrate that waterborne influences from macroalgae can even affect the settlement of *Acropora millepora* larvae on a crustose coralline alga, *Hydrolithon reinboldii*, known to induce settlement of larvae from a variety of corals, in particular acroporids (Morse et al. 1996). In turn, this suggests that coral settlement may be determined by several benthic algae in an assemblage and not just by the simple presence or absence of a few calcareous red algae that were previously thought to be the only algae inducing coral settlement (e.g. Morse et al. 1988, 1996, Heyward and Negri 1999).

In general, chemical and physical properties of the marine environment influence the settlement and behaviour of coral larvae (Harrison and Wallace 1990, Pawlik 1992, Maida et al.1995a, 1995b Raimondi and Morse 2000), thus it is not surprising that macroalgae affect coral settlement through waterborne chemical effects. In particular, macroalgae can influence the chemical composition, alkalinity to acidity ratio, and nutrient equilibrium of seawater as well as physical properties of marine habitats experienced by larvae (Jensen 1977, Carpenter et al. 1991, Amsler et al. 1992, McConnaughey et al. 2000). Both surface-bound and waterborne effects of algae have been shown to either chemically deter or induce the larval settlement of other invertebrates (Pawlik 1992, Steinberg et al. 2001, 2002, Steinberg and de Nys 2002). For example, on Hawai’ian coral reefs, the release of water-soluble chemicals by some algal species (*Ulva sp*., and *Sphacellaria sp*.) inhibited settlement and others (*Dictyota spp*.) even killed larvae of the fouling bryozoan, *Brugula neritina* and the polychaete *Hydroides elegans* (Walters et al. 1996). In contrast, water-soluble chemicals released by *Padina sp*. enhanced settlement of *H. elegans*, whereas, *Sargassum spp*. had no affect on *B. neritina* larvae (ibid).

Although my results provide clear evidence that algae affected coral settlement through waterborne chemicals, the nature of the chemical influences is unclear. Compounds known to induce invertebrate larvae to settle are generally primary metabolites such as carbohydrates, peptides or even nutrients and are commonly water-soluble, whereas deterrents are usually secondary metabolites that are insoluble (Steinberg et al. 2001). Studies of chemically mediated impacts of *L. variegata*, *C. fastigiata* and *Padina sp*. on other marine organisms may provide insights into the potential mechanisms by which these algae influenced settlement of coral larvae in my experiments. The cytotoxic diterpenoid chlorodesmin is a secondary metabolite present in *Chlorodesmis fastigiata* that deters herbivores from feeding on the algae (Wylie and Paul 1988, Hay et al. 1989, Paul et al. 1990). Thus, chlorodesmin possibly delayed coral settlement in my study, despite low solubility in seawater. *Lobophora variegata* is known to produce a variety of secondary metabolites such as phlorotannins (Stern et al. 1996, Arnold and Target 1998, Arnold et al. 2000) and bromophenols (Chung et al. 2003), which are believed to deter herbivores but possibly have other effects. Seawater passing over *Lobophora variegata* attracted *Diadema antillarum* (Solandt and Campbell 2001), which feeds preferentially on the alga (Tuya et al. 2001). Algae of the genus *Padina* have also been reported to have waterborne effects on invertebrate larvae and to contain secondary metabolites with herbivore deterrent and cytotoxic capacity (Renaud et al. 1990, Walters et al. 1996, Ktari and Guyot 1999, Chung et al. 2003). However, even closely related algal taxa may have different chemical effects on the settlement of invertebrate larvae (Steinberg et al. 2001, 2002, Steinberg and de Nys 2002).

It is also possible that bacteria or microflora associated with the surfaces of the algae caused the observed effects. In contrast to studies reporting that morphogens associated with calcareous and coralline algae induce settlement of invertebrate larvae, including corals (Morse et al. 1988, 1994), there is evidence that bacteria associated with these algae induce larval settlement (Johnson et al. 1991, 1997, Morse and Morse 1991, Johnson and Sutton 1994, Negri et al. 2001, Harder et al. 2002). The surfaces of *Lobophora variegata* support diverse bacterial communities (Jensen et al.1996), and although it is unknown how these affect coral settlement, there is evidence that bacteria associated with *Lobophora variegata* produce biologically active compounds that can affect invertebrates (Jiang et al. 1999).

The result that *Lobophora variegata* enhances coral settlement contrasts with reports that *L. variegata* competes with corals, overgrowing and killing recruits and mature colonies (de Ruyter van Stevenick et al. 1988, Hughes 1994a, Littler and Littler 1997a, Jompa and McCook 2002a, 2002b, pers. obs.). However, there is evidence that corals have defence mechanisms that prevent them from being overgrown by *L. variegata*, particularly in herbivore mediated interactions (de Ruyter van Stevenick et al. 1988; Jompa and McCook 2002a, 2002b). Thus, it may only be corals whose health is somehow compromised that are vulnerable in such competitive interactions. Other macroalgae also have apparently contrasting influences on corals. For example, some crustose coralline algae induce coral settlement (Morse et al. 1988, 1996), but most if not all crustose coralline algae can overgrow and kill coral recruits (Bak and Engel 1979, review McCook et al. 2001, personal observation) or dislodge recruits by sloughing epithelial layers (Littler and Littler 1999). However, my study emphasises that variable outcomes of coral-algae interactions are possible even within a single species of alga, such as *Lobophora variegata* (reviewed in McCook et al. 2001).

The enhancement of larval settlement by *Lobophora variegata* found in this study is consistent with the findings of a small number of other studies. Firstly, Morse et al. (1996) observed that, in some instances, treatments with fragments of *L. variegata* promoted first stage elongation of larvae from seven acroporid corals, even though larvae did not settle on the *L. variegata,* which was used as a control to investigate coral settlement on crustose coralline algae. Nonetheless, since first stage elongation of coral larvae precedes substrate testing and settlement (Harrison and Wallace 1990), these results suggest that *L. variegata* was inducing at least the first stages of settlement. Secondly, in a survey of the benthic biota surrounding coral recruits on inshore reefs of the Great Barrier Reef (Chapter 2), *L. variegata* was more frequently present and more abundant surrounding coral recruits than in background communities. Thirdly, the settlement inducer associated with *Hydrolithon reinboldii* is believed to be an insoluble carbohydrate present on the surface of the alga (Morse and Morse 1991, Morse et al. 1996), but larvae in my *Lobophora variegata* treatment displayed *substrate testing* responses immediately, and thus before they physically encountered *Hydrolithon reinboldii* surfaces, suggesting a waterborne influence not associated with *H. reinboldii*.

The limited capability of any experimental system to simulate field conditions means that extrapolation of these results to impacts on reefs should be qualified. Firstly, larvae had no alternative but to settle under experimental treatment conditions because they were restricted to confined volumes of water (petri dishes). In the field, coral larvae actively search the reef benthos before settling and can delay settlement to maximise chances of finding a suitable microhabitat (Harrison and Wallace 1990, Pawlik 1992, Raimondi and Morse 2000). However, if larvae fail to encounter suitable microhabitats, there is evidence they can metamorphose in sub-optimal conditions and even without a surface to settle on (reviewed in Harrison and Wallace, 1990). Thus, potentially more coral larvae settled under the deleterious effects of *Chlorodesmis fastigiata* in this experiment, because of lack of alternative microhabitats, than would settle close to the alga in the field. Secondly, there was no water circulation in experimental treatments, whereas water flow and hydrodynamics in the field can disperse and dilute waterborne chemical influences that affect invertebrate larvae (Pawlik 1992, Maida et al. 1994, 1995a, 1995b, Abelson and Denny 1997), as well as exchange resources and remove waste products (Vogel 1994). Thus chemical conditions in this experiment are likely to have been more homogenous than *in situ* and the effects more consistent.

4.4.1. Conclusion

In this study I have demonstrated, for the first time, that algae can influence coral settlement by means of waterborne chemical effects. This highlights an overlooked mechanism of coral-algae interaction with serious implications for coral recruitment on disturbed or degraded reefs, which are typically dominated by benthic algae. This study also shows that waterborne influences of algae on the behaviour and settlement of coral larvae are species-specific. The foliose brown alga *Lobophora variegata* (Lamouroux) enhanced settlement of *Acropora millepora* larvae by 50 % relative to control treatments. In contrast, the filamentous green alga *Chlorodesmis fastigiata* (C. Agardh - "Turtle weed") delayed coral settlement, indicating larvae would not settle close to *C. fastigiata* if provided with an alternative. However, *Padina sp.*, a foliose brown alga closely related to *Lobophora variegata*, had no apparent effect on coral settlement. The demonstration of waterborne effects by some algal species suggests that fleshy macroalgae have the potential to affect coral settlement before larvae reach the reef substrata, even on surfaces of a crustose coralline algae (*Hydrolithon reinboldii*) known to induce coral settlement, and even where the immediate settlement area is free of algal cover. Therefore, macroalgae that are present on degraded reefs as well as relatively “pristine” reefs may have previously unrecognised impacts on coral recruitment and thus on coral community recovery following disturbances.

Chapter 5: Early post-settlement survival and growth of *Acropora millepora* recruits in reef environments dominated by fleshy algae

5.1. Introduction

Algal turfs typically dominate degraded and disturbed coral reefs (Chapter 2), however assemblages of fleshy algae can develop from algal turfs and dominate reefs when herbivory is reduced (Hughes et al. 1987, 1999a, McCook 1999), or disputedly, when nutrients levels are enhanced (Lapointe 1997, Lapointe 1999). Thus, declines in herbivore populations through human overfishing and disease have facilitated the dominance of fleshy algae on many disturbed and degraded coral reefs worldwide (Hughes 1994a, Connell et al. 1997, McCook 1999, Wilkinson 2002). Moreover, assemblages of fleshy algae have hindered the recovery of disturbed coral populations by outcompeting remaining corals and fresh coral recruits (Hughes et al.1987. Hughes 1989, 1996, Connell 1997, Miller 1998, McCook et al. 2001), of which the latter is critical in facilitating the long-term decline of coral communities (Hughes and Tanner 2000). In particular, if coral recruits do not survive until they reach a reproductive size, they will fail to contribute to future generations of corals (Harrison and Wallace 1990, Hall and Hughes 1996). Therefore, it is important to understand the impact that assemblages of fleshy algae can have on coral recruitment and the survival and growth of juvenile corals, so that we can manage degraded reefs that are dominated by fleshy algae in ways that will facilitate the recovery of coral communities.

Until recently, investigations of the effects of fleshy algae on corals were generally “natural experiments”; studies in which treatments resulted from natural or semi-natural events in the environment (reviewed in McCook et al. 2001). For example, Jamaican coral reefs were widely dominated by fleshy algae after decades of reef degradation resulting from overfishing, sedimentation, eutrophication and pollution, combined with natural disturbances such as hurricane damage and mass-mortality of the herbivore, *Diadema antillarum* (Morrison 1988, Goreau 1992, Hughes 1994a). Taking advantage of this natural experiment, a number of studies found that widespread coral mortality freed substrata for algal colonisation (e.g. Goreau 1992), and that reduced herbivory (Hughes et al. 1999a and references therein), and/or arguably eutrophication (Lapointe 1997, 1999), enabled fleshy algal assemblages to outcompete remaining corals and even hinder coral recruitment (Hughes 1989, 1994a, 1996). However, the exact causes of reduced coral recruitment were unclear (Hughes and Tanner 2000). Interactions with fleshy algae may have reduced net coral recruitment through 1) reducing coral fertility and thus larval supply (Tanner 1995), 2) reducing coral settlement (Chapters 3 and 4), or 3) reducing survival of coral recruits (Hughes et al. 1987, Hughes 1989, 1996). Furthermore, given that survival of early life stages of corals can be hindered by stresses such as sedimentation (Rogers 1990, Babcock and Davies 1991, Gilmour 1999) and pollution (Negri and Heyward 2000, 2001, Negri et al. 2002), particularly when combined with algae (Chapter 3), it is not clear that coral recruitment was hindered solely by algae on Jamaican reefs. Therefore, to understand how fleshy algae can hinder coral recruitment requires experimental manipulations that separate potential factors (e.g. reduced grazing, pollution) and mechanisms (e.g. algal reduction of coral fertility, algal overgrowth of recruits) that may hinder coral recruitment in combination.

The logistical limitations of experimentally excluding herbivores from reefs has resulted in previous attempts at experimental field manipulations being either pseudo-replicated (Lewis 1986) or undertaken on spatial scales too small to reliably infer community effects (e.g. Miller and Hay 1996, McCook 1997). Thus studies that have previously investigated the effects of fleshy algae on coral recruitment provide limited insight into their effects on the survival and growth of coral recruits. Moreover, investigations of the effects of fleshy algae on coral recruits generally use coral recruits detected *in situ*, which for logistical reasons implies recruits are at least 5 mm in diameter (e.g. Bak and Engel 1979, Hughes et al. 1987, 1989, Babcock 1991). However, most coral recruits don’t reach detectable sizes *in situ* until at least 6 months of growth after settlement (Harrison and Wallace 1990, Babcock et al. 2003), thus very little is known about the impacts of fleshy algae on younger recruits, which are potentially two orders of magnitude smaller so may be susceptible to different influences.

A recent large-scale and replicated herbivore exclusion experiment by Hughes et al. (in progress) has used a novel design to overcome the problems of excluding herbivores from experimental plots on reefs. Large cages (5 m × 5 m × 6 m) and sides extending above high water levels, which made a cage ceiling unnecessary, reduced the effects of caging artefacts (e.g. reduced light and water flow). These cages provided a unique opportunity to test the impacts of fleshy algae on coral demographic processes (e.g. recruitment) *in situ* and at a community level. Moreover experimental manipulations were possible under field conditions of: 1) good water quality, by establishing the cages in a national park, which excluded the potential for eutrophication to promote fleshy algal dominance (e.g. Lapointe 1997, 1999), and 2) herbivore exclusion without the manipulation of other factors that might promote fleshy algal development or have adverse impacts on corals and other biota in the reef community.

In this study, I aim to investigate the effects of reef environments dominated by fleshy algae as a result of low herbivore densities, on coral recruits in their first four months following settlement. I specifically compare the survival and growth trajectories of newly settled *Acropora millepora* juveniles between large-scale experimental plots dominated by fleshy algae in herbivore exclusion cages and control plots composed of natural benthic communities without fleshy algae. This study has relevance for determining the impacts of overfishing and subsequent dominance of benthic communities by fleshy algae on the early survival of coral recruits. Understanding the mechanisms by which fleshy algae affect the survival and growth of the early life history stages of corals will provide important insights into: 1) the qualitative importance of algal impacts on different stages of coral recruitment (e.g. larval supply, settlement, early survival); 2) the potential and timescales for the recovery of degraded and disturbed coral reefs.

5.3. Methods

5.3.1. Study site

This study was conducted on the reef crest in Pioneer Bay, which is on the leeward side of Orpheus Island in the Central Section of the Great Barrier Reef Marine Park (18° 36.422’S, 146° 29.365’E; Figure 5.1). The site was selected because its highly protected status as a Marine Park B suggests that its herbivore populations and water quality should be relatively uncompromised by local human impacts. Coral cover at the site was relatively low (Figure 5.2) and dominant corals were massive *Porites spp*. (*P. australensis*, *P. lobata*, and *P. lutea*) and smaller favid colonies (particularly *Goniastrea retiformis*), whilst there were few *Acropora* colonies. Algal turf cover was extensive, and had developed on *in situ* dead corals and surfaces cleared of soft corals following the 1998 bleaching event (Berkelmans and Oliver 1999, Marshall and Baird 2000, Diaz-Pulido and McCook 2002). This algal turf cover provided a rich algal assemblage from which a fleshy algal assemblage could develop relatively quickly under a low grazing regime.

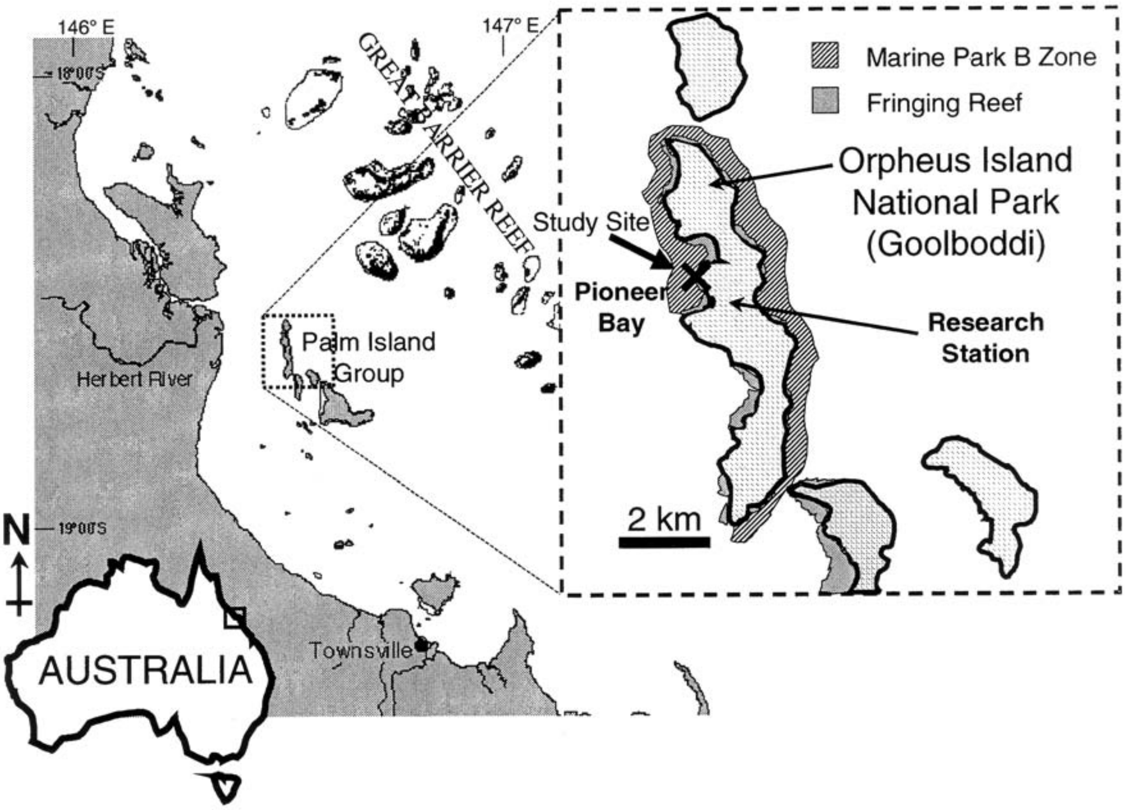

Figure 5.1. Study site on the reef crest in Pioneer Bay (18° 36.422’ S, 146° 29.365’ E) of Orpheus Island, located in the Palm Island Group on the Great Barrier Reef.

Figure 5.2. A) Large scale herbivore exclusion experiment established by Hughes et al. (in progress) at Orpheus Island. Cages have no top mesh and extend above the maximum annual tidal range. B) Environments dominated by fleshy algae inside the caged plots, C) environments with natural levels of algae inside the open plots.

The experimental design of the herbivore exclusion experiment involved replicate large plots (5 m × 5 m in basal area), which were fenced in January 2001 so that the tops of the fences extended above the high water level (Hughes et al. in progress, Figure 5.2). There were two types of controls; 1) partially caged plots, which were fenced on two sides and open on two sides (caging effect controls), and 2) open plots, which were simply marked with corner posts connected with a single wire (treatment controls). By the beginning of my study in December 2001, caged plots were dominated by fleshy algae in the genera *Sargassum* and *Padina* in contrast to the natural, unmanipulated algal communities in open and partially caged plots, which were dominated by algal turfs (L. McCook, pers. comm.). Smaller herbivores were able to access the caged plots through the caging mesh (2 cm), but it was assumed that their impact would be minimal in comparison to the impact of excluding larger herbivores (>2 cm in size).

5.3.2. Experimental design and approach

To investigate the effects of benthic assemblages dominated by fleshy algae on the survival and growth of coral recruits, I used a two-factor nested experimental design (Figure 5.3). The factor "algal dominance" was fixed and had two levels: plots dominated by fleshy algae (i.e. caged or ungrazed plots) and plots without fleshy algae but with natural levels of algae (i.e. uncaged or grazed plots). Four plots were nested within each level of algal dominance (plot: nested (random) factor). In each of these plots, I placed five panels of dead coral substrata (5 cm × 5 cm) upon the upper surface of which *Acropora millepora* recruits had settled. Larvae of *A. millepora* were raised and settled onto the panels in aquaria as outlined in Chapter 3. The number and location of *A. millepora* recruits were counted and mapped before the panels were placed in the experimental caged and uncaged plots.

The number of panels with coral recruits was limited, so it was not feasible to include the partially caged treatment in the design to test for caging artefacts without significantly compromising replication in the caged and open plot treatments. Because minimal caging artefacts have been found in the Hughes et al. study (T. Hughes, pers. comm.) and in previous experiments at the same location using the same caging mesh (McCook 1996, 1997, Jompa and McCook 2002a, 2002b), the benefits of retaining power to compare experimental treatments outweighed the benefits of including a partially caged treatment.

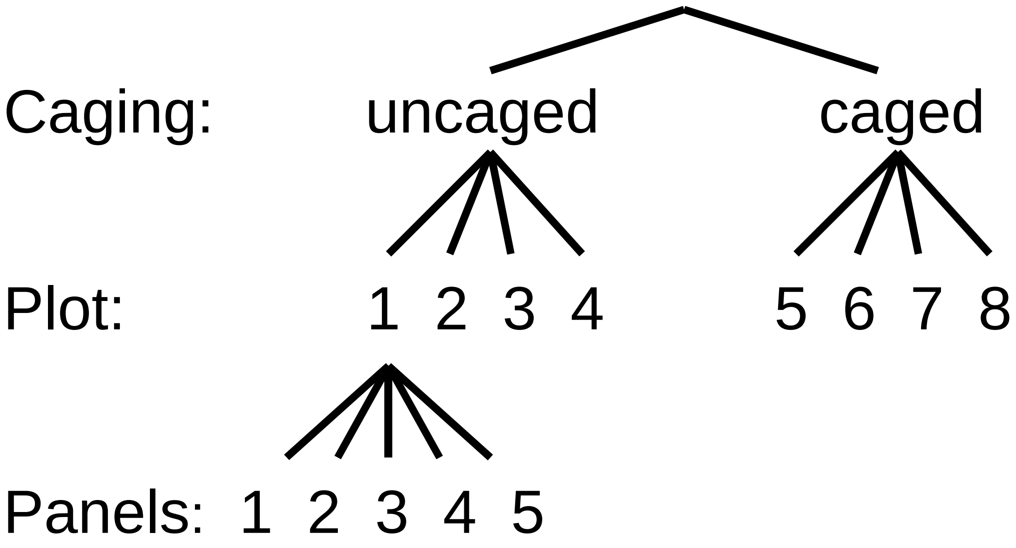

Figure 5.3. Experimental design to investigate the effects of reef environments dominated by fleshy algae on early post-settlement survival of the coral *Acropora millepora.*

5.3.3. Establishing and censusing the settlement panels

Five panels, each with an average of 15 coral recruits (± 1.5 SE), were randomly allocated to each of the four experimental and four control plots on substrata in between other ongoing experiments. Panels were bolted (with recruits upwards) to stainless steel plates attached to the substrata using masonry plugs (as per Hughes et al. 1999b, Mundy 2000). Panels were collected at 5-6 week intervals and transported under water to the Orpheus Island Research Station, where they were observed microscopically. Panels were censused and returned to the same bolts in the field within 24 hours.

5.3.4. Data analysis

Two response variables were recorded. The primary response variable was the percentage of recruits surviving at each observation relative to the original number of recruits. The secondary response variable was recruit size, measured as the total number of coral polyps per recruit. All observations were made using a dissecting microscope immediately after recruit settlement, and 40, 80 and 130 days after settlement.

To compare the survival of recruits between treatments, I used a nested ANOVA to compare the percentage of recruits surviving at 130 days after settlement and used graphs to compare recruit survival trajectories in each treatment. I used a one-way ANOVA to compare the size of 130-day old recruits between caged and uncaged treatments. Given the low numbers of recruits that survived to 130 days, there was insufficient replication to investigate variability in growth of recruits separately within or among panels, so variability due to these factors was incorporated into the caging treatments. Thus, I used mean recruit size per plot (instead of mean size per panel or recruit) as replicates for the analysis. To calculate the mean recruit size per plot, I summed mean recruit size per panel (for panels with surviving recruits) and divided this by the number of panels. This analysis of recruit growth is conservative, as it reduces the power of the analysis by using less degrees of freedom (residual df=6) than would have been possible if the number of surviving recruits had been used.

To confirm that differences in the percent survival of recruits were not contributed to by randomly allocating panels with more recruits to one treatment relative to another, I compared the number of recruits on panels at the onset of the experiment using a nested ANOVA. A similar comparison was not necessary for coral recruit size, as all recruits were at the one polyp stage at the beginning of this study. All data were tested for homogeneity of variance (Cochran's C test, $\alpha=0.05$), outliers and independence and normality of residuals (graphically). Transformations of the data were not necessary.

5.4. Results

5.4.1. Survival of coral recruits

Survival of coral recruits in environments dominated by fleshy algae was consistently greater than recruit survival in environments without fleshy algae, moreover, the magnitude of this difference increased throughout the study (Figure 5.4). Overall, approximately half of the coral recruits survived for the first 40 days in both treatments, however approximately 10% more recruits survived in the experimental plots dominated by fleshy algae. Eighty days after settlement, survival of recruits was almost twice as great in plots dominated by fleshy algae (39% recruit survival) in comparison to plots without fleshy algae (23% recruit survival). Finally, at 130 days after settlement, almost three times as many recruits survived in plots dominated by fleshy algae (28% ± 4.8% SE) compared to plots without fleshy algae (11% ± 3.3% SE), a difference that was statistically significant ($p<0.027$, Table 5.1 A). Heterogeneity of the reef environment within plots had minimal effect on the survival of coral recruits, as indicated by a lack of statistical significance for the nested factor, plot ($p=0.65$, Table 5.1 A).

Numbers of coral recruits on panels placed in each experimental plot at the beginning of the study did not differ between either plots or treatments ($p=0.969$ and $p=0.536$ respectively, Table 5.1 C). Thus initial differences in the number of coral recruits on each panel contributed minimally, if at all, to differences in the survival of coral recruits between treatments. Furthermore, evidence of grazing damage on panels in either treatment was minimal, amounting to one bite mark on a panel in one of the open plots, possibly because larger grazers (e.g. *Scaridae*) were deterred by the wing nuts and bolts fastening the panels. However, the development of epilithic algal communities on panels in both the caged and open plots was controlled, as a result of grazing by smaller herbivores that could access the caged plots.

Table 5.1. Results of analysis of variance tests to compare the effects of abundant upright macroalgae on **A**. the survival and **B.** the growth of *A. millepora* recruits compared 130 days after settlement **C**. The number of recruits on surfaces at the onset of the experiment is also compared between surfaces randomly allocated to different treatments. Cochran's C tests results of the homogeneity of variance are presented. Data are not transformed. Details of designs, analysis and treatment effects are explained in the text.

Comparison	**Source**	**Mean-Square**	**df**	***F*-ratio**	***P* value**	**Conclusion**
A. Survival	Treatment	2880.167		8.493	**0.027**	Significant
	Plot(treatment)	339.134	6	0.702	0.650	Not significant
	Error	483.249	32			
	Cochrans' C test: C=0.249, Ccrit=0.391, Homogeneity of variance accepted					
B. Growth	Treatment	99.238	1	8.365	**0.028**	Significant
	Error	11.864	6			
	Cochrans' C test: C=0.700, Ccrit=0.939, Homogeneity of variance accepted					
C. Number of recruits/surface (day 0)	Treatment	10.0	1	0.430	0.536	Not significant
	Plot(treatment)	23.267	6	0.216	0.969	Not significant
	Error	107.575	32			
	Cochrans' C test: C=0.284, Ccrit=0.391, Homogeneity of variance accepted					

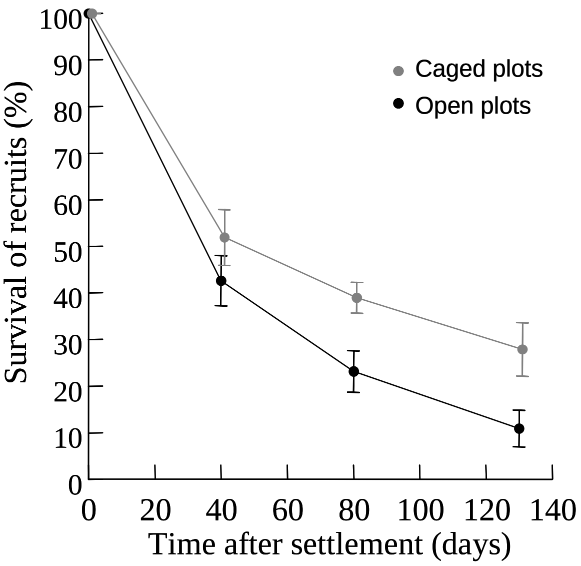

Figure 5.4. Graph showing trends in *A. millepora* recruit survival for 130 days after settlement in 1) caged plots with abundant upright macroalgae (primarily *Sargassum* and *Padina* species) (●, *i.e. grey lines)*; and 2) open plots with natural levels of macroalgae development (no upright macroalgae) (●, i.e. *black lines*). Observations were made at settlement (day 0) and 40, 80 and 130 days after settlement. Percent survival of recruits is relative to the number recruits which originally settled on each surface. Data are mean recruit survival ±SE for each treatment, calculated from the means of recruit survival for each of the four nested plots within each treatment.

5.4.2. Growth of coral recruits

Trajectories of coral recruit growth were similar in each treatment for up to 80 days after settlement, although mean recruit size was slightly larger (but only by approximately one polyp) in environments dominated by fleshy algae (Figure 5.5). The average size of coral recruits 40 days after settlement was 4 polyps (± 0.7 polyps SE) in plots dominated by fleshy algae and 2.9 polyps (± 0.5 polyps SE) in plots without fleshy algae. By 80 days after settlement, the average size of coral recruits had approximately doubled (8.3 ±1.2 polyps SE) in plots dominated by fleshy algae, whereas the average size of recruits in plots without fleshy algae was 6.9 polyps (± 0.7 polyps SE). Finally, between 80 and 130 days after settlement, the average size of coral recruits more than doubled again in plots dominated by fleshy algae (20.7 ± 2.8 polyps SE). In contrast, at

130 days after settlement the average size of coral recruits in plots without fleshy algae (7.7 polyps ± 0.7 polyps SE) remained relatively unchanged compared to observations made at 80 days after settlement. Thus coral recruits in treatments dominated by fleshy algae were nearly triple the size of coral recruits in treatments without fleshy algae at the end of the study (p=0.028, Table 5.1 B).

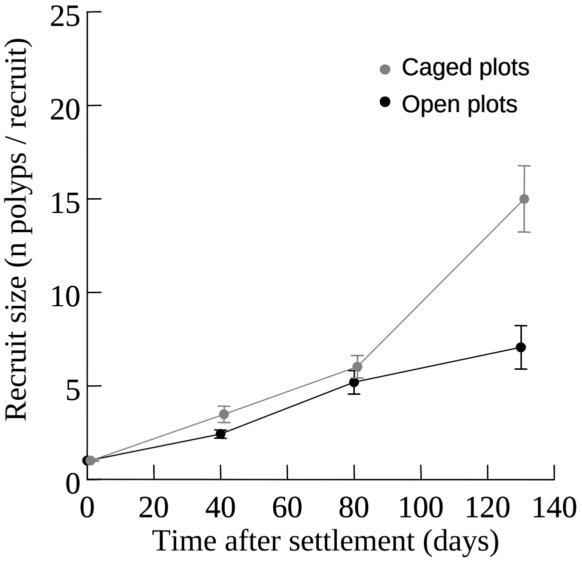

Figure 5.5. Graph showing trends in *A. millepora* recruit growth for 130 days after settlement in 1) caged plots with abundant upright macroalgae (primarily *Sargassum* and *Padina* species) (●*, i.e. grey lines)*; and 2) open plots with natural levels of macroalgae development (no upright macroalgae) (●, i.e. *black lines*). Observations were made at settlement (day 0) and 40, 80 and 130 days after settlement. Size of coral recruits is measured by the number of polyps and all recruits were only one polyp at settlement. Data are the means and standard error of recruit size. The four replicates for each treatment are the mean values for each nested plot (within treatment) as explained in the text.

5.5. Discussion

This study has shown that survival of newly settled *Acropora millepora* on fleshy algal dominated reef crests is consistently greater than on reef crests with turfing algae assemblages more typical of normal herbivore population densities, at least for the first four months following settlement at Orpheus Island in the summer of 2003 (Figure 5.4). Furthermore, coral recruits were also consistently larger in reef environments dominated by fleshy algae, growing to nearly triple the size of recruits in reef environments without fleshy algae within 130 days of settlement (Figure 5.5). Therefore, this study suggests that reef crest environments dominated by fleshy algae, as a consequence of depleted herbivore populations, may be more favourable (or less detrimental) to the survival and growth of young coral recruits than environments with natural levels of herbivores and algae. Initially, the results of this study appear to be inconsistent with those of previous studies that report reduced survival of coral recruits (Hughes et al. 1987, Hughes 1989, 1996) and reduced growth of established coral colonies (Tanner 1995) as a result of interactions with fleshy algae or in environments dominated by fleshy algae. However, there are several aspects of this study that differ to those of previous studies, highlighting that coral-algal interactions are complex and may vary with a number of life history and environmental factors, as discussed more fully below.

Patterns of greater recruit survival in plots dominated by fleshy algae are unlikely to have been the result of reduced grazing damage in the caged plots, given that grazer damage to experimental panels was similarly minimal or non-existent in the uncaged, control plots. Previous studies have reported damage and even the complete removal of coral recruits as a result of herbivores grazing on algae surrounding them (Brock 1979, Sammarco 1980, Rylaarsdam 1983, Miller and Hay 1998). However, two factors suggest that grazer damage to the recruits may have been similar in both experimental treatments. First, panels in the caged plots were not completely ungrazed as smaller herbivores could access the cages through the mesh, and secondly, it is possible that wing-nuts protruding above the panels deterred larger herbivores (e.g. *Scaridae*) from grazing on panels in the open plots by obstructing bite access. In addition, the greater growth of coral recruits in plots dominated by fleshy algae compared to plots without fleshy algae further indicates that the former represented a more favourable, or at least less stressful, growth environment for the young recruits (Meesters et al. 1994, Hall 1997).

The result that survival and growth of coral recruits was greater in environments dominated by fleshy algae is consistent with a few previous studies that have observed greater coral survival and calcification in environments dominated by fleshy algae (reviewed in McCook et al. 2001). Firstly, Jompa and McCook (1998) observed less bleaching on established corals shaded by *Sargassum spp*. canopies compared to nearby unshaded corals. Given that elevated seawater temperatures and a significant mass-bleaching event were observed on the Great Barrier Reef between January and March of 2002 (http://www.gbrmpa.gov.au, Berkelmans et al. in press), it is possible that coral recruits also benefited from shade provided by fleshy algae canopies in this study. However, no significant coral bleaching was observed at the experimental sites or in the vicinity of this study (T. Hughes pers. comm.). Secondly, McConnaughey et al. (2000) found that non-calcareous fleshy algae stimulated coral calcification by increasing the alkalinity:acidity ratio of seawater, which affects the efficiency of CO_2 generation required for coral calcification. Thus, it is possible that fleshy algae stimulated calcification of coral recruits in this study, accounting for the greater growth of coral recruits in the plots dominated by fleshy algae.

The patterns of coral recruit survival and growth that were observed in this study could be specific to the small size that recruits achieve within 4 months of settlement (<5 mm diameter). The small size of recruits reduced their chances of being overgrown and abraded by contact with the fleshy algae, *Sargassum spp*. and *Padina spp*., the species that dominated the caged plots (e.g. Jackson 1979, Steneck and Dethier 1994). These algae have relatively small holdfasts and upright morphologies and are not known to produce allelochemicals that affect corals (McCook et al. 2001, but see Walters et al. 1996), thus overtopping or shading is the most likely mechanism by which they competed with coral recruits in this study (reviewed in Carpenter 1990, McCook et al. 2001). However, since light intensity in shallow waters can exceed levels required by corals, leading to photo-inhibition (Buddemeier and Kinzie III, 1976, Lesser 1996, 1997), shading may have a positive rather than a negative impact on small recruits. In addition, corals can adapt to low light intensity with changes in the concentrations of photosynthetic pigments, which reduces the chances of shade having negative impacts on recruits (Barnes and Chalker 1990). Furthermore, River and Edmunds (2001) observed slower growth rates in colonies of *Porites porites* that were shaded and abraded by *Sargassum spp.*, but detected no significant change in coral growth when corals were only shaded and not abraded. Thus, if fleshy algae primarily affected coral recruits with shade, the deleterious effects on coral recruits may have been minimal in this study.

The impacts of fleshy algae on patterns of recruit survival and growth observed in this study could be reversed as corals grow older and increase in size. Jackson (1979) predicted that as benthic organisms grow larger, they are more likely to encounter and interact with other benthic organisms, thus abrasion and overgrowth of coral recruits by fleshy algae is more likely as they grow larger. The recruits in this study are smaller than recruits investigated in other studies, because the latter have been “natural experiments” that detected the impacts of fleshy algae on *in situ* recruits larger than 5 mm in diameter (e.g. Hughes 1989, 1996, reviewed in Harrison and Wallace 1990, McCook et al. 2001). Furthermore, reversals in the survival and growth patterns of coral recruits have been observed in coral recruits approximately 4 months after settlement (Babcock and Mundy 1996), which coincides with the end of this study and precedes observations in studies that detected recruits *in situ* (e.g. Hughes 1989, 1996). Therefore the results of this study are specific to newly settled coral recruits, and complement rather than contradict those of previous studies that have found that fleshy algae reduce the survival and growth of older coral recruits and established corals (e.g. Hughes 1989, 1996, Tanner 1995).

5.5.1. Conclusion

In conclusion, this study has found that the survival and growth of *Acropora millepora* recruits, up to four months after settlement, can be greater in environments dominated by fleshy algae (*Sargassum spp.* and *Padina spp.*), particularly when seawater temperatures are elevated. These findings contradict the paradigm that fleshy algae generally have deleterious impacts on corals and illustrate that the outcomes of coral-algae interactions can vary with life history stage and size of corals, species-specific influences of the algae, and with environmental factors. Furthermore, my results emphasise that the context of reef degradation is important in determining the outcome of coral recruit-algae interactions, because in my study reef degradation resulted from the exclusion of large (> 2cm) herbivores and predators alone (i.e. “overfishing”), whereas in other studies of coral recruit-algae interactions reefs are potentially degraded by several factors (e.g. sedimentation, overfishing, pollution).

Chapter 6. General Discussion

6.1. Algal associations with coral recruits on inshore reefs of the Great Barrier Reef

Surveys of benthic organisms close to versus distant from algal recruits on inshore reefs of the Great Barrier Reef (GBR) suggest that corals generally recruit into habitats dominated by algal turfs, and to a lesser extent into habitats dominated by crustose coralline algae and the brown alga *Lobophora variegata*. These algae were more abundant close to coral recruits than distant from recruits regardless of the regional differences that existed between the reefs surveyed (e.g. latitude, terrestrial run-off impacts, Chapter 2). Thus, I suggest these algae promoted successful coral recruitment to a greater extent than other benthic biota (e.g. soft corals, hard corals, sponges), although the surveys don’t distinguish whether they actually enhanced coral recruitment or merely hindered it less than other biota, such as hard and soft corals. Other algae were also observed close to coral recruits but were less frequent and less abundant. Nonetheless, some were identified that potentially favoured coral recruitment (*Amphiroa spp*. *Dictyota spp*. *Turbinaria spp*. and Cyanophyta) or hindered coral recruitment (*Padina spp*., *Laurencia spp*., *Peyssonnelia spp*., and *Chnoospera spp*.). Despite trends for these algae to favour or hinder coral recruitment, the algal dominance of microhabitats where corals recruited indicates that to understand coral recovery processes on inshore reefs, experimental manipulations are required to identify mechanisms by which these algae influence coral settlement and the early stages of coral recruitment.

6.2. Algal impacts on coral settlement and the implications for the recovery of degraded and disturbed reefs

As a result of the association found between coral recruits and algal turfs (Chapter 2), I investigated impacts of algal turfs on coral settlement and found that sediments combined with algal turfs reduced coral settlement, but the effects of different algal turfs varied (Chapter 3). A newly established (<6 weeks growth) and relatively ungrazed algal turf reduced coral settlement in its own right. In contrast, a well-established (up to 3 years) and grazed algal turf only reduced coral settlement when combined with sediments. Since algal turfs had been established on *in situ* dead corals following the 1998 bleaching event, these results provide a good indication of mechanisms that influence coral settlement on degraded reefs following disturbances such as mass-bleaching events or crown-of-thorns starfish outbreaks (Price 1975, McClanahan et al. 2001, Diaz-Pullido and McCook 2002). However, the result that an ungrazed algal turf, even though it was newly established, hindered coral settlement in its own right, whereas a grazed algal turf that was well established did not hinder coral settlement, highlights the importance of grazing in mediating the impacts of algae on coral recruitment. Therefore, my results suggest it is most likely that algal turfs reduce coral settlement on reefs in high sediment environments and on reefs where grazing is low, perhaps as a result of overfishing or disease (e.g. Hughes 1994a).

In Chapter 4, I demonstrated that one fleshy brown alga can enhance coral settlement (*Lobophora variegata*), whilst another had no effect on coral settlement (*Padina sp.*), and that a green alga can delay, thus potentially hinder coral settlement (*Chlorodesmis fastigiata*) with waterborne chemical influences. Furthermore, the influences of these algae affected coral settlement on the crustose coralline alga *Hydrolithon reinboldii*, which is known to induce coral settlement (Morse et al. 1996). Therefore, coral settlement may be determined by several algae in a benthic assemblage, and not solely by the presence of the few, primarily calcareous red algae that can induce coral settlement (Morse et al. 1988, 1996, Heyward and Negri 1999). Waterborne chemical influences (including allelopathy) of algae on coral settlement has not been demonstrated before, even though they are reported for many other invertebrates (reviewed in Pawlik 1992, Steinberg et al. 2001, 2002, Steinberg and de Nys 2002), thus these findings have added another level of complexity to the understanding of coral recovery on degraded and disturbed reefs. My results indicate that algae can affect coral settlement through waterborne influences, thus before larvae reach the reef substrata and even where the immediate area of settlement is free of algae. This may be one of the reasons algal phase shifts can be relatively stable and associated with the long-term demise of coral populations (e.g. Hughes 1994a, Hughes and Tanner 2000). However, the species-specific influences observed for *Lobophora variegata* and *Chlorodesmis fastigiata*, and the lack of influence observed for *Padina sp.*, indicates that there may be considerable heterogeneity of waterborne chemical influences on coral settlement from algal assemblages. My study has furthered understanding of coral recruitment and reef recovery processes by demonstrating waterborne chemical influences from algae can affect coral settlement. Nonetheless, more experimental manipulations to identify chemical influences of algae characteristic of degraded reefs (other than the three algae of my study) are required to facilitate management of reef recovery processes.

The results of Chapters 3 and 4 provide evidence that benthic algae which are not competitively superior to established corals, specifically filamentous algal turfs and the filamentous alga *Chlorodesmis fastigiata* (McCook 2001, McCook et al 2001, Jompa and McCook 2003a, 2003b), can hinder coral settlement. Thus, these algae may prevent or slow down coral recovery following disturbance, facilitating algal dominance on such reefs (see reviews McCook 1999, McCook et al. 2001). Furthermore, the finding that algal turfs are more likely to hinder coral settlement if combined with sediments is consistent with reports that multiple stresses can lead to the failure of reef recovery (Connell 1997, Hughes and Connell 1999). Thus, to understand the recovery potential of degraded and disturbed reefs it is important to identify the mechanisms of algal influence on coral recruitment, bearing in mind that several may affect coral recruitment simultaneously even from a single alga (e.g. abrasion, chemical influences, shading), and that outcomes of algal influence on coral recruitment may differ for different coral life stages (e.g. settlement, early recruit survival).

The result that waterborne chemical influences from benthic algae affected the settlement of coral larvae on a crustose coralline alga (*Hydrolithon reinboldii*) known to induce coral settlement (Chapter 4), indicates that influences from the benthic community surrounding the surface upon which corals settle may also control rates of coral settlement. Thus knowledge of the distribution of algae known to induce coral settlement (e.g. *Hydrolithon reinboldii*; Morse et al. 1996) may provide limited insight into the potential for coral settlement unless the distributions of benthic biota that can have waterborne influences on coral settlement are also known. However, surprisingly few such biota have been identified, and these include the algae *Lobophora variegata*, *Chlorodesmis fastigiata* (Chapter 4), and potentially *Dictyota spp*., and *Laurencia spp*. (Chapter 2), the soft corals *Sinularia flexibilis* and *Sarcophyton glaucum* (Maida et al. 1995a, 1995b) and the hard coral *Tubastrea faulkneri* (Koh and Sweatman 2000). Therefore, this area of chemical marine ecology requires investigations to identify biota that can hinder or promote coral settlement if the distribution of suitable settlement surfaces for corals is to be used to manage or understand coral recovery processes.

6.3. Algal impacts on the survival of coral recruits and implications for the recovery of degraded and disturbed reefs

The findings that algal turfs dominate the microhabitats where coral recruits are found (Chapter 2) and that filamentous algae turfs can hinder coral settlement (Chapter 3), raise the question: "How do algal turfs affect coral recruit survival?" Theoretically algal turfs can overgrow, shade, abrade and have allelopathic effects on coral recruits (reviewed in McCook et al. 2001). However, factors that influence the fitness of either corals (e.g. sedimentation, pollution) or algae (e.g. herbivory) may determine the relative competitiveness of coral recruits and algal turfs, and thus the outcomes of their interactions (e.g. McCook 1999, McCook et al. 2001). For example, Littler and Littler (1997a) reported both coral recruits overgrowing algal turfs and algal turfs overgrowing coral recruits. However, McCook (2001) experimentally determined that the massive coral *Porites lobata* was competitively superior to algal turfs and Diaz-Pulido and McCook (2002) experimentally demonstrated that algal turfs only established on dead coral surfaces and not on live coral surfaces. Nonetheless, this outcome could be reversed if environmental stresses (e.g. high temperatures, sedimentation) reduce coral fitness. For example, sediments stress corals (e.g. Rogers 1990) and tend to accumulate in algal turfs (Purcell 2000), thus increasing the ability of algal turfs to smother and overgrow coral recruits and other organisms such as crustose coralline algae (Steneck 1997, Smith et al. 2001). Finally, the taxonomic composition of algal turfs can also be important in determining impacts on coral recruit survival. For example, Jompa and McCook (2003a, 2003b) investigated the effects of mixed algal turfs on massive *Porites* *spp.* corals, but singled out the filamentous alga *Anotrichium tenue* as, solely, it could damage or kill coral tissue allelopathicaly whilst overgrowing the coral, yet mixed algal turf assemblages did not overgrow corals. Therefore environmental stresses (e.g. sedimentation) and the presence of specific algal taxa (e.g. *Anotrichium tenue*) could enable algal turfs to kill coral recruits, whilst in general algal turfs may have less severe impacts on coral recruits resulting in the frequent association of coral recruits with algal turfs (Chapter 2).

In Chapter 5, survival and growth of *Acropora millepora* recruits up to 4 months after settlement were favoured in reef environments dominated by fleshy algae (principally *Sargassum spp*. and *Padina spp*.) that developed from algal turf assemblages over less than twelve months of reduced grazing. Nonetheless, my study of early recruit survival and growth was undertaken in a protected reef environment (Marine Park Zone B) with few human related impacts (e.g. pollution, nutrient inputs, elevated sediment stress) at a time when elevated seawater temperatures caused corals to bleach throughout much of the Great Barrier Reef (Berkelmans et al. in press). Other studies of coral recruit survival on reefs dominated by fleshy algae (Jamaican reefs), as a results of factors such as pollution, sedimentation, and nutrient inputs (Goreau 1992, Hughes 1994a, Lapointe 1997) have attributed the cause of failed coral recruit survival to reef dominance by fleshy algae (e.g. Hughes et al. 1987, Hughes 1989, 1996). The contrast in coral recruit survival between my study and these other studies suggests that abnormally high temperatures constitute an additional environmental stress which plays an important role in determining the outcome of coral recruit survival in reef environments dominated by fleshy algae.

Differences in recruit survival between my study (Chapter 5) and others that found reduced coral recruit survival on reefs dominated by fleshy algae (e.g. Hughes et al. 1987, Hughes 1989, 1996) also suggest that the size of coral recruits involved and the specific algae involved determine the mechanisms of coral recruit-algae interaction and the outcome of coral recruit survival. As a result of their relatively small size (<5 mm diameter) the coral recruits in my study were less likely to physically encounter benthic algae and thus be overgrown or abraded (see review by Jackson 1979) compared to larger recruits (> 5mm diameter) in other studies (e.g. Hughes et al. 1987, Hughes 1989, 1996). Thus in my study mechanisms of coral recruit-algal interaction most likely to reduce recruit survival (e.g. abrasion and overgrowth of the coral recruits) were less likely, in particular as *Sargassum spp*. and *Padina spp*. are relatively upright and have relatively small holdfasts. Although *Sargassum spp*. and *Padina spp*. were also present on degraded Jamaican reefs, the composition of other algae (e.g. *Dictyota spp*., *Laurencia spp*., *Lobophora spp*.) was also relatively high (Hughes et al. 1987, Hughes 1994a, Steneck 1994). These algae are less upright than *Sargassum spp*. and *Padina spp.* thus are more likely to overgrow or abrade small coral recruits as a result of their morphology (reviewed in McCook et al. 2001). Moreover, several algae of the genera *Dictyota* and *Laurencia* are known to have allelopathic effects (Paul et al. 2001, Van Alstyne et al. 2001, Cronin 2001), which suggests these algae are likely to reduce coral recruit survival. Thus, the different features of both the coral recruits and the algae involved in interactions, as well as the abnormal seawater temperatures are likely to explain differences in coral recruit survival.

6.4. Summary

My initial survey indicated that on inshore reefs of the Great Barrier Reef corals may have no alternative but to recruit into habitats dominated by algae, in particular algal turfs, crustose coralline algae, and the brown alga *Lobophora variegata*, which were more abundant close to coral recruits versus distant from recruits. These positive associations with coral recruits suggest these algae either favour coral recruitment or hinder coral recruitment less than other biota, such as soft corals and hard corals. Subsequently, I experimentally investigated the impacts of key algae (e.g. algal turfs, *Lobophora variegata*) on coral recruitment. First I found that sediments in algal turf assemblages reduced coral settlement but the effects of algal turfs differed. A newly established (<6 weeks growth) and relatively ungrazed algal turf reduced coral settlement in its own right. In contrast, a well established (up to 3 years) and grazed algal turf only reduced coral settlement when combined with sediments. Secondly, I demonstrated waterborne chemical influences from algae on coral settlement and that these affected settlement even on the crustose coralline alga *Hydrolithon reinboldii*, which is known to induce coral settlement. Moreover the influences were species-specific, the brown alga *Lobophora variegata* enhanced coral settlement whilst another brown alga (*Padina sp*.) had no discernible effect on coral settlement, and the filamentous green alga *Chlorodesmis fastigiata* delayed coral settlement, indicating intermediate deleterious effects. Finally, I found coral recruits survived and grew more up to four months after settlement amidst fleshy algae assemblages that had developed from ungrazed algal turfs, and when seawater temperatures were elevated, thus contradicting the paradigm that fleshy algae generally hinder coral recruitment. My research suggests that environmental stresses that operate simultaneously and at larger spatial scales (e.g. sedimentation, elevated sea temperatures) to mechanisms of direct algal influence on coral recruitment can alter the outcome of algal impacts on coral settlement and recruit survival. Therefore, to determine the recovery potential of a degraded reef we must consider the specific algae present and how they influence different stages of coral recruitment (e.g. larval settlement, early survival), whilst also considering the environmental context and that several mechanisms of algal influence, even from one alga, may simultaneously determine the outcome of coral recruitment.

Bibliography

Abelson, A., and Denny, M. (1997). Settlement of marine organisms in flow. *Annu. Rev. Ecol. Syst.* **28**:317-339.

Aceret, T. L., Sammarco, P. W., and Coll, J. C. (1995). Toxic effects of alcyonacean diterpenes on scleractinian corals. *J. Exp. Mar. Biol. & Ecol.* **188**:63-78.

Adey, W. H. (1998). Coral reefs: Algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. *J. Phycol.* **34**:393-406.

Airoldi, L. (1998). Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. *Ecology* **79**:2759-2770.

Airoldi, L. (2000). Effects of disturbance, life histories, and overgrowth on coexistance of algal crusts and turfs. *Ecology* **81**:798-822.

Amsler, C. D., Reed, D. C., and Neushel, M. (1992). The microclimate inhabited by macroalgal propagules. *J. Brit. Phycol. Soc.* **27**:253-270.

Arnold, T. M., and Targett, N. M. (1998). Quantifying in situ rates of phlorotannin synthesis and polymerization in marine brown algae. *J. Chem. Ecol.* **24**:577-595.

Arnold, T. M., and Targett, N. M. (2000). Evidence for metabolic turnover of polyphenolics in tropical brown algae. *J. Chem. Ecol.* **26**:1393-1410.

Babcock, R. (1991). Comparative demography of three species of scleractinian corals using age and size-dependent classifications. *Ecol. Monogr.* **61**:225-244.

Babcock, R., Baird, A., Piromvaragorn, S., Thomson, D. P., and Willis, B. L. (2003). Identification of Scleractinian coral recruits from Indo-Pacific Reefs. *Zool. Stud.* **42**:1-15.

Babcock, R., and Davies, P. (1991). Effects of sedimentation on settlement of *Acropora millepora*. *Coral Reefs* **9**:205-208.

Babcock, R., and Heyward, A. J. (1986). Larval development of certain gamete-spawning scleractinian corals. *Coral Reefs* **5**:111-116.

Babcock, R., and Mundy, C. (1996). Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinian corals. *J. Exp. Mar. Biol. & Ecol.* **206**:179-201.

Baird, A. H., Babcock, R., and Mundy, C. P. (2003). Habitat selection by larvae influences the depth distribution of six common coral species. *Mar. Ecol. Prog. Ser.* **252**:289-293.

Baird, A. H., and Hughes, T. P. (2000). Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understory assemblages. *J. Exp. Mar. Biol. & Ecol.* **251**:117-132.

Bak, R. P. M., and Engel, M. S. (1979). Distribution, Abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Mar. Biol.* **54**:341-352.

Barnes, D. J., and Chalker, B. E. (1990). Calcification and photosynthesis in reef-building corals and algae. Pages 109-132 *in* Dubinsky, Z., editor. *Ecosystems of the world 25: Coral Reefs*. Elsevier, New York 109-132.

Bellwood, D. R., and Hughes, T. P. (2001). Regional-scale assembly rules and biodiversity of coral reefs. *Science* **292**:1532-1534.

Berkelmans, R., De'ath, G., Kininmonth, S., and Skirving, W. J. (in press). A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: Spatial correlation, patterns and predictions. *Coral Reefs*.

Berkelmans, R., and Oliver, J. K. (1999). Large-scale bleaching of corals on the Great Barrier Reef. *Coral Reefs* **18**:55-60.

Berner, T. (1990). Coral-Reef Algae. Pages 253-264 *in* Dubinsky, Z., editor. *Ecosystems of the World 25: Coral Reefs*. Elsevier, Amsterdam253-264.

Birkeland, C. (1977). The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Pages 15-21 *in* 3rd Int Symp Corals Coral Reefs Proc, Miami.

Brock, R. E. (1979). An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. *Mar. Biol.* **51**:381-388.

Brown, B. E. (1997). Disturbances to reefs in recent times. Pages 354-378 *in* Birkeland, C., editor. *Life and Death of Coral Reefs*. Chapman & Hall, New York354-378.

Brown, B. E., and Howard, L. S. (1985). Assessing the effects of "Stress" on reef corals. *Adv. Mar. Biol.* **22**:1-63.

Bryant, D., Burke, L., McManus, J., and Spalding, M. (1998). 'Reefs at risk: a map-based indicator of the threats to the world's coral reefs'. World Resources Institute, International Center for Living Aquatic Resources Management, World Conservation Monitoring Centre, and United Nations Environment Programme, Washington D.C.

Buddemeier, R. W., and Kinzie III, R. A. (1976). Coral Growth. *Ocean. Mar. Biol. Ann. Rev.* **14**:183-225.

Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P., and Menge, B. A. (1996). Recruitment and the local dynamics of open marine populations. *Ann. Rev. Ecol. & Syst.* **27**:477-500.

Carpenter, R. C. (1990). Competition between marine macroalgae: a physiological perspective. *J. Phycol.* **26**:6-12.

Carpenter, R. C., Hackney, J. M., and Walter, A. H. (1991). Measurements of primary productivity and nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow. *Limn. Ocean.* **36**:40-49.

Carpenter, R. C., and Williams, S. L. (1993). Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral fore reef environment. *Limn. Ocean.* **38**:687-694.

Cheroske, A. G., Williams, S. L., and Carpenter, R. C. (2000). Effects of physical and biological disturbances on algal turfs in Kaneohe Bay, Hawaii. *J. Exp. Mar. Biol. & Ecol.* **248**:1-34.

Chung, H. Y., Ma, W. C. J., Ang, P. O., Kim, J. S., and Chen, F. (2003). Seasonal variations of bromophenols in brown algae (*Padina arborescens, Sargassum siliquastrum, and Lobophora variegata*) collected in Hong Kong. *J. Agric. Food Chem.* **51**:2619-2624.

Clare, A. S. (1996). Marine natural product antifoulants: status and potential. *Biofouling* **9**:211-229.

Connell, J. H. (1997). Disturbance and recovery of coral assemblages. *Coral Reefs* **16 Suppl.**:S101-113.

Connell, J. H., Hughes, T. P., and Wallace, C. C. (1997). A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol. Monogr.* **67**:461-488.

Cronin, G. (2001). Resource allocation in seaweeds and marine invertebrates. Pages 325-353 *in* McClintock, J. B. and Baker, B. J., editors. *Marine Chemical Ecology*. CRC Press, Boca Raton, Florida 325-353.

Crossland, C. J. (1981). Seasonal growth of *Acropora cf. formosa* and *Pocillopora damicornis* on a high latitude reef (Houtman Abrolhos, Western Australia). Pages 663-668 *in* Proceedings of the Fourth International Coral Reef Symposium, Manila.

de Nys, R., and Steinberg, P. D. (1999). Role of secondary metabolites from algae and seagrasses in biofouling control. Pages 223-244 *in* Fingerman, M., Nagabhushanam, R., and Thompson, M.-F., editors. *Recent advances in marine biotechnology, Vol. III*. Science Publishers, Enfield, New Hampshire223-244.

de Ruyter van Steveninck, E. D., Van Mulekom, L. L., and Breeman, A. M. (1988). Growth inhibition of *Lobophora variegata* (Lamouroux) Womersley by *scleractinian* corals. *J. Exp. Mar. Biol. & Ecol.* **115**:169-178.

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

Done, T. J. (1983). Coral zonation: its nature and significance. Pages 107-147 *in* Barnes, D. J., editor. *Perspectives on coral reefs*. Brian Clouston Publisher, Townsville107-147.

Done, T. J. (1992). Phase shifts in coral communities and their ecological significance. *Hydrobiologia* **247**:121-132.

Duggins, D. O., Eckman, J. E., and Sewell, A. T. (1990). Ecology of understory kelp environments. II effects of kelps on recruitment of benthic invertebrates. *J. Exp. Mar. Biol. & Ecol.* **143**:27-45.

Eckman, J. E., Duggins, D. O., and Sewell, A. T. (1989). Ecology of an understory kelp environment: I. effects of kelps on flow and particle transport near the bottom. *J. Exp. Mar. Biol. & Ecol.* **129**:173-187.

Engelhardt, U., Miller, I., Lassig, B. R., Sweatman, H., and Bass, D. (1997). Crown-of-thorns starfish (*Acanthaster planci*) populations in the Great Barrier Reef World Heritage Area: status report 1995-1996. Pages 158-184 *in* State of the Great Barrier Reef World Heritage Area Workshop, Townsville.

Furnas, M. (2003). Catchments and corals: terrestrial run-off to the Great Barrier Reef. Australian Institute of Marine Science, Townsville.

Gilmour, J. (1999). Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral. *Mar. Biol.* **135**:451-462.

Gleason, M. G. (1996). Coral recruitment in Moorea, French Polynesia: the importance of patch type and temporal variation. *J. Exp. Mar. Biol. & Ecol.* **207**:79-101.

Goreau, T. J. (1992). Bleaching and Reef Community Change in Jamaica: 1951-1991. *Amer. Zool.* **32**:683-695.

Goreau, T. J., and Hayes, R. M. (1994). Coral bleaching and ocean "hot spots". *Ambio* **23**.

Hadfield, M. G. P., V.J. (2001). Natural chemical cues for settlement and metamorphosis of marine-invertebrate larvae. Pages 431-461 *in* McClintock, J. B.

B., B.J., editor. *Marine Chemical Ecology*. CRC Press, Boca Raton, Florida431-461.

Hall, R. V. (1997). Interspecific differences in the regeneration of artificial injuries on scleractinian corals. *J. Exp. Mar. Biol. & Ecol.* **212**:9-23.

Hall, V. R., and Hughes, T. P. (1996). Reproductive Strategies of Modular Organisms: Comparative studies of reef-building corals. *Ecology* **77**:950-963.

Harder, T., Lau, S. C. K., Dahms, H.-U., and Qian, P.-Y. (2002). Isolation of bacterial metabolites as natural inducers for larval settlement in the marine polychaete *Hydroides elegans* (Haswell). *J. Chem. Ecol.* **28**:2029-2044.

Harrison, P. L., and Wallace, C. C. (1990). Reproduction, Dispersal and Recruitment of scleractinian corals. Pages 133-207 *in* Dubinsky, Z., editor. *Ecosystems of the World 25: Coral Reefs*. Elsevier, Amsterdam133-207.

Hatcher, B. G. (1983). Grazing in coral reef ecosystems. Pages 164-179 *in* Barnes, D. J., editor. *Perspectives on coral reefs*. A.I.M.S., Townsville, Australia164-179.

Hatcher, B. G. (1990). Coral reef primary productivity: A hierarchy of pattern and process. *Trends Ecol. Evol.* **5**:149-155.

Hay, M., Pawlik, J., Duffy, J., and Fenical, W. (1989). Seaweed-herbivore-predator interactions: Host-plant specialization reduces predation on small herbivores. *Oecologia* **81**:418-427.

Hay, M. E. (1997). The ecology and evolution of seaweed-herbivore interactions on coral reefs. *Coral Reefs* **16 Suppl.**:S67-S76.

Heyward, A. J., and Negri, A. P. (1999). Natural Inducers for coral larvae metamorphosis. *Coral Reefs* **18**:273-279.

Hodgson, G. (1990). Sediment and the settlement of larvae of the reef coral *Pocillopora damicornis*. *Coral Reefs* **9**:41-44.

Hodgson, G. (1994). Letters: Coral Reef Catostrophe. *Science* **266**:1930-1931.

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Fresh. Res.* **50**:839-866.

Hughes, T. P. (1989). Community structure and diversity of coral reefs: the role of history. *Ecology* **70**:275-279.

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

Hughes, T. P. (1994b). Response to Hodgson (1994) and Ogden (1994). *Science* **266**:1932-1933.

Hughes, T. P. (1996). Demographic approaches to community dynamics: a coral reef example. *Ecology* **77**:2256-2260.

Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J. B. C., Kleypas, J. A., Marshall, P. A., Nystrom, M., Palumbi, S. R., Pandolfi J. M., Rosen, B., and Roughgarden, J. (2003). Climate change, human Impacts, and the resilience of coral reefs. *Science* **301**:929-933.

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Harriott, V. J., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, J. E., and Willis, B. L. (2002). Detecting regional variation using meta-analysis and large scale sampling: latitudinal patterns in recruitment. *Ecology* **83**:436-451.

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, J. E., and Willis, B. L. (1999b). Patterns of recruitment and coral abundance along the Great Barrier Reef. *Nature* **397**:59-63.

Hughes, T. P., and Connell, J. H. (1999). Multiple stressors on coral reefs : A long-term perspective. *Limn. Ocean.* **44**:932-940.

Hughes, T. P., and Jackson, J. B. C. (1985). Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.* **55**:141-166.

Hughes, T. P., Reed, D. C., and Boyle, M. (1987). Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *J. Exp. Mar. Biol. & Ecol.* **113**:39-59.

Hughes, T. P., Szmant, A. M., Steneck, R., Carpenter, R. C., and Miller, S. (1999a). Algal blooms on coral reefs: what are the causes? *Limn. Ocean.* **44**:1583-1586.

Hughes, T. P., and Tanner, J. E. (2000). Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* **81**:2250-2263.

Jackson, J. B. C. (1979). Morphological Strategies of Sessile animals. Pages 499-555 *in* Larwood, G. R., B. R., editor. *Biology and Systematics of colonial organisms*. Academic Press, London & New York499-555.

James, N. P., Wray, J. L., and Ginsburg, R. N. (1988). Calcification of encrusting aragonite algae (Peyssonneliaceae): implications for the origin of late Paleozoic reefs and cements. *J. Sed. Petrol.* **58**:291-303.

Jensen, A. (1977). Chemical conditioning of seawater by algal growth and development. Pages 329-336 *in* Faulkner, D. J., Fenical, W.H., editor. *Marine Natural Products Chemistry*. Plenum Press, New York329-336.

Jensen, P. R., Kauffman, C. A., and Fenical, W. (1996). High recovery of culturable bacteria from the surfaces of marine algae. *Mar. Biol.* **126**:1-7.

Jiang, Z. D., Jensen, P. R., and Fenical, W. (1999). Lobophorins A and B, new antiinflammatory macrolides produced by a tropical marine bacterium. *Bioorg. & Med. Chem. Let.* **9**:2003-2006.

Johnson, C. R., Lewis, R. E., Nichols, D.S., and Degnan, B.M. (1997).Bacterial induction of settlement and metamorphosis in marine invertebrates. 2 pp1219-1225 *in* 8th Int Symp Corals Coral Reefs Proc, Panama.

Johnson, C. R., Muir, D. G., and Reysenbach, A. L. (1991). Characteristic bacteria associated with surfaces of coralline algae: a hypothesis for bacterial induction of marine invertebrate larvae. *Mar. Ecol. Prog. Ser.* **74**:281-294.

Johnson, C. R., and Sutton, D. C. (1994). Bacteria on the surface of crustose coralline algaeinduce metamorphosis of the crown-of-thorns starfish *Acanthaster planci*. *Mar. Biol.* **120**:305-310.

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

Jompa, J., and McCook, L. J. (2002a). The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). *Limn. Ocean.* **47**:527-534.

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

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

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

Karlson, R. H. (1999). Dynamics of coral communities. Kluwer Academic Publishers, Dordrecht, Netherlands.

Koh, E. G. L., and Sweatman, H. (2000). Chemical warfare among scleractinians: bioactive natural products from *Tubastrea faulkneri* Wells kill larvae of potential competitors. *J. Exp. Mar. Biol. & Ecol.* **251**:141-160.

Krug, P. J., and Manzi, A. E. (1999). Waterborne and surface-associated carbohydrates as settlement cues for larvae of the specialist marine harbivore *Alderia modesta*. *Biol. Bul.* **197**:94-103.

Ktari, L., and Guyot, M. (1999). A cytotoxic oxysterol from the marine alga Padina pavonica (L.) Thivy. *J. App. Phycol.* **11**:511-513.

Lang, J. C., and Chornesky, E. A. (1990). Competition between scleractinian reef corals - a review of mechanisms and effects. Pages 209-252 *in* Dubinsky, Z., editor. *Coral reefs - Ecosystems of the World 25*. Elsevier, Amsterdam209-252.

Lapointe, B. E. (1997). Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefsin Jamaica and southeast Florida. *Limn. Ocean.* **42**:1119-1131.

Lapointe, B. E. (1999). Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs (Reply to the comment by Hughes et al.). *Limn. Ocean.* **44**:1586-1592.

Lesser, M. P. (1996). Elevated temperatures and ultraviolet radiation cause oxidative stress and inhibit photosynthesis on symbiotic dinoflagellates. *Limn. Ocean.* **41**:271-283.

Lesser, M. P. (1997). Oxidative stress causes coral bleaching during exposure to elevated temperatures. *Coral Reefs* **16**:187-192.

Lewis, S. M. (1986). The role of herbivorous fishes in the organisation of a carribbean reef community. *Ecol. Monogr.* **56**:183-200.

Littler, M. M. (1980). Morphological form and photosynthesis performances of marine macroalgae: tests of a functional/form hypothesis. *Bot. Mar.* **22**:161-165.

Littler, M. M., and Littler, D. S. (1980). The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Amer. Nat.* **116**:25-44.

Littler, M. M., and Littler, D. S. (1984). Models of tropical reef biogenesis: The contribution of algae. *Progr. Phycol. Res.* **3**:323-363.

Littler, M. M., and Littler, D. S. (1997a). Disease-induced mass mortality of crustose coralline algae on coral reefs provides rational for the conservation of herbivorous fish stocks. Pages 719-724 *in* 8th Int Symp Corals Coral Reefs Proc, Panama.

Littler, M. M., and Littler, D. S. (1997b). Epizoic red alga allelopathic (?) to a Caribbean coral. *Coral Reefs* **16**:168.

Littler, M. M., and Littler, D. S. (1999). Epithallus sloughing: a self-cleaning mechanism for coralline algae. *Coral Reefs* **18**:204.

Macintyre, I. G. (1997). Reevaluating the role of crustose coralline algae in the construction of coral reefs. Pages 725-730 *in* 8th Int Symp Corals Coral Reefs Proc, Panama.

Maida, M., Coll, J. C., and Sammarco, P. W. (1994). Shedding new light on scleractinian coral recruitment. *J. Exp. Mar. Biol. & Ecol.* **180**:189-202.

Maida, M., Sammarco, P. W., and Coll, J. C. (1995a). Effects of soft corals on scleractinian coral recruitment. I: directional allelopathy and inhibition of settlement. *Mar. Ecol. Prog. Ser.* **121**:191-202.

Maida, M., Sammarco, P. W., and Coll, J. C. (1995b). Preliminary evidence for directional allelopathic effects of the soft coral *Sinularia flexiblis*(Alcyonacea: Octocorallia) on scleractinian coral recruitment. *Bull. Mar. Sci.* **56**:303-311.

Marshall, P. A., and Baird, A. H. (2000). Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* **19**:155-163.

McClanahan, T. R. (2000). Bleaching damage and recovery potential of Maldivian coral reefs. *Mar. Pol. Bul.* **40**:587-597.

McClanahan, T. R., Muthiga, N. A., and Mangi, S. (2001). Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* **19**:380-391.

McConnaughey, T. A., Adey, W. H., and Small, A. M. (2000). Community and environmental influences on reef coral calcification. *Limn. Ocean.* **45**:1667-1671.

McCook, L. J. (1996). Effects of herbivores and water quality *Sargassum* distribution on the Great Barrier Reef: cross-shelf transplants. *Mar. Ecol. Prog. Ser.* **139**:179-192.

McCook, L. J. (1997). Effects of herbivory on zonation of *Sargassum sp.* within fringing reefs of the central Great Barrier Reef. *Mar. Biol.* **129**:713-722.

McCook, L. J. (1999). Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* **18**:357-367.

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

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

McCook, L. J., and Price, I. R. (1996). Macroalgal distributions on the Great Barrier Reef: a review of patterns and causes. Pages 38-46 *in* The Great Barrier Reef, Science, Use and Management. CRC, GBRMPA, Townsville.

McCook, L. J., and Price, I. R. (1997). The state of the algae of the Great Barrier Reef: what do we know? Pages 194-204 *in* Wachenfeld, D. R., Oliver, J. K. & Davis, K., editor. State of the Great Barrier Reef World Heritage Area Workshop. GBRMPA, Townsville.

McCook, L. J., Price, I. R., and Klump, D. W. (1997). Macroalgae on the GBR: causes or consequences, indicators or models of reef degradation? Pages 1851-1856 *in* 8th Int Symp Corals Coral Reefs Proc, Panama.

McEnroe, F. J., Robertson, K. J., and Fenical, W. (1977). Diterpenoid synthesis in brown seaweeds of the family *Dictyotaceae*. Pages 179-189 *in* Faulkner, D. J. and Fenical, W. H., editors. *Marine Natural Products Chemistry*. Plenum Press, La Jolla, California179-189.

Meesters, E. H., Noordeloos, M., and Bak, R. P. M. (1994). Damage and regeneration: links to growth in the reef building coral *Montastrea annularis*. *Mar. Ecol. Prog. Ser.* **112**:119-128.

Miller, M. W. (1998). Coral/seaweed competition and the control of reef community structure within and between latitudes. *Ocean. Mar. Biol. Ann. Rev.* **36**:65-96.

Miller, M. W., and Hay, M. E. (1996). Coral-seaweed-grazer-nutrient interactions on temperate reefs. *Ecol. Monogr.* **66**:323-344.

Miller, M. W., and Hay, M. E. (1998). Effects of fish predation and seaweed competition on the survival and growth of corals. *Oecologia* **113**:231-238.

Morrison, D. (1988). Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology* **69**:1367-1382.

Morse, A. N. C. (1991). How do planktonic larvae know where to settle? *Amer. Sci.* **79**:154-167.

Morse, A. N. C. (1992). Role of algae in the recruitment of marine invertebrates. Pages 385-404 *in* John, D. M., Hawkins, S. J. & Price, J. H., editor. *Plant-animal interactions in the marine benthos*. Clarendon Press, Oxford; 385-404.

Morse, A. N. C., Iwao, K., Baba, M., Shimoike, K., Hayashibara, T., and Omori, M. (1996). An ancient chemosensory mechanism brings new life to coral reefs. *Biol. Bul.* **191**:149-154.

Morse, D. E., Hooker, N., Morse, A. N. C., and Jensen, R. A. (1988). Control of larval metamorphosis and recruitment in sympatric agariciid corals. *J. Exp. Mar. Biol. & Ecol.* **116**:193-217.

Morse, D. E., and Morse, A. N. C. (1991). Enzymatic characterisation of the morphogen recognised by *Agaricia humilis* (scleractinian coral) larvae. *Biol. Bul.* **181**:104-122.

Morse, D. E., Morse, A. N. C., Raimondi, P. T., and Hooker, N. (1994). Morphogen-based chemical flypaper for *Agaricia humilis* coral larvae. *Biol. Bul.* **186**:172-181.

Mundy, C., and Babcock, R. (1998). Role of light intensity and spectral quality in coral settlement: Implications for depth-dependent settlement? *J. Exp. Mar. Biol. & Ecol.* **223**:235-255.

Mundy, C. N. (2000). An appraisal of methods used in coral recruitment studies. *Coral Reefs* **19**:124-131.

Negri, A. P., and Heyward, A. J. (2000). Inhibition of fertilization and larvalmetamorphosis of the coral Acropora millepora (Ehrenberg, 1834) by petroleum products. *Mar. Pol. Bul.* **41**:420-427.

Negri, A. P., and Heyward, A. J. (2001). Inhibition of coral fertilisation and larval metamorphosis by trybutyltin and copper. *Marine Environmental Research* **51**:17-27.

Negri, A. P., Smith, L. D., Webster, N. S., and Heyward, A. J. (2002). Understanding ship-grounding impacts on a coral reef: potential effects of anti-fouling paint contamination on coral recruitment. *Mar. Pol. Bul.* **44**:111-117.

Negri, A. P., Webster, N. S., Hill, R. T., and Heyward, A. J. (2001). Metamorphosis of broadcast spawning corals in response to bacteria isolated from crustose algae. *Mar. Ecol. Prog. Ser.* **223**:121-131.

Ogden, J. C. (1994). Letters: Coral Reef Catastrophe. *Science* **266**:1931.

Paul, V. J., Cruz-Riviera, E., and Thacker, R. W. (2001). Chemical Mediation of Macroalgal-Herbivore Interactions: Ecological and Evolutionary Perspectives. Pages 227-265 *in* McClintock, J. B. and Baker, B. J., editors. *Marine Chemical Ecology*. CRC Press, Boca Raton: 227-265.

Paul, V. J., Nelson, S. G., and Sanger, H. R. (1990). Feeding preferences of adult and juvenile rabbitfish *Siganus argenteus* in relation to chemical defenses of tropical seaweeds. *Mar. Ecol. Prog. Ser.* **60**:23-34.

Pawlik, J. R. (1992). Chemical ecology of the settlement of benthic marine invertebrates. *Ocean. Mar. Biol. Ann. Rev.* **30**:273-335.

Price, I. N. (1975). The development of algae on the skeletons of reef-building corals. Pages 181-191 *in* Anonymous, editor. Crown-of-thorns starfish seminar proceedings. Australian Government Publishing Service Canberra.

Purcell, S. W. (2000). Association of epilithic algae with sediment distribution on a windward reef in the northern Great Barrier Reef, Australia. *Bull. Mar. Sci.* **66**:199-214.

Raimondi, P. T., and Morse, A. N. C. (2000). The consequences of complex larval behaviour in a coral. *Ecology* **81**:3193-3211.

Renaud, P. E., Hay, M. E., and Schmitt, T. M. (1990). Interactions of plant stress and herbivory: intraspecific variation in the susceptibility of a palatable versus an unpalatable seaweed to sea urchin grazing. *Oecologia* **82**:217-226.

Richmond, R. H. (1993). Coral reefs - present problems and future concerns resulting from anthropogenic disturbance. *Amer. Zool.* **33**:524-536.

Rittschoff, D. (1990). Peptide-mediated behaviours in marine organisms: Evidence for a common theme. *J. Chem. Ecol.* **16**:261-267.

River, G. F., and Edmunds, P. J. (2001). Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. *J. Exp. Mar. Biol. & Ecol.* **261**:159-172.

Rogers, C. S. (1990). Responses of coral reefs and reef organisms to sedimentation. *Mar. Ecol. Prog. Ser.* **62**:185-202.

Rylaarsdam, K. W. (1983). Life histories and abundance patterns of colonial corals on Jamaican reefs. *Mar. Ecol. Prog. Ser.* **13**:249-260.

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

Sammarco, P. W., and Carleton, J. H. (1981). Damselfish territoriallity and coral comunity structure: reduced grazing, coral recruitment and effects of coral spat. Pages 525-535 *in* 4th Int Symp Corals Coral Reefs Proc.

Schmitt, T. M., Hay, M. E., and Lindquist, N. (1995). Constraints on chemically mediated coevolution: Multiple functions for seaweed secondary metabolites. *Ecology* **76**:107-123.

Sheppard, C. R. C. (1988). Similar trends, different causes: responses of corals to stressed environments in Arabian seas. Pages 297-302 *in* Proc. 6th Int. Coral Reef Symp., Townsville.

Smith, J. E., Smith, C. M., and Hunter, C. L. (2001). An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* **19**:332-342.

Solandt, J. L., and Campbell, A. C. (2001). Macroalgal feeding characteristics of the sea urchin Diadema antillarum Phillipi at Discovery Bay, Jamaica. *Carib. J. Sci.* **37**:227-238.

Steinberg, P. D., and de Nys, R. (2002). Chemical mediation of colonization of seaweed surfaces. *J. Phycol.* **38**:621-629.

Steinberg, P. D., de Nys, R., and Kjelleberg, S. (2001). Chemical Mediation of Surface Colonization. Pages 355-387 *in* McClintock, J. B. B., B.J., editor. *Marine Chemical Ecology*. CRC Press, Boca Raton, Florida: 355-387.

Steinberg, P. D., de Nys, R., and Kjelleberg, S. (2002). Chemical cues for surface colonization. *J. Chem. Ecol.* **28**:1935-1951.

Steinberg, P. D., and R., d. N. (2002). Chemical mediation of colonization of seaweed surfaces. *J. Phycol.* **38**:621-629.

Steneck, R. S. (1994). Is herbivore loss more damaging to reefs than hurricanes? Case studies from two coral reef systems (1978-1988). Pages 220-226 *in* Ginsburg, R. N., editor. Proc. Conf. on the Colloquium on Global Aspects of Coral Reefs: Health Hazards, and History, University of Miami, Miami.

Steneck, R. S. (1997). Crustose corallines, other algal functional groups, herbivores and sediments: complex interactions along reef productivity gradients. Pages 695-700 *in* 8th Int Symp Corals Coral Reefs Proc, Panama.

Steneck, R. S., and Dethier, M. N. (1994). A functional group approach to the structure of algal-dominated communities. *Oikos* **69**:476-498.

Stern, J. L., Hagerman, A. E., Steinberg, P. D., and Mason, P. K. (1996). Phlorotannin-protein interactions. *J. Chem. Ecol.* **22**:1877-1899.

Strong, A. E., Kearns, E. J., and Gjovig, K. K. (2000). Sea Surface Temperature Signals from Satellites - An update. *Geo. Res. Let.* **27**:1667-1670.

Sweatman, H., Cheal, A., Coleman, G., Delean, S., Fitzpatrick, B., Miller, I., Ninio, R., Osborne, K., Page, C., and Thompson, A. (2001). Long-term monitoring of the Great Barrier Reef, Status Report 5. Australian Institute of Marine Science, Townsville, Australia.

Sweatman, H., Cheal, A., Coleman, G., Fitzpatrick, B., Miller, I., Ninio, R., Osborne, K., Page, C., Ryan, D., Thompson, A., and Tomkins, P. (2000). Long-term monitoring of the Great Barrier Reef, Status Report 4. Australian Institute of Marine Science, Townsville, Australia.

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

Targett, N. M. (2001). Impact of environmental changes on the production of brown algal phlorotannins. *J. Phycol.* **37**:48.

Tuya, F., Martin, J. A., Reuss, G. M., and Luque, A. (2001). Food preferences of the sea urchin *Diadema antillarum* in Gran Canaria (Canary Islands, central-east Atlantic Ocean). *J. Mar. Biol. Assoc. U. K.* **81**:845-849.

Underwood, A. J. (1997). Experiments in ecology:their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge.

Van Alstyne, K. L., Dethier, M. N. & Duggins, D. O. (2001). Spatial Patterns in Macroalgal Chemical Defenses. Pages 301-324 *in* McClintock, J. B. B., B.J., editor. *Marine Chemical Ecology*. CRC Press, Boca Raton, Florida: 301-324.

Veron, J. E. N. (2001). Corals of the World. Austalian Institute of Marine Science, Townsville, Australia.

Vogel, S. (1994). Life in moving fluids: the physical biology of flow, 2nd edition. Princeton University Press, Princeton, N. J.

Wachenfeld, D. R., et al. (2003). State of the Great Barrier Reef World Heritage Area: http://www.gbrmpa.gov.au. Great Barrier Reef Marine Park Authority, Townsville Australia.

Wachenfeld, D. R., Oliver, J. K., and Morrissey, J. I. (1998). State of the Great Barrier Reef World Heritage Area. Great Barrier Reef Marine Park Authority, Townsville Australia.

Walters, L. J., Hadfield, M. G., and Smith, C. M. (1996). Waterborne chemical compounds in tropical macroalgae: positive and negative cues for larval settlement. *Mar. Biol.* **126**:383-393.

Wells, J. W. (1956). Scleractinia. Pages 328-480 *in* Moore, R. C., editor. *Treatise on invertebrate paleontology*. University of Kansas Press:328-480.

Wilkinson, C. R. (1993). Coral reefs are facing widespread extinctions: can we prevent these through sustainable management practices? Pages 11-21 *in* 7th Int Symp Corals Coral Reefs Proc, Guam.

Wilkinson, C. R. (1999). Global threats to coral reef functioning and existence: review and predictions. *Mar. Freshwater Res.* **50**:867-878.

Wilkinson, C. R. (2000). Status of coral reefs of the world: 2000. A.I.M.S., Townsville.

Wilkinson, C. R. (2002). Status of coral reefs of the world: 2002. A.I.M.S., Townsville.

Williamson, J. E., de Nys, R., Kumar, N., Carson, D. G., and Steinberg, P. D. (2000). Induction of metamorphis in the sea urchin *Holopneustes purpurascens* by a metabolite complex from the algal host *Delisea pulchra*. *Biol. Bul.* **198**:332-345.

Willis, B. L., Babcock, R., Harrison, P. L., Oliver, J. K., and Wallace, C. C. (1985). Patterns in the mass spawning of corals on the Great Barrier Reef from 1981 to 1984. Pages 343-348 *in* 5th Int Symp Corals Coral Reefs Proc, Tahiti.

Willis, B. L., Babcock, R. C., Harrison, P. L., and Wallace, C. C. (1997). Experimental hybridization and breeding incompatibilities within the mating systems of mass spawning reef corals. *Coral Reefs* **16 Suppl.**:S53-S65.

Wolanski, E., Richmond, R., McCook, L. J., and Sweatman, H. (2003). Mud, Marine Snow and Coral Reefs. *Amer. Sci.* **91**:44-51.

Wright, A. D., Coll, J. C., and Price, I. R. (1990). Tropical marine algae. 7. The chemical composition of marine algae from North Queensland waters. *J. Nat. Prod.* **53**:845-861.

Wylie, C. R., and Paul, V. J. (1988). Feeding preferences of the surgeonfish Zebrasoma flavescens in relation to chemical defenses of tropical algae. *Mar. Ecol. Prog. Ser.* **45**:23-32.