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Resilience and Recovery of Coral Communities on an Isolated Reef System in Western Australia Following a Catastrophic Mortality Event

Thesis submitted by

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Statement of the contribution of others

During my postgraduate studies, overall supervision was provided by Professor Terry Hughes (TPH) and Dr Andrew Heyward (AJH). This research was primarily funded by Australian Institute of Marine Science.

Other collaborations: Numerous people have assisted with my PhD research over the years; many by providing simulating intellectual input (see Acknowledgements). However, some have co-authored research papers that resulted from my postdoctoral research.

Chapter 3: James Bird undertook the modelling to hindcast the water temperatures at Scott Reef in 1998. Steve Delean provided assistance with statistics. TPH, and AJH provided editorial and research input. Currently, a paper is in preparation (see Appendix 1, research paper #13).

Chapter 4: TPH and AJH and James Gilmour provided editorial assistance and intellectual input. Currently a paper is in review (see Appendix 1, paper #11).

Chapter 5: Max Rees and AJH and James Gilmour provided input into this chapter and are co-authors in the resultant research paper (Appendix 1, paper #9).

Chapter 6: Steve Delean assisted with the statistical analysis. My supervisors contributed to the intellectual work. This chapter forms part of a research paper that is in review (see Appendix 1, paper #12).

Chapter 7: Richard Brinkman assisted in downloading and representing the drogue track data.

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Abstract

Coral reefs are increasingly exposed to disturbances acting over a range of spatial scales. At a global scale, there is growing concern that a changing climate will affect the long-term health and resilience of coral reefs. Climate change is predicted to increase seawater temperatures and cause extensive and recurrent mass bleaching of corals. In 1998, seawater temperature anomalies in the world's oceans affected a large proportion of coral reefs, many of which suffered catastrophic levels of mortality. This thesis provides quantitative data on the direct impacts of a severe bleaching event at an isolated reef system, Scott Reef in northwest Australia, during the actual period of elevated seawater temperatures and in the months and years following it. I assess the recovery of coral communities in the five years following the disturbance, including the changes in recruitment, benthic cover and population size-structures. Overall, this thesis provides a key dataset to further our understanding of the impacts of severe bleaching events on coral communities and the processes of replenishment and recovery.

While many studies have documented the patterns of bleaching among species of corals at the time of elevated sea-water temperatures few have shown how these patterns of bleaching vary during the period of elevated sea-water temperatures and directly following it. To determine the short- and longer-term effects of bleaching on the community structure of corals, I quantified the changes in the percentage cover of different taxa, three and six months after a mass-bleaching event, at the Scott Reef system. The overall result of the mass bleaching event at Scott Reef was a major shift in community structure from one dominated by a diverse range of scleractinian and alcyonarian corals to one dominated by turf and coralline algae. It resulted in the death of the majority of zooxanthallae corals at all of the study locations at Scott Reef, with relative decreases in the mean cover of hard corals of between 75% and 89%, depending on the reef habitat and depth. In addition, major differences were seen in the timing of mortality between different genera of corals.

In addition, I investigate how the severe bleaching event at the Scott Reef affected recruitment rates of corals, and consequently, the resilience of the resident coral communities. Coral cover and rates of sexual recruitment were quantified from two years before to five years after the bleaching event. The mass mortality of hard corals in 1998 caused a 97% decrease in recruitment rates at the Scott Reef system decreasing from a mean of 39.1 (± 12.6 *s.e.*) recruits yr^{-1} prior to the beaching to a mean of 1.3 (± 0.2 *s.e.*) after it. I attribute this decline in coral recruitment to both the extent and severity of the bleaching and the loss of reproductive corals on Scott Reef, and the isolation (> 240 km) of the reef system. Satellite-tracked drogues released in the region showed larval transport times to the Scott Reef system are likely to be greater than 25 days, longer than the optimal competency period for most coral larvae.

To understand changes in percent coral cover I measured the changes in the number of colonies of different size and/or stage classes of three common groups of corals at the Scott Reef system. The data showed that the bleaching event affected all life stages (ie juvenile, small adults and large adults) of each coral group surveyed. In addition, the number of juvenile corals in the families Acroporidae and Pocilloporidae five years after the bleaching was unexpectedly high, given the very low rates of recruitment.

To elucidate the recovery of the reef communities at Scott Reef I quantified the changes in their structure over nine years; four years before and five years after the catastrophic bleaching event. Almost six years after the bleaching, percentage cover of hard corals had returned to approximately 40% of their pre-bleaching cover and the community was returning to its previous percent cover, with evidence of an increasing rate of recovery in the later years. In fact, coral communities at some monitoring sites had almost returned to their pre-bleaching precent cover by 2003. It is likely that the survival and growth rates of corals at the Scott Reef system are relatively high. As a consequence, the coral communities are recovering, and at a faster rate than would be predicted, based in the severity of the bleaching event and the reduction in coral recruitment rates. In part, I attribute this recovery to the lack of many anthropogenic stressors that reduce the population growth rates of corals and promote the growth of competitors. These results suggest the resilience of coral communities to extreme, but infrequent (decadal) disturbances, and highlight the potential extent to which human activities may be compromising this resilience elsewhere.

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Chapter 1: GENERAL INTRODUCTION

Coral reefs are under threat as the scale and severity of anthropogenic impacts increases (Knowlton 2001, Hughes *et al.* 2003, Bellwood *et al.* 2004). One of the greatest threats to the long-term health of coral reefs, globally, is climate change, which is predicted to increase the temperature of the world's oceans dramatically in the next 50 years (Hoegh-Guldberg 1999, Sheppard 2003). Elevated water temperatures stress corals, causing them to expel their symbiotic algae (bleach) and in many instances, die (Hoegh-Guldberg and Smith 1989, Glynn 1991, Coles and Brown 2003). Reports of mass-mortality as a result of thermally induced coral bleaching date back to the early 1980's (Glynn 1984), and were at the time, viewed as rare events. This is supported by the limited oral history of bleaching events amongst indigenous fishing communities (see Hoegh-Guldberg 1999).

In the 1990's, there were numerous reports of major coral bleaching events (e.g., Gleason 1993, Fitt and Warner 1995, Fagerstom and Rougerie 1994, Hoegh-Guldberg and Salvat 1995, Brown *et al.* 1996). However, it wasn't until 1998 that the full potential geographical scale of thermal bleaching on coral reefs became evident. During 1998, there were temperature anomalies of at least 1 ^{o}C in most of the world's tropical waters, and in many cases temperatures were elevated by 2 to 5 ^{o}C (Sheppard 2003). The elevated water temperatures resulted in the mass bleaching of corals on reefs around the globe, and in many instances caused shifts from reefs dominated by corals to ones dominated by algae (Marshall and Baird 2000, McClanahan 2000, Loya *et al.* 2001, Aronson *et al.* 2002, Kayanne *et al.* 2002). Wilkinson (2000) estimated that 16% of all coral reefs were severely bleached in 1998 as a result of thermal stress. On the Great Barrier Reef, over 85% of inshore reefs were affected, although many recovered quickly (Berklemens and Oliver 1999). The greatest impact from the bleaching in 1998 was in the Indian Ocean, where it was estimated that one in three reefs were destroyed (Wilkinson 2000).

Following the dramatic die-off of corals in 1998, there has been much debate about the resilience of coral reefs if sea-water temperatures continue to rise (Hoegh-Guldberg 1999, Knowlton 2001, Hughes *et al.* 2003, Pandolfi *et al.* 2003, Folke *et al.* 2004). It has been argued that thermal stress, coupled with overfishing and eutrophication pressures (in many instances) will cause coral ecosystems to permanently shift to an alternate state, in which they are dominated by thermally-tolerant species of coral or by other taxa such as algae. However, our understanding of the short- and long-term responses of reef ecosystems to elevated seawater temperatures is poor.

To address the current gap in knowledge about the resilience of coral reefs in the face of increasing seawater temperatures, research needs to focus on four key areas. Firstly, accurate models predicting the changes in sea-water temperatures around coral reefs are required. These models need to examine the magnitude, duration and periodicity of elevated seawater temperatures anomalies. While these models are beginning to be developed (see Sheppard 2003), further refinements are needed to ensure future models are more robust and quantitative.

Secondly, the potential for reef organisms to acclimatise or adapt to increasing seawater temperatures must be investigated further. Adaptation or acclimatisation to elevated waters can be facilitated by either the host (e.g. coral) or the symbiont (e.g. zooxanthallae), and both should be assessed (see Rowan *et al.*1997, Baker 2001). Of particular interest, is the observed ability of most species of coral to survive high temperatures in some regions, but bleach and die at the same temperatures in other regions (see Hughes *et al.* 2003). Whether acclimatisation or adaptation can occur at the same rate as predicted climate change also needs to be determined.

Thirdly, we need to fully understand the short-term, direct, impacts of thermally induced bleaching on coral reefs, especially for severe bleaching events that are predicted to become common (Hoegh-Guldberg 1999, Sheppard 2003). The spatial and temporal variability in the rates of bleaching and post-bleaching mortality needs to be better understood. For example, while we have anecdotal reports of 30% of all Indian Ocean reefs being destroyed during 1998, we know little of the temporal and spatial the scale of the impacts on populations, communities and habitats (Wilkinson 2000). Additionally, there is a poor understanding of how observed patterns of bleaching and mortality among coral species during and shortly after the time of elevated water temperatures reflect the longer-term changes in community structure.

Finally, quantitative data need to be collected on the effects of bleaching on the processes that normally facilitate the recovery and replenishment of coral reefs. Few studies have assessed the long-term (ie. years) recovery of reef communities following severe bleaching events (however see Brown and Suharsono 1990) and little research has been undertaken on the impact of thermally induced bleaching on different life-histories stages of corals (ie. reproduction, growth, recruitment). Bleaching probably reduces colony fecundity (Michalek-Wagner and Willis 2001, Baird and Marshall 2000), but there is a poor understanding of the consequences for reproductive output and recruitment at the scale of the entire reef or regions.

This thesis concentrates on the last two research topics; assessing the short- and long-term effects of a mass bleaching event, and the effects of thermally-induced bleaching on the demographic processes that facilitate the recovery of communities from such a disturbance. Studies were undertaken at the Scott Reef system, an isolated group of reefs on the edge of the continental shelf, 270 km off the mainland of northwestern Australia (Figure 1.1). This system consists of North and South Scott Reef (S14^{o} 04’, E121^{o} 46’) and Seringapatam Reef (S13^{o} 40’, E121^{o} 59’). North Reef and South Reef are separated by a 5 km wide channel that reaches depths of 400 – 700 m. South Reef is crescent shaped, with a distance of 28 km between separating the east and west hooks (Figure 1.3). A permanent unvegetated sand cay (Sandy Islet) measuring approximately 1 km by 100 m is located on the eastern hook. The South Reef lagoon is extensive and between 20 and 50 m depth. The shallow reef flat is emergent at low tide and provides a barrier against the prevailing south-westerly swell and wind. North Reef has an annular structure and is 16 km long and 14 km wide and encloses a deep lagoon of up to 28 m depth. Numerous coral outcrops are found within North Reef lagoon. Like South Reef, the extensive reef flat at North Scott Reef is emergent at low tide. Two small channels, one on the southern edge and one on the eastern edge, connect the lagoon to the open ocean (Figure 1.3).

Seringapatam Reef is located 40 kilometres northwest of Scott Reef. Seringapatam Reef is an annular structure, 8 km long and 9 km wide with a deep lagoon that reaches approximately 30 m depth. A small channel on the north-eastern edge of the reef connects the lagoon to the open ocean. Scott Reef and Seringapatam Reef have been described as shelf atolls which rise up from the steep continental slope (Berry and Marsh 1986). This slope position of the reefs means that water depths of 400 m are found on the eastern side of the reef and 700 m depths on the western side (Figure 1.2). Within this region, the closest reefs are the Ashmore group 240 km to the north and Rowley Shoals 400 km the south.

Sea surface temperatures at the Scott Reef system are far warmer than similar latitude reefs on the Great Barrier Reef or higher latitude reefs off Western Australia. Surface seawater temperatures at Scott Reef ranged from a minimum of 27.2^{o}C to a maximum of 29.7^{o}C between 1968 and 1996 and were at their lowest from June to September and at their highest in November to December and March to April (Figure 1.4).

Interestingly, water temperature drop during January and February, presumably as a result of increased cloud cover. Wind speeds are at their lowest pre- and post-monsoon (Figure 1.4). The tidal cycle at the Scott Reef system is semi-diurnal, with a spring range of approximately 4.5 m.

The isolation of the Scott Reef system, coupled with the lack of commercial fishing or a resident human population, means its ecological communities have remained relatively pristine. Within this system, suitable habitats for coral communities are extensive, with 440,000 hectares of hard substrata in water less than 30 metres depth. The communities of coral at Scott Reef are highly diverse, with 233 species of scleractinian corals from 56 genera recorded (Veron 1986).

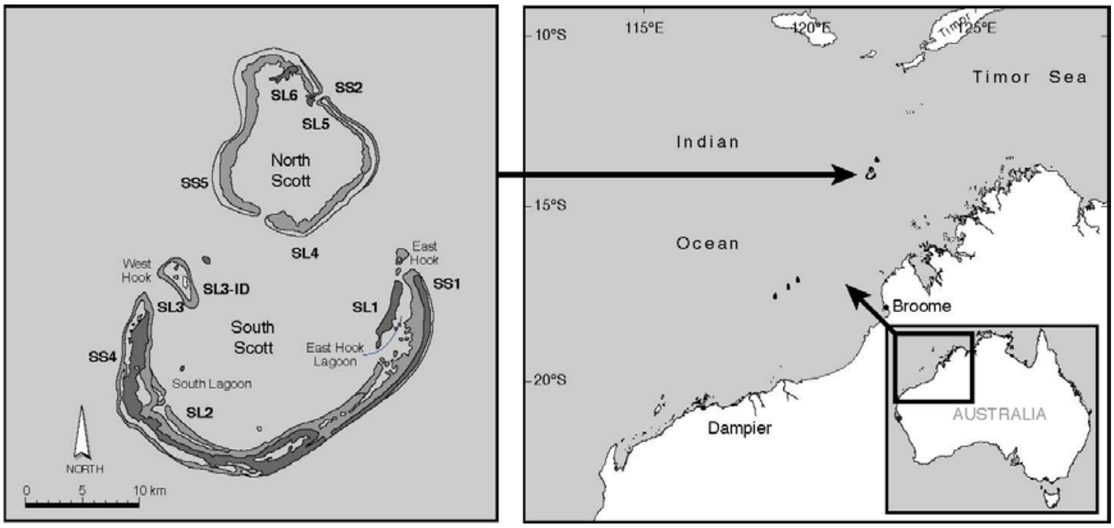

Figure 1.1 Location of the Scott Reef system

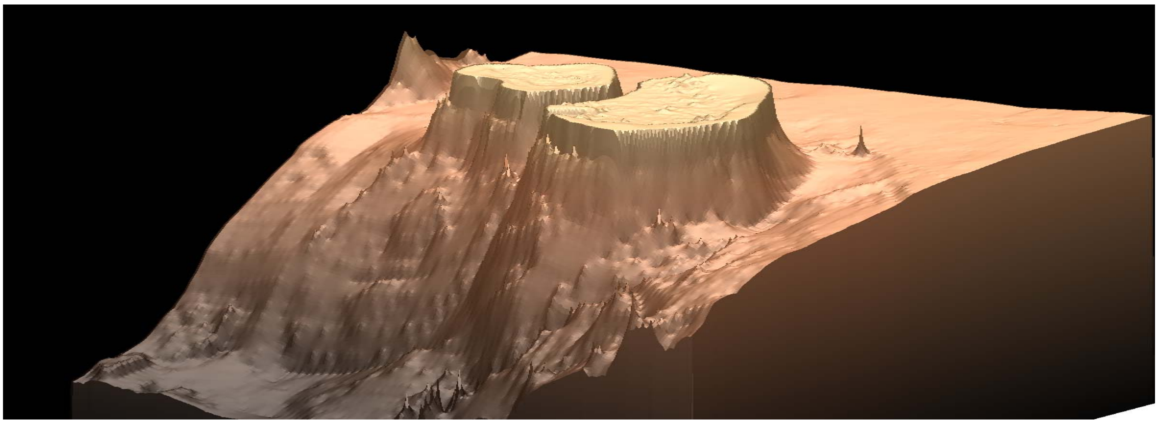

Figure 1.2 **Three-dimensional figure of the Scott Reef system showing the steep continental slope (provided R. Brinkman, AIMS).**

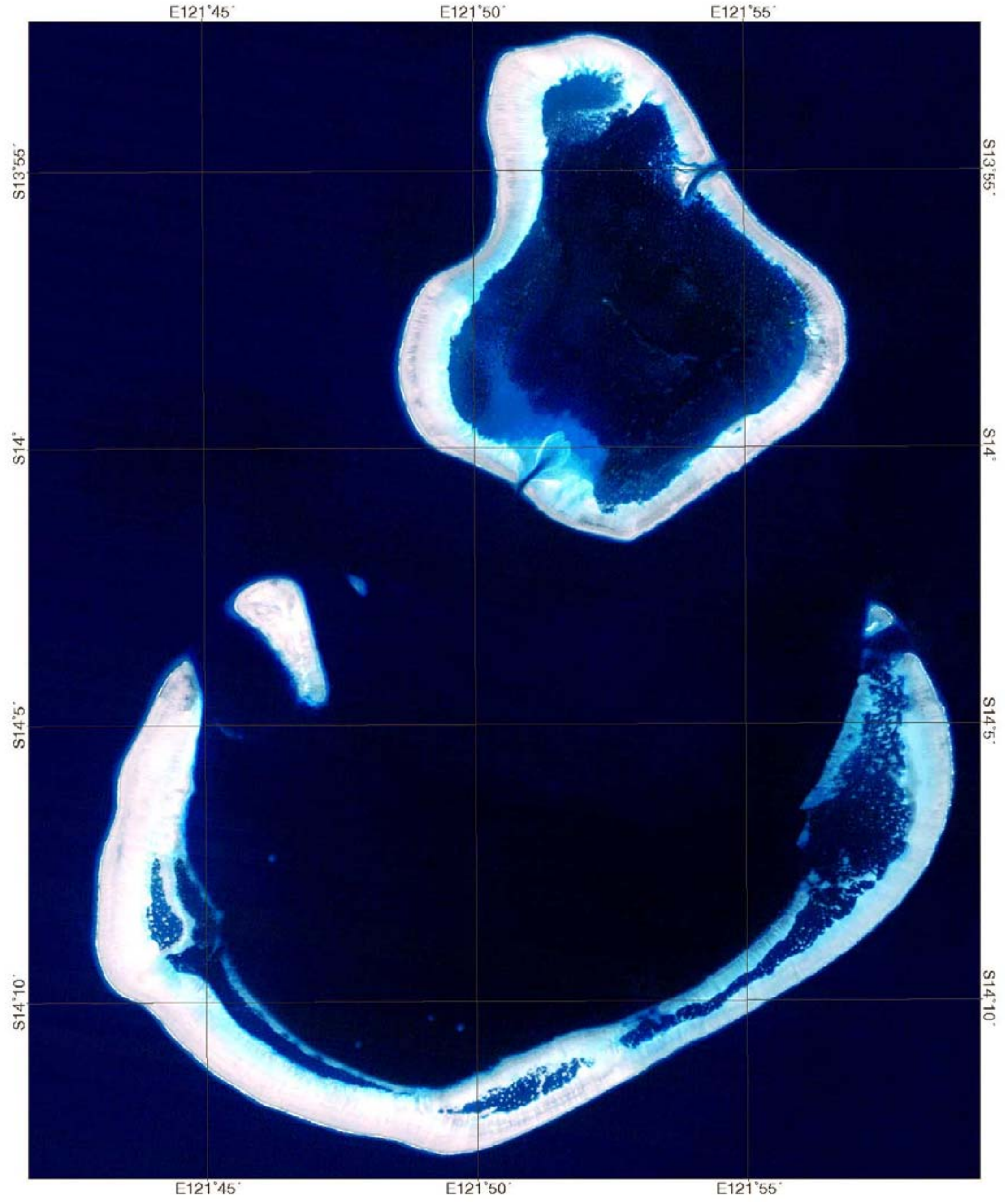

Figure 1.3 Dual enhanced Landsat image of Scott Reef (11/1993) provide by WA DOLA.

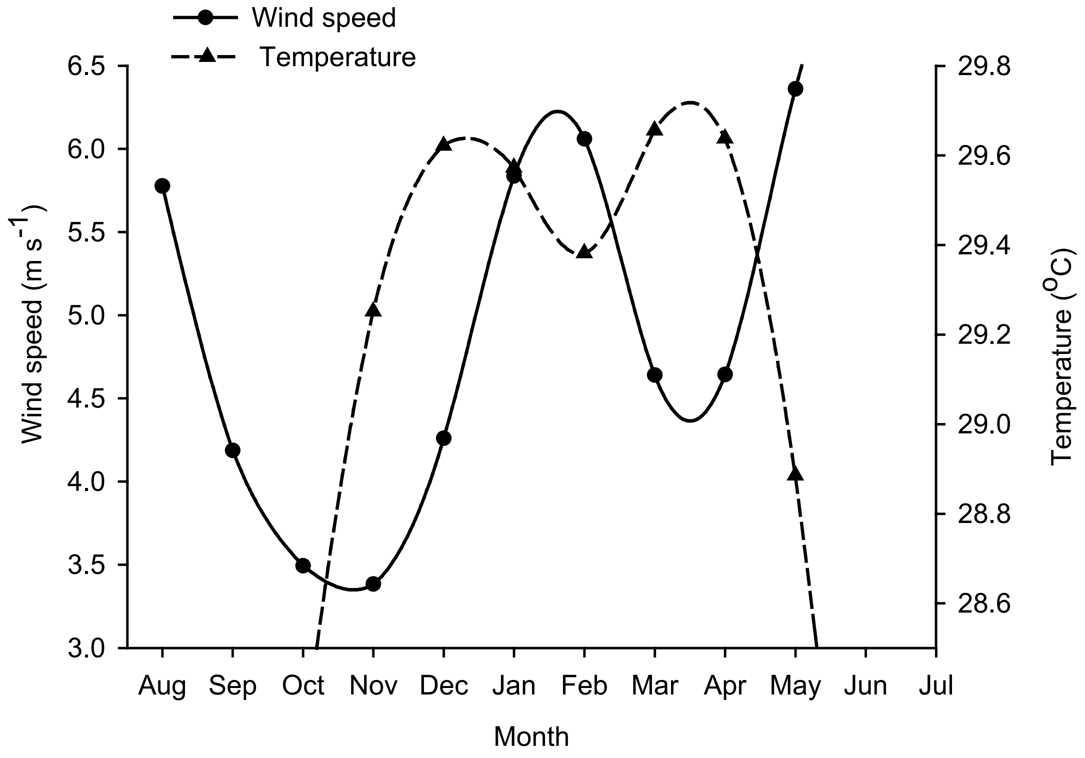

Figure 1.4 **Mean monthly sea-water temperatures and wind speeds at Scott Reef. Sea-water temperatures are mean monthly values obtained from the Hadley Centre Sea Surface Temperature data set (HadiSST1) from 1990 to 2000, and wind speeds are mean monthly averages obtained from the NOAA Earth Systems Research Laboratory, Physical Sciences Division, from 1968 to 1996. The times of multi-specific spawning are October/November and March/April.**

1.1 THESIS OUTLINE

This thesis quantifies the effects of a severe, large-scale bleaching event on short- (months) and long-term (years) structure of coral communities at the Scott Reef system. In addition, I assess the impacts of the bleaching event on the rates of coral recruitment at this system and make predictions about the resilience of Scott Reef to increasing sea-water temperatures around the world.

In Chapter 2, I discuss the seasonality of reproduction of hard corals from *Genus Acropora* at Scott Reef, and determine whether the genus spawns in autumn at the same time as most corals on high latitude reefs of Western Australia (Simpson *et al.* 1991, Babcock *et al.* 1994). These data enabled the long-term studies on coral recruitment at the Scott Reef system to be conducted.

In Chapter 3, I describe the short-term impacts of a thermally induced bleaching event at Scott Reef in 1998 on coral communities. I assessed the susceptibility of different coral taxa to elevated water temperatures over a range of temporal and spatial scales, and document shifts in the benthic communities over a three and six month period.

In Chapter 4, I assess the impact of the bleaching event on the rates of sexual recruitment to Scott Reef, which is an important demographic parameter influencing recovery. I quantify rates of recruitment over eight years at Scott Reef, three years before the mass-bleaching and for five years after it.

In Chapter 5, I discuss the impact of the mass bleaching on the population size-structure of three important coral taxa at Scott Reef. I assess whether the bleaching event caused size-dependent mortality and changes in the size-structure of populations.

In Chapter 6, I examine the long-term dynamics of Scott Reef’s benthic communities, assessing changes in community structure four years prior to a catastrophic bleaching event and for five years after it. These data provide insights into the resilience of coral reefs to catastrophic bleaching events, and raise concerns about their future should sea-water temperatures continue to increase around the world.

In Chapter 7, I investigate the extent to which the coral communities at Scott Reef may be reproductively isolated from other reefs in the region. Using satellite-tracked drogues, I estimate the transport times of coral larvae between isolated reef systems of northwest Australia. Using these data, and studies on larval competency, I make predictions about whether the coral communities at Scott Reef are largely self-seeded.

In Chapter 8, I broadly summarise the findings of the previous chapters and discuss the implications for their resilience of coral reefs in a changing climate. In addition, I suggest research that would further elucidate the future trajectory of coral reef ecosystems.

Chapter 2: TIMING OF SPAWNING AND RECRUITMENT AT AN ISOLATED REEF SYSTEM

2.1 INTRODUCTION

For most coral species, their clonal nature means populations can be maintained by a combination of sexual and asexual reproduction (Harrison and Wallace 1990; Hughes *et al.* 1992). The relative importance of these two modes of reproduction to population maintenance is highly species-dependent, with some species heavily reliant on colony fragmentation or fission (Highsmith 1982, Smith and Hughes 1999). However, even these species are dependent on sexual reproduction for initial establishment of populations following severe disturbances that cause local populations to become extinct, such as cyclones, predatory outbreaks or thermal induced bleaching. In order, to adequately understand the processes of replenishment and recovery of coral communities we require information on patterns of reproduction and recruitment.

One of the major objectives of this thesis is to assess annual variability in the rates of coral recruitment at an isolated reef system in NW Australia, Scott Reef. Given the expense of undertaking research at Scott Reef, I wish to identify the seasonality of coral reproduction and recruitment in the Genera *Acropora* at Scott Reef and then concentrate my sampling during those seasons each year to determine the longer-term patterns of coral recruitment. Currently no data exists on seasonality of coral reproduction at Scott Reef.

Corals belonging to the Genera *Acropora* are hermaphroditic, that is, having both male and female gonads in the same polyp. Two modes of reproduction are found within the Genus *Acropora*. Firstly, some acroporid species release sperm into the water column and fertilise their eggs internally. Development of the embryo takes months and larvae are released competent to settle onto the reef immediately (Kojis 1986). The other mode of reproduction, the predominant one for acroporids, is via broadcast spawning, where colonies release both eggs and sperm into the water column. Fertilisation is external and the embryos develop during this planktonic stage, before being able to settle back upon the reef. In general, *Acropora* larvae are competent to settle four to five days after initial fertilisation (Wallace 1999; Negri and Heyward 1999).

Broadcast spawning acroporids corals have been found to undergo a single gametogenic cycle every year. This annual reproductive cycle for *Acropora* broadcast spawners is likely to be related to the long development cycle of the oocytes, with studies assessing the gametogenic cycles having found that oocytes take approximately 9 – 10 months to develop (Wallace 1985, Dai *et al.* 1992, Shimoke *et al.* 1992). However, it should be noted that these studies where conducted on reefs in subtropical regions. Whether acroporids corals in warmer water, closer to the equator are able to undergo more that one gametogenic cycle per year is unknown.

Most broadcast spawning acroporids at particular reefs usually release their eggs and spawn over a number of nights during a particular lunar month every year. On eastern Australia reefs this mass spawning and recruitment of corals occurs in late spring (Willis *et al.* 1985, Wallace 1985, Babcock *et al.* 1986), whereas corals on high latitude reefs of the west coast spawn and recruit in early autumn (Simpson *et al.* 1991, Babcock *et al.* 1994). Determining the extent to which this pattern of coral spawning and recruitment applies to Scott Reef corals requires that cycles of both reproduction and recruitment to be quantified seasonally and over a number of years. To determine seasonality of reproduction and recruitment at Scott Reef I assess the seasonality of reproduction of two common acroporids, *Acropora specifera* and *A. hyacinthus*. At the subtropical Houtman Abrolhos Islands, Western Australia, *A. specifera* has been found to spawn in 10-11 nights after the full moon in March (Babcock *et al.* 1994). Alternatively, this species spawns three nights after the full moon in May in Taiwan

(Dai *et al.* 1992). For *A. hyacinthus*, spawning has been documented to happen throughout the year depending on the location (see Wallace 1999). In Western Australia, *A. hyacinthus* has been found *to* spawn approximately eight nights after the full moon in March at higher latitude reefs (Simpson 1985).

In addition, I assess the seasonality of actual recruitment of acroporids at Scott Reef in 1996 and 1997 using settlement plates. Most studies assessing *Acropora* recruitment via settlement plates have found that highest pulses of recruitment are associated with multi-species spawning periods. Within this study, deployment of settlement plates is timed to occur when *Acropora* species are found to be spawning.

2.2 MATERIAL AND METHODS

2.2.1 Seasonality of Reproduction

To assess the seasonality of reproduction, oogenic cycles were quantified for the hermaphroditic spawning corals *Acropora hyacinthus* and *A. specifera* which are abundant at Scott Reef and have a wide geographic distribution (Wallace 1999). Colonies of each species at two sites at Location SL3 (Figure 2.1) were randomly sampled at intervals between three and five months over almost four years. As a result different colonies were sampled on each trip. During sampling trips, two branches (>8 cm) were collected from the central region of 10 colonies of each species, and the presence of pigmented (pink/red) eggs with polyps recorded. Samples were fixed in a solution of 10% formalin and seawater for a minimum of one month. Each sample was sub-sampled and this sample was decalcified in a solution 7.5% hydrochloric acid over a period of 2-3 days. The now decalcified sample was then dissected using a binocular microscope. At least ten polyps were extracted from each sample using a pair of forceps. On a wax dissecting dish each polyp was teased open to reveal the mesenteries containing the oocytes. Gently using two fine long steel pins the eggs were extracted from the mesenteries of each polyp. If eggs were presented, each egg was measured in five random polyps using a calibrated eyepiece micrometer. Eggs were recorded as as being small (100–300µm), medium (300–500µm) and large (500-700µm). Testes were not measured in this study due to time limitations and having access to histological facilities.

In addition to quantifying the oogenic cycles of two study species, replicate colonies of a range of other *Acropora* species were sampled haphazardly during all trips to determine whether they had large, pigmented eggs, from which inferences about the times of spawning were drawn. Each colony was sampled at three locations near the centre of the colony and only colonies larger than 10 centimetres were sampled, to avoid sampling juvenile colonies (Hall and Hughes 1996). *In-situ* assessment of the seasonality of reproduction of individual colonies was undertaken based on whether cream/pink eggs were present or not. Species observed to have more than 20% of colonies spawning in a season where judged to be participating in the multi-specific spawning event for that season.

2.2.2 Seasonality of Recruitment

In order, to assess the seasonality of recruitment of broadcast spawning corals at Scott Reef, 18 settlement panels were deployed on the reef slope on the eastern edge of South Reef at a depth of nine metres. Three sets of six panels were deployed 50 metres apart. Within each set, panels were randomly placed approximately one metre apart. These settlement panels were simple terracotta tiles (110mm x 110mm x 10mm) attached to the reef (see Mundy, 2000), two weeks (± 4 days) prior to the predicted mass spawning in autumn and spring and were collected 6 weeks later (± 5 days) in 1996 and 1997. Following collection, settlement panels were bleached and coral recruits from the Family Acroporidae were identified using a dissecting microscope. To compare the rates of sexual recruitment between the predicted spawning times, data was log-transformed and analysed using a repeated measures ANOVA (SPSS v12).

2.3 RESULTS

2.3.1 Evidence of an autumn spawning

During autumn of each year some *Acropora hyacinthus* and *A. spicifera* colonies had mature eggs (Figure 2.2A). In January 1996, 100% of *A. spicifera* and 60% of the *A. hyacinthus* colonies that were sampled had medium sized eggs (Table 2.1). In early March 1997 and 1998, 90% of all colonies (100% of *A. spicifera* and 70 % of *A. hyacinthus*) had large eggs (Figure 2.2, Table 2.1). Colonies of both species were observed to spawn in late March or early April of these years.

At the end of March 1996, 40% of *A. spicifera* colonies had large eggs, whereas all *A. hyacinthus* colonies had empty mesenteries. These data, coupled with the full moon falling early in March, suggest a split-spawning for 1996; with *A. hyacinthus* colonies and some *A. spicifera* colonies spawning after the full moon in March, and the remaining *A. specifera* colonies spawning after the full moon in April.

2.3.2 *Evidence of a spring spawning*

A second mass spawning event occurred at Scott Reef during spring of each year, however, the numbers of colonies and species that participated in this spawning was apparently fewer than those spawning in the autumn spawning. Colonies of *A. spicifera* and *A. hyacinthus* had large eggs prior to the predicted dates of spawning (Table 2.1). Gametogenesis for spring spawners began sometime between May and August in both 1996 and 1997, since all samples collected in May contained no eggs. By early August of 1995 and 1996, 70% of *A. spicifera* and 80% of *A. hyacinthus*; and 100% of *A. spicifera* and 60% of *A. hyacinthus* had small eggs, respectively. In late August 1997, 50% of colonies of both species had small eggs. By October 1995 and 1996, 100% of *A. spicifera* and 80% of *A. hyacinthus*; and 60% of *A. spicifera* and 50% of *A. hyacinthus*, had large eggs, respectively (Figure 2.2A, Table 2.1). These eggs were presumably spawned at the end of October or early November. Small eggs were found in *A. spicifera* colonies at the end of November and in *A. hyacinthus* in mid-December 1997 (Table 2.1) and probably represent the onset of oogenesis for spawning in autumn the following year.

2.3.3 *Evidence of a two spawning events*

Data collected for seasonality of reproduction of acroporids, including *A. hyacinthus* and *A. specifera* at Scott Reef indicates that two multi-species spawning events occur each year. Nineteen species of *Acropora* were found to spawn at Scott Reef in both spring and autumn (Table 2.2). The majority of colonies within a species were found to be reproductive in autumn. In contrast, in spring only a minority of colonies were reproductive within an individual species.

2.3.4 Seasonality of coral recruitment

Major differences were seen in recruitment rates between spring and autumn (Figure 2.2B; ANOVA, F = 87.57, d.f = 1,360, p < 0.005). Coral recruitment of acroporids occurred predominately in autumn following the March/April spawning. Averaged rates of acroporid recruitment in 1996 and 1997 were 27.5 (± 5.6 *s.e.*) and 10.5 (± 2.9 *s.e.*) recruits per panel in autumn and spring, respectively. Overall 94% of all acroporids recruits counted during this study recruited in autumn, with the remaining 6% recruiting during spring.

2.4 DISCUSSION

Corals at Scott Reef can potentially spawn bi-annually. The first spawning in early autumn at the same time as other reefs further south in Western Australia, and the second, in spring, at the same time as reefs on the Great Barrier Reef. On the Great Barrier Reef, gametogenesis in hermaphroditic corals takes approximately 6 to 9 months (e.g. Heyward and Collins 1985, Wallace 1985), but in the warmer waters of Scott Reef this period of gametogenesis may be shorter. Between July 1995 and December 1998 the mean sea-surface temperature at Scott Reef was very warm with an average of 29.1ºC, and a maximum of over 32ºC (at 15 m depth, see Chapter 3). Based on the number of days required for eggs to develop from modal size classes of approximately 200 to 700 µm between censuses, oogenesis may take less than five months at Scott Reef. Consequently, there is sufficient time for two gametogenesis cycles to allow for an autumn and a spring spawning.

What remains to be determined is whether individual colonies at Scott Reef have; 1) one gametogenic cycle a year and spawn in autumn or spring or 2) two cycles a year and spawn at both times or 3) variable number of cycles (ie one or two) depending on environmental conditions. Additionally, there may be years when individual colonies do not spawn. It is unlikely that all colonies have only one gametogenic cycle a year as well over 50% of all colonies had mature eggs in spring and autumn. It is also unlikely that all colonies have two gametogenic cycles a year because at no time did where all colonies, of either species, have reproductive during both spring and autumn. The most probable pattern of reproduction is that most colonies of both species participate in the autumn spawning, making it the dominant spawning event, with a lower and more variable proportion of colonies also participating in the spring spawning.

Additional sampling at Scott Reef revealed that in addition to the two acroporid species sampled intensely, many other species participated in two short and distinct periods of multi-specific spawning each year, in contrast to the single mass spawning previously documented on most reefs around Australia (Harrison and Wallace 1990, Simpson *et al.*1991, Babcock *et al.* 1994). More than one multi-specific spawning event within a year has also been reported on other reefs around the world, such as those adjacent to Papua New Guinea (Oliver et al. 1988), Singapore (Guest 2005) and Kenya (Mangubhi and Harrison 2006).

Variation in the proportion of species and colonies participating in the spring spawning may be explained by the amount of energy required for gamete production and development. The gametogenic cycle must be initiated at least five months prior to spawning, and environmental conditions during this period are likely to be critical in determining whether gametes mature and spawn. If conditions during gametogenesis are unsuitable, then the developing eggs may be reabsorbed before they mature (Szmant-Froelich *et al.* 1980, Oliver *et al.* 1988). Alternatively, colonies of spawning corals experiencing warm waters and high food availability may reproduce more than once a year (Szmant-Froelich *et al.* 1980, Glynn *et al.* 2000).

Here, I have shown that reproductive output of *Acropora hyacinthus* and *A. specifera* at Scott Reef is bi-modal with autumn being the dominant spawning period. In addition, 22 other acroporid species were found to spawn in both spring and autumn at Scott Reef, however for most of these species less than 50% of colonies spawned during spring. Not surprisingly the highest levels of *Acropora* recruitment are associated with the autumn spawning event. For example in 1996, 94% of *Acropora* recruitment was associated with the autumn spawning, with remaining 6% recruiting in spring. This major difference in recruitment rates between seasons is likely a result of the majority of species spawning in spring. As a consequence, recruitment rates probably reflect a strong reproductive output/ recruitment relationship.

Future research needs to address whether corals found at higher latitudes in Western Australia spawn and recruit in both November and March. All data to date indicates this is unlikely. Corals spawn in autumn at higher latitude reefs in Western Australia. For example, Simpson *et al.* (1988) found 27 species that spawn in early autumn at Dampier Reefs and no species gravid in spring. In addition, reproductive studies at the Abrolhos Islands, further south of Dampier, found 94 of 107 sampled species spawned in March Babcock *et al.* 1994).

The question of causative factors for seasonality in spawning and recruitment of scleractinian corals is still to be addressed. Current evidence suggests corals on high latitudes reefs in Western Australia spawn in autumn, while corals on east coast of Australia spawn in spring. Whether the Scott Reef region is a transition zone between east coast reefs (ie. spring spawning) and west coast reefs (ie. autumn spawning) requires further sampling, especially on reefs in northern Australia. Interestingly weather conditions at Scott Reef at the time of the multi-species spawning events, in spring and autumn, are likely to maintain larva close to their parental reef. That is water temperatures are high, thereby potentially allowing faster larval development to competency (to settle) and relatively low wind speeds, which would limit the dispersal of larvae on wind-driven currents (Figure 2.3). Whether these factors are causative for the timing of multi-spawning events around the world remains to be determined. However, selection pressure on the timing of reproduction could be high if spawning at times of higher water temperatures and lower wind-driven currents leads to an increased likelihood of successful settlement (by remaining close to their natal reef).

Table 1.1 The presence and size of eggs within colonies of *Acropora hyacinthus* and *A. spicifera*. Five polyps from ten colonies of each species were sampled from each census.

Year	Month	Day	Species	Modal size (µm)	Size range (µm)	Number with eggs (n = 10)
1995	August	5	*A. spicifera*	200	200-400	7
			A. hyacinthus	200	100-300	8
	October	15	*A. spicifera*	600	500-700	10
			A. hyacinthus	700	500-700	8
1996	January	28	*A. spicifera*	400	400-600	10
			A. hyacinthus	400	400-500	6
	March	29	*A. spicifera*	700	700	4
			A. hyacinthus			0
	May	21	*A. spicifera*			0
			A. hyacinthus			0
	August	1	*A. spicifera*	200	100-300	6
			A. hyacinthus	200	200	2
	October	29	*A. spicifera*	600	500-600	6
			A. hyacinthus	600	600	5
1997	March	10	*A. spicifera*	600	600 – 700	9
			A. hyacinthus	700	500-700	9
	May	5	*A. spicifera*			0
			A. hyacinthus			0
	August	24	*A. spicifera*	200	100-300	5
			A. hyacinthus	100	100-200	5
	December	15	*A. hyacinthus*	200	200-300	7
1998	March	4	*A. spicifera*	700	600-700	10
			A. hyacinthus	600	600	7
	November	24	*A. spicifera*	200	100-300	6

Table 2.2 Species observed to spawn or have pigmented eggs during one or more years in Autumn (March / April), and Autumn and Spring (October / November). In each sample, more than 3 colonies of each species were investigated, and for each species between 20 and 95% of colonies were observed or inferred to participate in the spawning in Autumn or Spring

Autumn		**Autumn and Spring**
Acropora	*abrolhosensis*	
	acuminata	
	anthoceris	
	aspera	**X**
	cerealis	**X**
	cytherea	**X**
	digitifera	
	elseyi	
	formosa	
	florida	**X**
	gemmifera	**X**
	grandis	
	horrida	
	humilis	**X**
	hyacinthus	**X**
	intermedia	**X**
	indonesia	
	listeri	
	loisettea	
	microphthalma	
	millepora	**X**
	monticulosa	**X**
	muricata	**X**
	nana	**X**
	nasuta	
	nobilis	
	polystoma	**X**
	pulchra	
	robusta	**X**
	samoensis	**X**
	secale	
	selago	**X**
	specifera	**X**
	subulata	**X**
	tenuis	**X**
	valida	

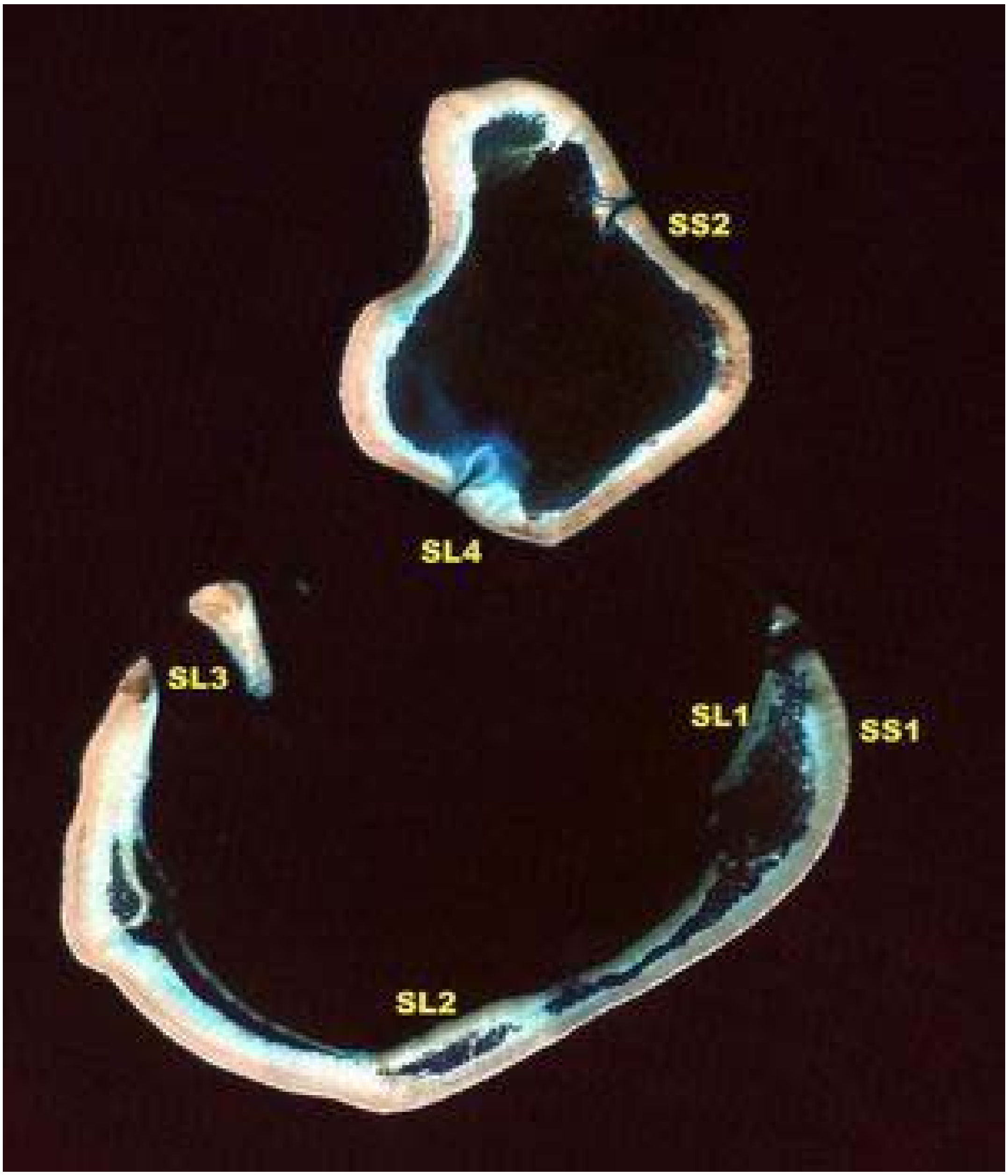

Figure 2.1 Location of study sites at Scott Reef

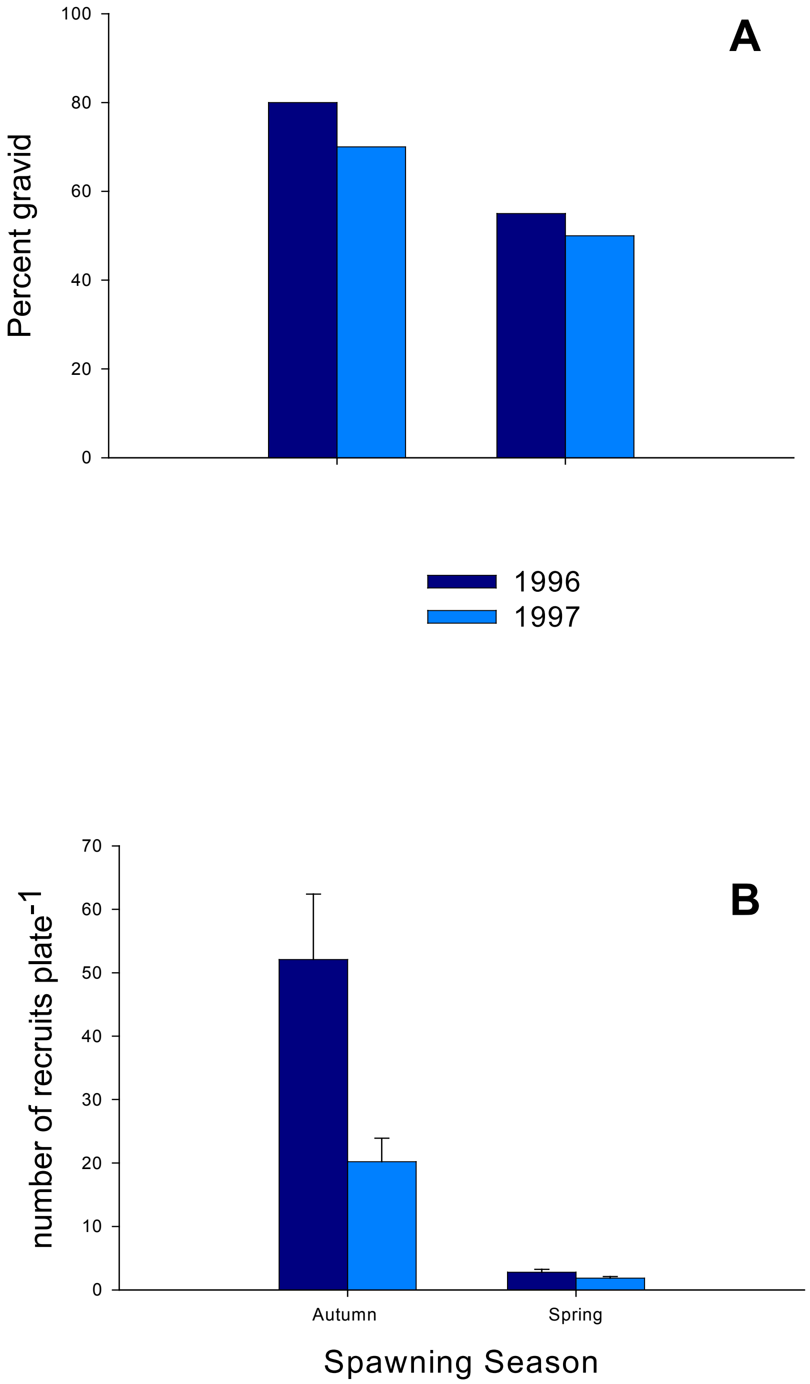

Figure 2.2 **Seasonality of reproduction and recruitment of acroporid corals at Scott Reef in 1996 and 1997; A) Mean percentage of colonies (A. hyacinthus and A. spicifera) with mature eggs prior to the predicted dates in spring and autumn, B) Rate of acroporid recruitment, measured as the number of juvenile corals per settlement panel at Scott Reef in 1996 and 1997.**

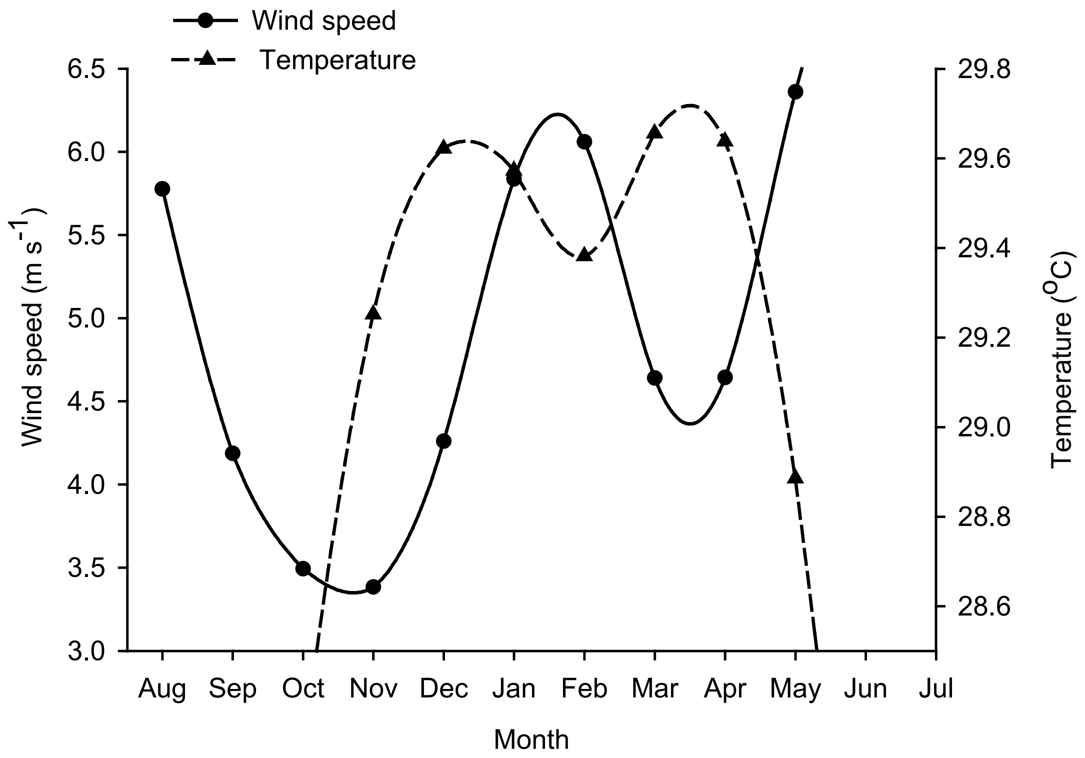

Figure 2.3 **Mean monthly sea-water temperatures and wind speeds at Scott Reef. Sea-water temperatures are mean monthly values obtained from the Hadley Centre Sea Surface Temperature data set (HadiSST1) from 1990 to 2000, and wind speeds are mean monthly averages obtained from the NOAA Earth Systems Research Laboratory, Physical Sciences Division, from 1968 to 1996. The times of multi-specific spawning are October/November and March/April.**

Chapter 3: SHORT-TERM RESPONSE OF CORAL COMMUNITIES TO A SEVERE BLEACHING EVENT

3.1 INTRODUCTION

Corals reef ecosystems around the world are under greater threat as the intensity and spatial scale of anthropogenic impacts increases (Wilkinson 2000, 2002). Reefs are being increasingly exposed to anthropogenic impacts that range from point sources (eg sewage, Grigg 1994; oil spills Vogt 1995) to those acting over a regional scale (eg. overfishing, Hughes 1994; corallivore outbreaks; Moran 1986, Turner 1994). In 1997-1998, we saw that reefs can be impacted on a global scale as a result of unprecedented warming of the world's oceans (Hoegh-Guldberg 1999, Wilkinson 2000).

When corals are exposed to elevated sea-water temperatures, they may respond by expelling their symbiotic algae and/or pigments (i.e. bleach) and potentially, die. The 1997-98 mass-bleaching event resulted in severe or catastrophic damage to 16% of the world's coral reefs (Wilkinson, 2000). The impact was greatest in the Indian Ocean, where 45% of reefs were destroyed. This unprecedented loss of cover, biodiversity, and reef structure led many to question the long-term resilience of coral reef ecosystems in the face of a warming climate (see reviews by Knowlton 2001, Hughes *et al.* 2003, Bellwood *et al.* 2004).

Differences in susceptibilities of corals to elevated water temperatures has resulted in predictions of major shifts to alterative communities dominated by bleaching-resistant species (Hoegh-Guldberg and Salvat 1995; Marshall and Baird 2000; Loya *et al.* 2001; Kayanne *et al.* 2002). Generally, pocilloporids and acroporids are most susceptible to bleaching, whereas faviids and poritids are less likely to bleach, or may suffer partial mortality rather than being killed outright after bleaching (Baird and Marshall 1998). The different susceptibilities of species can cause shifts in the structure of communities from ones dominated by branching species to ones dominated by massive poritids and faviids (Aronson 2002, McClanahan *et al.* 2004). After very severe bleaching episodes most coral species may die and reefs can undergo a complete phase-shift, with corals largely being replaced by algae (Wilkinson 2000; 2002).

While many studies have documented the patterns of bleaching among species of corals at the time of elevated sea-water temperatures, few have shown how these patterns of bleaching vary during the period of elevated sea-water temperatures and directly following it. To determine the short- and longer-term effects of bleaching on the community structure of corals, I quantified the changes in the percentage cover of different taxa, three and six months after a mass-bleaching event, at a group of reefs that were free of other confounding anthropogenic disturbances. In addition, I quantified the overall impacts of the bleaching event at a range of habitats and depths. The results were used to determine the spatial, temporal and taxonomic variability in the patterns of bleaching following a severe bleaching event.

3.2 MATERIAL AND METHODS

3.2.1 Water Temperatures

From 1996, water temperatures at 16 metres depth were directly quantified using a temperature logger at one location (Location SL4; Figure 3.1). Additionally, a depth-temperature profile was hindcast for Scott Reef from February 1998 until the end of June 1998, when the NOAA AVHRR (advanced very high resolution radiometer) satellite data indicated that water temperatures were well above normal. Bird *et al.* (2004) hindcast seawater temperatures during the 1998 bleaching event to a depth of 50 metres at Scott Reef after analysing *in-situ* tide, water temperature, air temperature, pressure, humidity, bathymetry, and other data collected from regional weather stations.

3.2.2 Long-term monitoring of coral communities

Monitoring sites were established at 9 metres depth to quantify the short- and long-term dynamics of benthic communities at Scott Reef. Monitoring sites were first established in 1994 at six locations at Scott Reef (SL1, SL2, SL3, SL4, SS1, SS2; Figure 3.1). Each location consisted of three sites, approximately 500 metres apart. Each site consisted of five permanent 50 metre transects, each separated by 10 metres. Transects followed the contour of the reef slope and were marked by steel rods at 10 metre intervals. All monitoring locations were surveyed during November 1997 and November 1998. Additionally, to assess the short-term response of benthic communities to the mass-bleaching event that occurred in March/April 1998, the first site at each location was surveyed between 27 June and 5 July 1998 at SL1, SL2, SL3 and SL4 (Figure 3.1). At each survey, a 50 metre tape was laid along each transect and a 30 cm belt of reef filmed using an underwater video camera. The video footage was analysed using a fixed-point sampling technique. The videotape was stopped at 50 regular intervals along each transect and the benthic organisms under five fixed points were recorded, giving a total of 250 points per transect. The percentage cover of benthic organisms was then calculated. Qualitative surveys were conducted during two additional trips; 26 February to 6 March, and 16 May to 24 April 1998.

In addition to the reef slope habitat, surveys were conducted at a range of other habitats to provide a more extensive understanding of the short-term effects of the thermal bleaching on coral communities. At locations SL1, SL2 and SL3, the reef crest (0 - 1 m), lower reef crest (2 - 4 m), and upper reef slope (5 - 6 m) habitats were surveyed in 1997 and 1999 (Table 1). At each location, within each habitat were six, 20 m transects permanently marked by steel rods. All transects were filmed and analysed as previously mentioned, but the video footage was paused at 20 regular intervals and the benthic organisms at five fixed points was recorded. In addition, the shallow (4 - 11 m) lagoonal habitats at two locations at North Scott and one location at Seringapatam were surveyed in 1999, and at each location were 20 randomly chosen sites consisting of three 50 m transects placed haphazardly at intervals of approximately 15 m. Mortality from the 1998 bleaching event was calculated by estimating the area of colonies that had recently died and was covered in either turf or coralline algae.

3.2.3 Statistical Analysis

To compare changes in percent cover and recruitment of hard corals among locations, before and after the 1998 thermal bleaching, a set of customised contrasts were tested using linear mixed-effects models. The models were fitted using the /MIXED command and the contrasts using the /TEST command in SPSS statistical software. The data used in the models were repeated site-level measurements (ie. mean of 5, 50 m transects) of *Soft Coral*, *Fire Coral (Milleporidae)*, *Hard Coral* and hard coral families; *Acroporidae*, *Poritidae* or *Pocilloporidae*, using the November 1997, June 1998 and November 1998 censuses. To satisfy model assumptions percent cover data for Families Acroporidae, Pocilloporidae, Milliporidae (fire coral) and total soft coral cover were transformed using a square root function prior to fitting the model, while hard coral and Family Poritidae data remained untransformed. The importance of temporal autocorrelation in the residuals was determined by fitting models both with and without first-order autoregressive correlation structure and then selecting the optimal model using Akaike Information Criteria (AIC; Burnham and Anderson 1998). For each coral taxa, mixed-effects models tested if significant changes occurred between; a) November 1997 and June 1998, b) June 1998 and November 1998, c) November 1997 and November 1998.

Two principal component analyses (PCA) on transformed (square root) percent cover data compared the impact of the bleaching event on the structure of benthic communities at Scott Reef (S-Plus, Statistical Sciences 1999). The first PCA illustrated changes in the community structure at four locations (SL1, SL2, SL3, SL4) between November 1997, June 1998 and November 1998. The second PCA illustrated the overall changes in community structure at all locations before the bleaching (November 1997) and, after it, at all six monitoring locations (November 1998). Vectors representing the benthic groups, and arrows representing the mean direction of change in benthic groups, were superimposed on each PCA bi-plot. The length of these vectors represents the overall importance of each taxonomic group and the direction of each vector indicates the location in which the vector is important in determining overall community structure.

3.3 RESULTS

3.3.1 Elevated sea-surface temperatures

Seawater temperatures at Scott Reef in 16.3 metres water depth were consistently above 30 °C from mid-March until the end of April 1998 (Figure 3.2). While it is not usual for water temperatures at this depth to be above 30 °C at Scott Reef, it is likely to be highly unusual for the temperature to be this high for such an extended period of time. For example, in November 1996, the hottest month for that year, water temperatures at the same depth and location were above 30 °C for days rather than months.

Sea surface temperatures derived from the NOAA/NASA Pathfinder satellite were 2 to 4 °C above the monthly mean at Scott Reef between March and the beginning of April 1998. Hindcasted temperature models indicated that temperatures reached 34 °C at the sea surface and 32 °C in depths of 20 metres between March and May 1998 at Scott Reef (Figure 3.3A). And on many occasions during this period, temperatures were up to 5 °C above expected. The hindcast model indicated that the water began to heat significantly in the middle February 1998 (Figure 3.3A). By the first week of March, the water column down to 20 metres, had heated up to approximately 31 °C. Major heating of the water column occurred from the middle of March, with surface waters reaching 34 °C. Strong winds in early to mid March caused the downward heating of the warm water. As a result, water temperatures at 20 metres reached 31 °C, two to three degrees above what would be expected (Figure 3.3B). As the water column continued to mix, the abnormally warm waters were pushed deeper and deeper. By late April, water at 30 metres depth was 2 °C warmer than expected. However, by the end of April, water temperatures had dropped below 31 ^{o}C in the top 20 metres, less than one degree above expected.

3.3.2 Qualitative observations of coral bleaching of Scott Reef

In late February 1998, there was no evidence of bleaching at Scott Reef, despite above average water temperatures in the shallows (see Figure 3.3). However, by the middle of May 1998, the benthic communities at Scott Reef had undergone dramatic changes. At locations SL1, SL2 and SL3, almost all branching acroporids had died and their skeletons had been colonised by filamentous algae. Soft corals and fungiids had bleached and were bright green. The tissue of many soft corals appeared to be dissociating, and piles of spicules remained following tissue necrosis. Most massive *Porites* colonies had bleached, but there was little evidence of partial or whole colony mortality. In some instances, areas of *Porites* colonies had not bleached, or had paled rather than fully bleached, but there was no apparent pattern to the bleaching, which had occurred on the top, sides and base of some colonies.

By late June 1998, almost every coral colony down to 30 metres depth had bleached (Figure 3.4). Soft corals were still dying, leaving piles of spicules. *Porites* colonies were still white, with most suffering some partial mortality. On the reef crest, in 1 to 3 metres depth, few live corals remained. For example, in a 60 minute search on the reef crest at location SL1, only seven coral colonies were found alive (but still bleached); *Seriatopora hystix* (2), *Goniastrea favulus* (3) and *Goniopora spp.* (2). Not a single acroporid colony was found alive in less than 6 metres at SL1. Isoporids (mostly *Acropora bruggemanni*) had disappeared from locations SS1 and SS2, where they had dominated prior to the bleaching. Extensive stands of staghorn coral (mainly *Acropora muricata*, *A. intermedia*, *A. abrolhosensis*) had died. Fungiids at all sites had bleached either bright orange or green, but had not died. The only major survivors three months after the onset of bleaching were the poritids and the soft corals. The rates of bleaching and mortality of corals were apparently lower at Location SL3 where some of the bleached acroporids were still alive. In some cases, either the corallivore *Drupella sp.*, or black band disease, was killing some of the survivors, especially at location SL2. Filamentous algae had quickly overgrown the exposed skeletons of dead corals. The communities at Scott Reef approximately 3 months after the elevated water temperatures were dominated by filamentous algae, interspersed with bleached coral colonies.

By late October 1998, all surviving corals had regained their zooxanthallae and their colour, including the *Porites* and soft corals that were slow to bleach. However, most *Porites* colonies had undergone some partial mortality, and numerous large colonies had died, especially in the lagoon at North Scott. Some of the dead colonies in the lagoon measured up to 8 metres around the base. A colony of *Pavona minuta* that measured 20 metres around the base had also died. Much of the filamentous algae that had colonised dead skeletons had been replaced by crustose coralline algae. Despite the partial mortality of some *Porites*, all observations indicated that there would be no further direct mortality of corals caused by the bleaching, and the direct effects of the elevated water temperatures between March and June had passed.

3.3.3 Quantitative impacts of the mass bleaching: the first six months

Major differences were observed in the timing of mortality between different taxa. Mortality of both hard and soft corals was greatest between November 1997 and June 1998, when seawater temperatures were abnormally hot (Table 3.2, Figure

3.5). However, after seawater temperatures had returned to normal, hard and soft corals continued to die in significant numbers. For example, of the total loss of hard corals, as a result of the mass bleaching, 87% occurred when the water was abnormally hot (ie pre-June 1998) and 13% after the water the water had returned to normal temperatures (Table 3.2, Figure 3.5). Similarly, soft corals continued to die, in significant numbers, after seawater temperatures had returned to normal (post June 1998), with 10% of overall soft coral mortality occurring after June 1998.

Within the hard coral group there were some major differences in the timing of mortality associated with the mass-bleaching (Table 3.2, Figure 3.6). The fire coral, Milleporidae and the scleractinian families Acroporidae and Pocilloporidae all died during the period of elevated seawater temperatures. For example, Family Acroporidae suffered an 84% reduction in percent cover between November 1998 and June 1998 census and showed no significant change in cover following this census. Similarly the fire coral, Milleporidae suffered mortality rates of 95% prior to June 1998 and showed no significant change in cover. If colonies of these taxa (fire coral and Acroporidae) and also Family Pocilloporidae survived the period of elevated temperatures at Scott Reef (pre-June), then they continued to survive. In contrast, mean percent cover of Family Poritidae dropped, significantly after the June 1998 census, when water temperatures had returned to normal (Table 3.2, Figure 3.6). Between June and November 1998, 42% (by mean percent cover) of Family Poritidae died, dropping in cover from 7.2% (± 1.1 s.e.) to 4.3% (± 1.0 s.e.) by November 1998. Interestingly, Family Poritidae suffered no decrease in mean percent cover between March and June 1998 when the water temperatures were unusually elevated.

Multivariate analysis illustrated the major changes in the structure of benthic communities at Scott Reef that had occurred by the June census, during the period of elevated water temperatures (indicated by the length of the arrow 1-2 for each monitoring location; Figure 3.7). The small changes in the community structure between the June and November censuses were mostly driven by the slower rates of bleaching and mortality of the Poritidae (MNA) and soft corals (SC). Consequently, the extent to which the structure of the communities changed at each location between the June and November censuses varied according to the relative abundance of the Poritidae and soft corals. Locations with very few poritids and soft corals (e.g. SL2) changed little, whereas locations where many poritids and soft corals underwent larger changes (indicated by the length of the arrow 2-3; Figure 3.7). However, the most dramatic changes in community structure occurred between November 1997 and June 1998 during the period of elevated seawater temperature.

3.3.4 Overall effects of bleaching events on benthic communities

The mass bleaching event at Scott Reef resulted in a major shift in community structure from one dominated by a diverse range of scleractinian and alcyonarian corals to one dominated by turf and coralline algae. Evidence of this benthic community shift across all locations is show in the movement from coral-dominated communities (left of Figure 3.7) to communities dominated by turf and coralline algae (right of Figure 3.7) in multivariate space. It resulted in the death of the majority of zooxanthallae corals at all of the study locations at Scott Reef, with relative decreases in the mean cover of hard corals of between 75% and 89%, depending on the reef habitat and depth (Table 3.1).

The mean percentage cover across all reef slope locations decreased by 78% for the hard corals and 84% for the soft corals, between the censuses in November 1997 and 1998 (Figure 3.8). On average, hard and soft corals constituted over 50%

of the benthic community in November 1997, which decreased to 12% a year later. The dead skeletons of hard corals were colonised by turf algae and to a lesser extent by coralline algae. By November 1998, these algae had become the dominant benthic organism. While mortality of corals following the bleaching was severe across all of Scott Reef, there was some variation among locations (Figure 3.8). Reef Slope locations SL3 and SL4 had relative decreases in cover of approximately 50%, whereas the relative decreases in cover were > 75% at the remaining four locations. There was a similar pattern of variability among locations for both the hard and soft corals.

Major differences in the overall susceptibility of different coral taxa to bleaching were found at Scott Reef. The fire coral, *Millepora sp*. suffered almost local extinction, with only a few colonies being found at location SL3 following the bleaching. In addition, branching acroporids and pocilloporids had relative decreases in mean cover of > 75% across all locations (Table 3.2). However, massive and sub-massive corals survived far better, although their relative decreases in mean cover were still greater than 50%. The only group of corals that had relative decreases in cover of less than 50% were the fungiids, which decreased by 25%, but the fungiids were uncommon and generally occupied less than 1.2 % mean cover overall.

Differences in susceptibility of corals caused major changes in the structure of the hard coral communities from November 1997 to November 1998 (Figure 3.9). Overall, there was a dramatic shift in the community structure at all locations from communities dominated by corals to dominance by turf and coralline algae (FS). However, there was some variability in the degree of change at different locations; the smallest changes were at locations SL3 and SL4, and the largest changes at locations SS1, SS2 and SL2 (Figure 3.9). The smaller arrows in Figure 3.9 indicate less change in the community structure (SL3, SL4) than locations with longer arrows which had larger changes to community structure (SS1, SS2, SS3). Despite differences in the magnitude of the change, the types of changes in community structure were consistent among all the locations as a result of the mass bleaching event reflecting the scale of the disturbance and its impact across all of Scott Reef.

3.4 DISCUSSION

The temperature anomaly at Scott Reef in 1998 was extreme, with water temperatures 3 to 4 ^{o}C higher than expected (Figure 3.3). The result was the bleaching of almost all hard and soft corals to a depth of at least 30 metres, in contrast to many other bleaching events around the world where many corals on parts of the reef did not bleach, or only partially bleached (Marshall and Baird 2000, Kanyanne *et al.* 2002). The scale and severity of the bleaching at Scott Reef was probably a consequence of both the maximum water temperatures and the duration of heating. The shallow water (< 20 metres) around Scott Reef was unusually warm (> 1^{o}C) for at least 11 weeks. The elevated water temperatures and the mass-bleaching resulted in dramatic changes in the benthic communities at Scott Reef. The cover of hard and soft corals decreased by approximately 80%, and within six months turfing and coralline algae were the dominant benthic organisms across Scott Reef.

Overall mortality of hard corals was extreme with rates of mortality between 74 and 89 percent depending on the reef habitat. Without a doubt this was one of the most severely impacted reefs, both regionally and globally, during the 1998 elevated seawater temperature event. For example, one of the worst bleached reefs on the Great Barrier Reef only suffered levels of mortality between 38% and 0% depending on species (Marshall and Baird 2000). On Japanese reefs overall mortality rates of hard corals reached levels of 61-79% depending on the reef (Fujioka 1999, Loya *et al.* 2001). Whereas on Kenyan reefs rates of coral mortality varied between 0% and 85% depending on the reef (McClanahan *et al.* 2001).

In mild bleaching events, massive corals such as the poritids and faviids may not bleach, or may partially bleach, whereas many branching corals may totally bleach and die (McField 1999, Marshall and Baird 2000, Kayanne et al 2002). Massive corals may be better able to withstand elevated water temperatures because they are able to retract polyps into their thick walls and shade their tissue and resident symbionts (Hoegh-Guldberg 1999, Loya *et al.* 2001) or, alternatively, they may possess more temperature tolerant zooxanthallae (Rowan *et al.*, 1997; Fabricius *et al.*, 2004; Rowan, 2004) or florescent coral pigments that photoprotect tissue (Salih *et al.* 2000, Brown *et al.* 2002). However, unlike most other studies, the temperature anomaly was so severe at Scott Reef that all taxa possessing symbiotic algae, even those thought to be relatively temperature tolerant, bleached down to depth of 30 metres.

While the bleaching at Scott Reef was so severe that all corals bleached, there were major differences in the subsequent mortality rates between coral genera. The acroporids and pocilloporids suffered the highest rates of mortality across all study sites, while the fire coral, *Millepora sp.* became almost locally extinct at Scott Reef. In contrast, the massive poritids were least affected. These differences in survival among taxa are likely to be a result of a number of primary and secondary responses to the bleaching event. Corals, in the first instance, are likely to suffer cellular damage as a direct result of the thermal stress that causes the expulsion of the resident symbionts (see reviews by Hoegh-Guldberg 1999, Coles and Brown 2003). In the longer-term of weeks to months, the secondary effects of bleaching could also prove lethal. For example, many corals derive a large portion of their nutrient requirements from their endosymbionts (Muscatine *et al.* 1981, Bythell 1988, Muscatine 1990), so colonies that remain without their zooxanthellae for a long time period will potentially starve to death. In addition, bleached corals are by definition highly stressed, and are more susceptible to disease or predators (also see Baird and Marshall 2002). For example, many corals, especially at location SL2 contracted black band disease during the bleaching event.

While there were major differences in the overall mortality rates of taxa as a result of the mass bleaching event, there was some interesting variability in the timing of the deaths between taxa. Most corals (eg. Acroporidae, Faviidae, Pocilloporidae) at Scott Reef died during the period of elevated sea-surface temperature, between the censuses in April and June 1998. Coral mortality during this period is likely to be related to direct cellular damage. However, most Poritidae and soft corals died between June and November, after the water temperature had returned to normal levels. Obviously, this delayed mortality of Poritidae and soft corals is unlikely to be directly attributable to cellular damage resulting directly from the bleaching event. These data suggest that bleached Poritidae and soft corals may have compounds such as florescent coral pigments or heat shock proteins that can protect colonies from bleaching induced cellular damage (Salih *et al.* 2000, Dove *et al.* 2001, Brown *et al.* 2002). The mechanism that allowed most Poritidae and soft coral colonies to initially survive the bleaching when water temperatures were elevated needs to be investigated. However, in many instances, these taxa were unable to escape secondary mortality agents, most likely starvation or pathogens, after water temperatures had returned to normal.

This study has shown the need to investigate the secondary responses of some taxa that were previously thought to be bleaching resistant to protracted thermal induced bleaching events. In addition, it highlights the need for repeated surveys over extended periods, well beyond the time of elevated water temperatures, to properly evaluate the consequences of mass bleaching.

This study assessed changes in populations of hard and soft corals and hydrocorals at Scott Reef using changes in overall mean percentage cover. However, these data fail to highlight different rates of whole- and partial-colony mortality between taxa as a result of the bleaching. Most strikingly, branching acroporids, pocilloporids and the fire coral, *Millepora sp.* mostly suffered whole-colony mortality, whereas most massive poritids and faviids, suffered partial-colony mortality. Thus, far fewer genotypes of the massive corals were lost from Scott Reef than for the branching corals. In most cases, massive colonies were fragmented into numerous daughter colonies through partial mortality, so there were comparatively small decreases in the number of genotypes, despite the large decreases in percentage cover. The recovery of populations of poritids and faviids is likely to be facilitated by growth of numerous daughter colonies, in addition to the production of sexual recruits by the survivors of reproductive size. However, the reproductive output of the resident populations of poritids and faviids is likely to be reduced through the process of reverse puberty when large colonies are reduced to numerous small daughter colonies (see Harrison and Wallace 1990, Smith and Hughes 1999).

In contrast to the massive corals, most of the acroporids, pocilloporids and the fire coral *Millepora sp.* suffered whole-colony mortality. Accordingly, populations of these taxa are likely to have experienced a dramatic reduction in genotypic diversity and density, and are likely to suffer reduced rates of sexual recruitment due to the negative effects of sperm dilution at the time of spawning (Levitan and Peterson 1995). Recruitment failure following the mortality of most colonies of branching corals is even more likely at at Scott Reef, because it is an isolated reef system. The populations of corals at Scott Reef are more likely to be reliant on self-seeding for population maintenance than other reefs that are part of an interconnected system (eg Great Barrier Reef; see Chapter 5).

The recovery of the coral communities at Scott Reef is likely to be slowed because of both the severity and scale of the bleaching event. Major disturbances to coral reefs usually kill corals in particular habitats. For instance, crown of thorns (*Acanthaster planci*) outbreaks predominately affect reef slope communities (De'ath and Moran 1998), and cyclones tend to impact on communities on exposed reef crests and slopes (Connell *et al.* 1997; Bries *et al.* 2004, Halford *et al.* 2004). As a consequence, most major disturbances leave some habitats or coral communities unaffected. These communities can provide recruits that facilitate the recovery of the affected habitats. However, the bleaching of corals at Scott Reef resulted in the death of most corals across all habitats, including the lagoon, reef crest and slope communities. Thus, the combination of the scale and severity of the bleaching event, and the isolation of Scott Reef, means rates of sexual recruitment are likely to remain low for many years and, as a consequence, the coral communities are likely to take a long time to fully recover.

In conclusion, catastrophic bleaching events, such as the one at Scott Reef in 1998, affect all taxa possessing symbiotic algae, across all habitats on a reef, and are far more damaging than other disturbances whose affects may be species- or site-specific. As a consequence, recovery from massive bleaching events is likely to take longer than for other disturbances. In the case of isolated reef systems, such as Scott Reef, recovery times are likely to be measured in decades, rather then years, and rely on there being no further disturbances of similar magnitude during the recovery period.

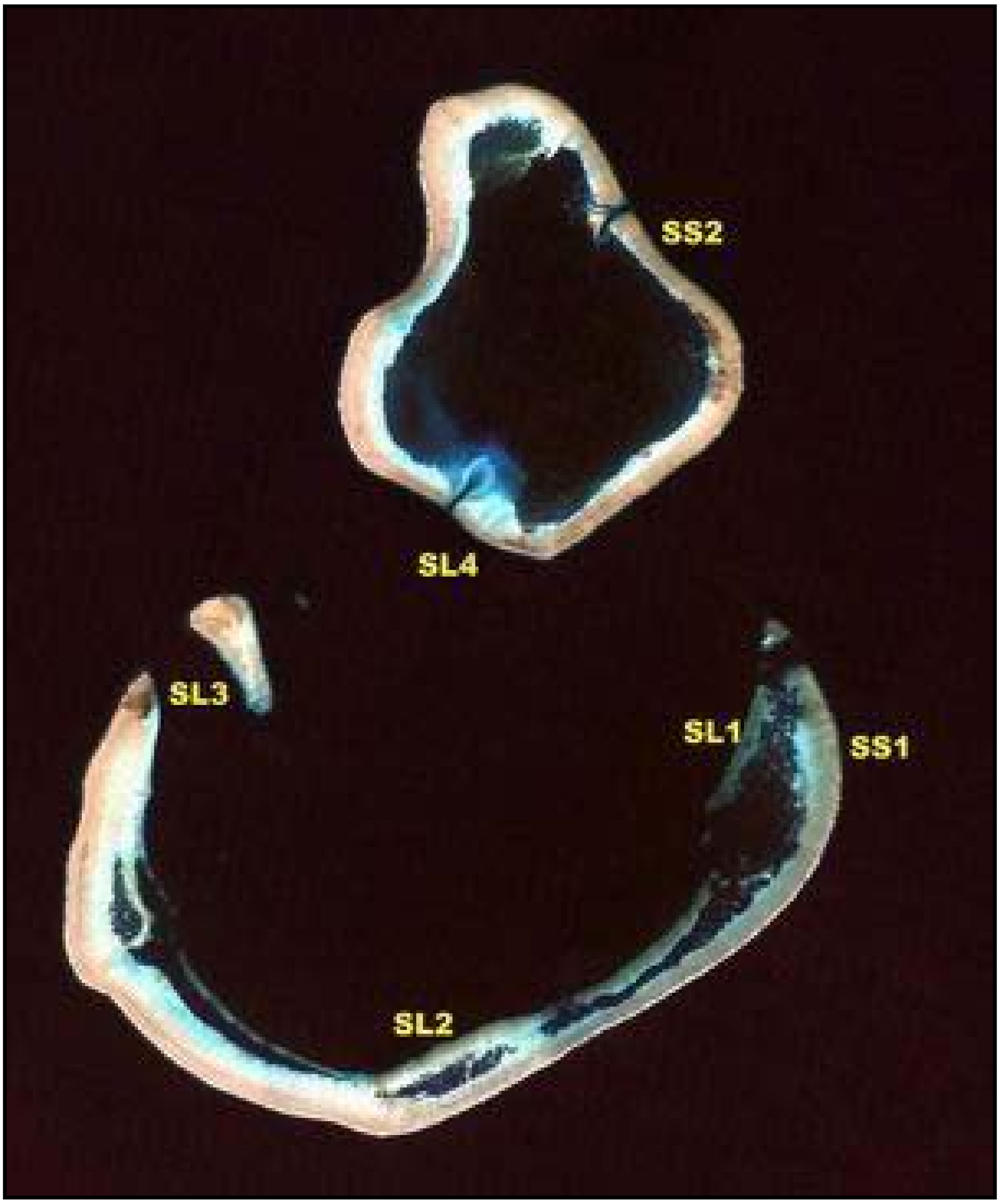

Figure 3.1 Location of monitoring sites at Scott Reef

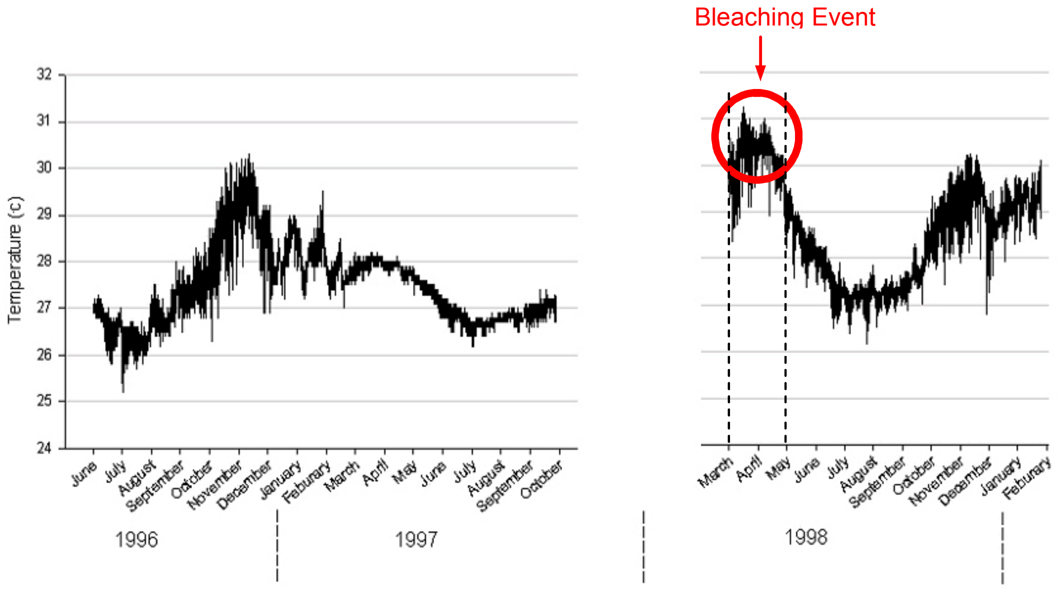

Figure 3.2 **Temperature data from depth of 16 metres of Location SL4 showing the high spike in water temperatures between March and May 1998.**

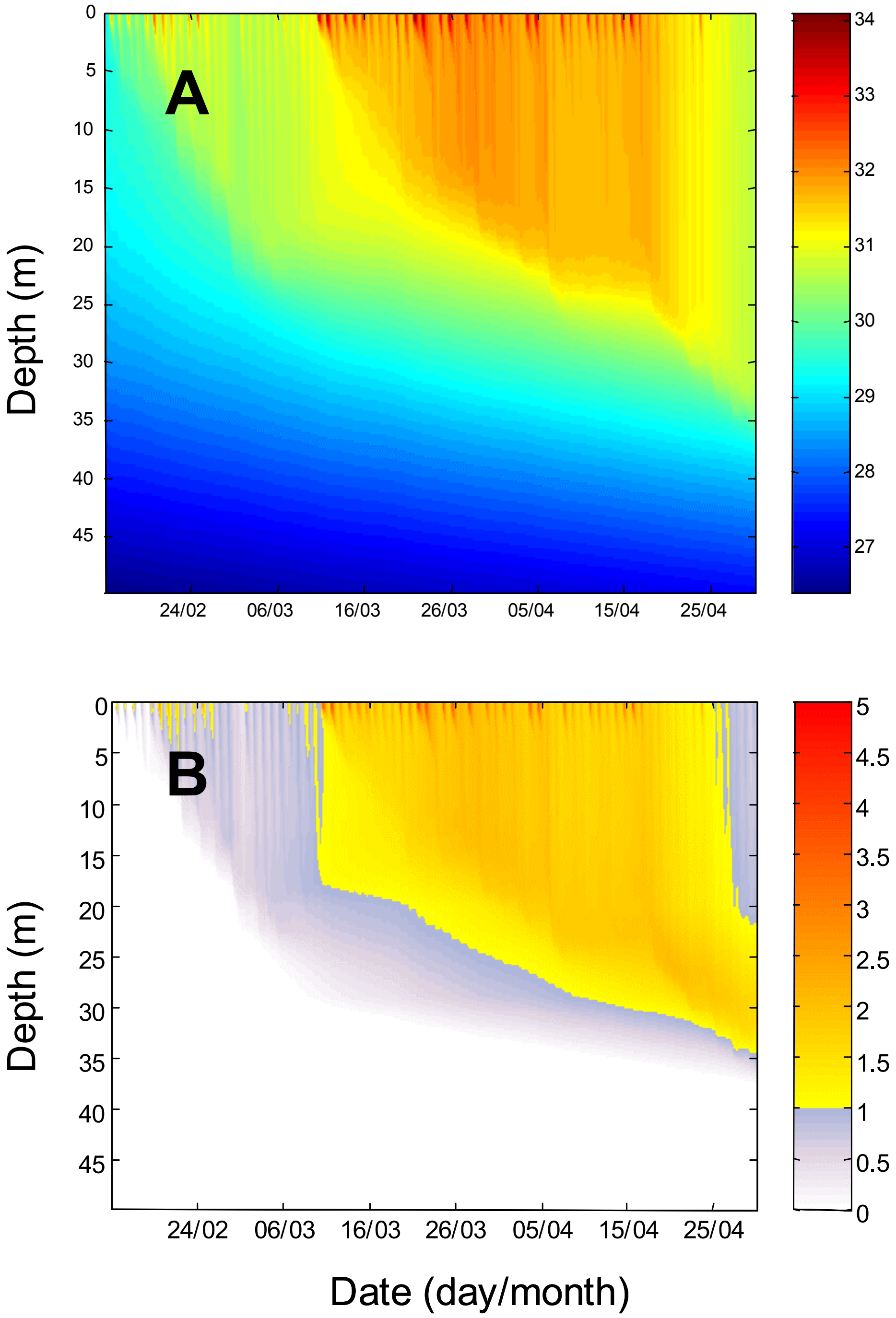

Figure 3.3 **Modelled temperature profile at Scott Reef for the period February - April 1998. A) absolute temperature; B) degrees above expected sea-surface water temperature.**

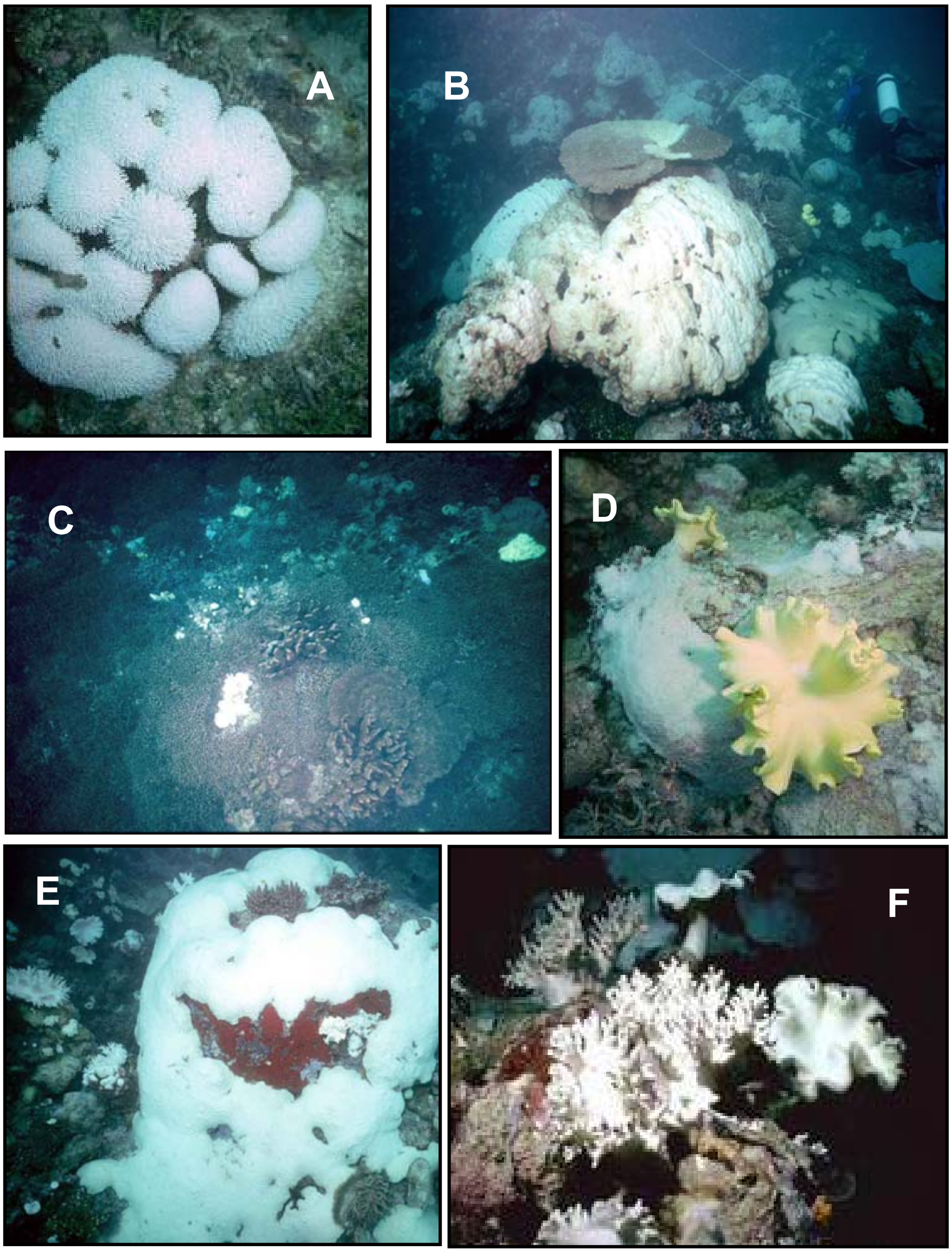

Figure 3.4 **Thermal induced coral bleaching at Scott Reef in June 1998, two months after the initial onset of the event; A) a bleached *Goniopora sp.* colony, B) a bleached community (SL4) in nine metres depth, C) all acroporids colonies have died and only bleached soft coral can be seen remaining, D) a bleached *Sacrophyton* soft coral surrounded by spicules from dead soft coral colonies, E) *Diploastrea helipora* colony surrounded by bleached soft corals, F) bleached soft corals**

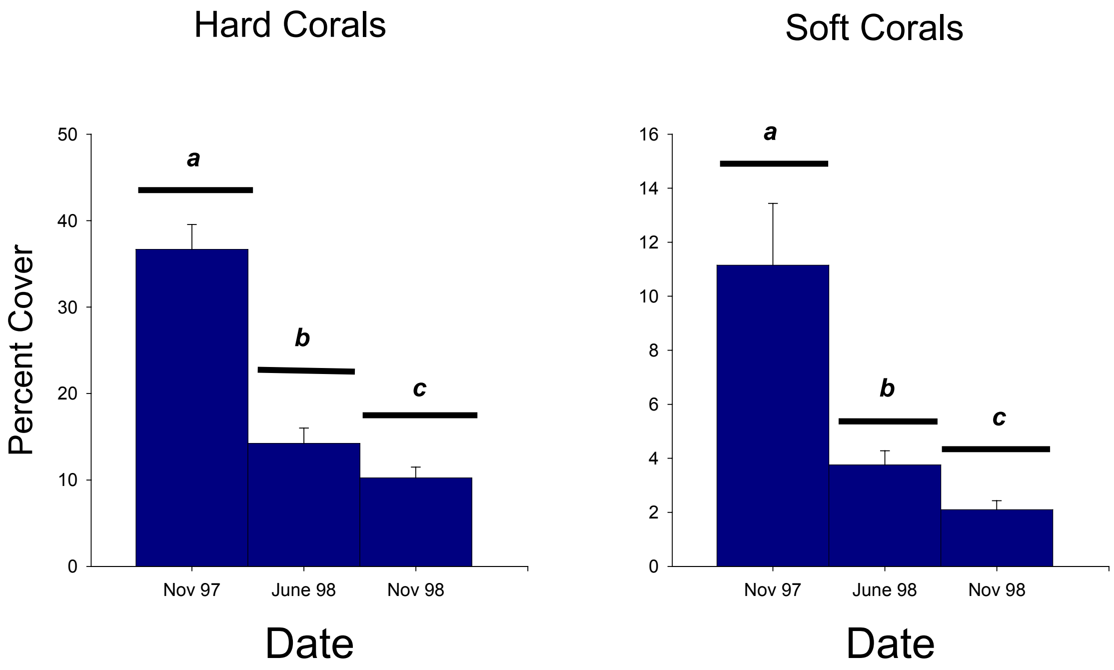

Figure 3.5 **Mean percent cover (± std error) of all hard and soft corals at Scott Reef during three surveys between November 1997 and November 1998. Lines represent means that are not significantly different ($p < 0.05$, Table 3.3).**

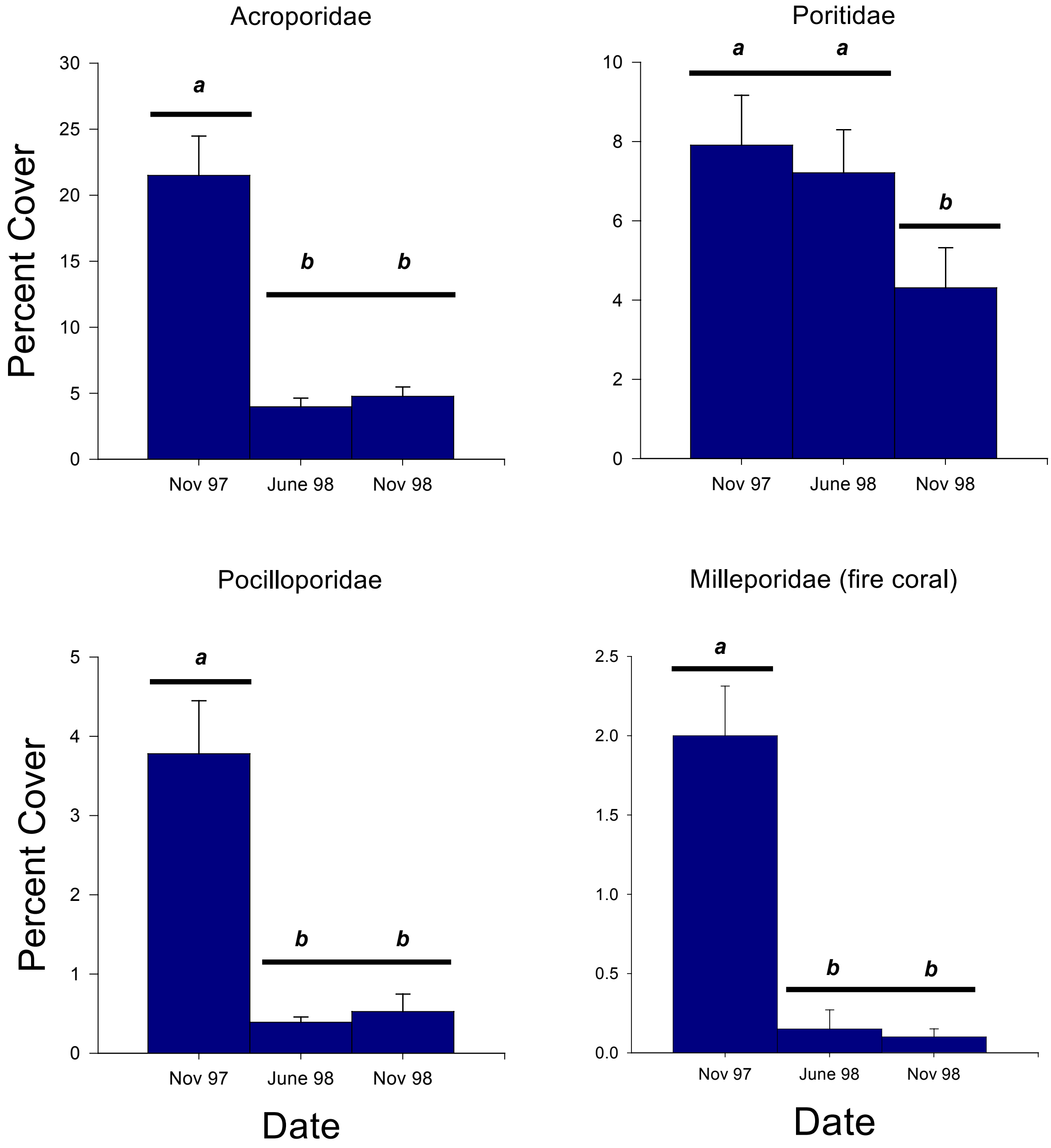

Figure 3.6 **Mean percent cover (± std error) of four major coral taxa at Scott Reef during three surveys between November 1997 and November 1998. Lines represent means that are not significantly different ($p < 0.05$, Table 3.3).**

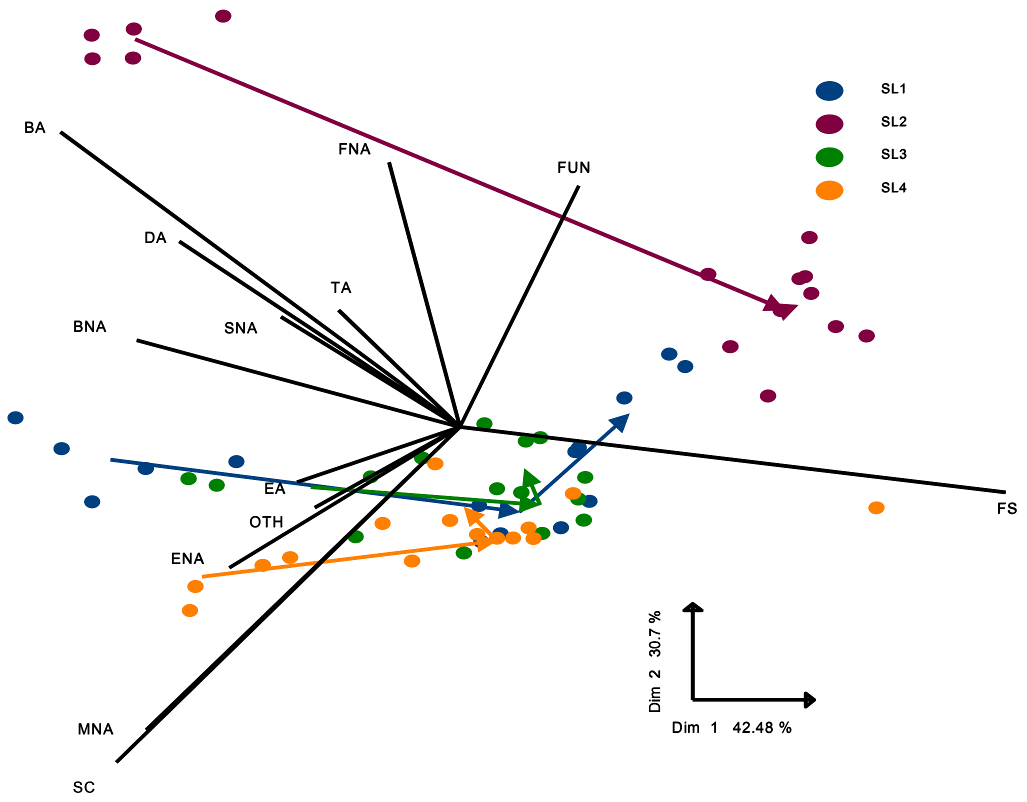

Figure 3.7 **PCA bi-plot of benthic community changes, as a result of the thermally-induced bleaching event at four locations at Scott Reef. Arrowed lines represent the shift in benthic communities at each location from time 1 to time 3. BA: Branching Acroporidae; DA: Digitate Acroporidae; TA: Tabulate Acroporidae; EA: Encrusting Acroporidae; SNA: Submassive non-Acroporidae; FNA: Foliose non-Acroporidae; BNA: Branching non-Acroporidae; ENA: Encrusting non-Acroporidae; MNA: Massive non-Acroporidae; FUN: Fungiidae; SC: Soft Coral; FS: Turf and Coralline algae**

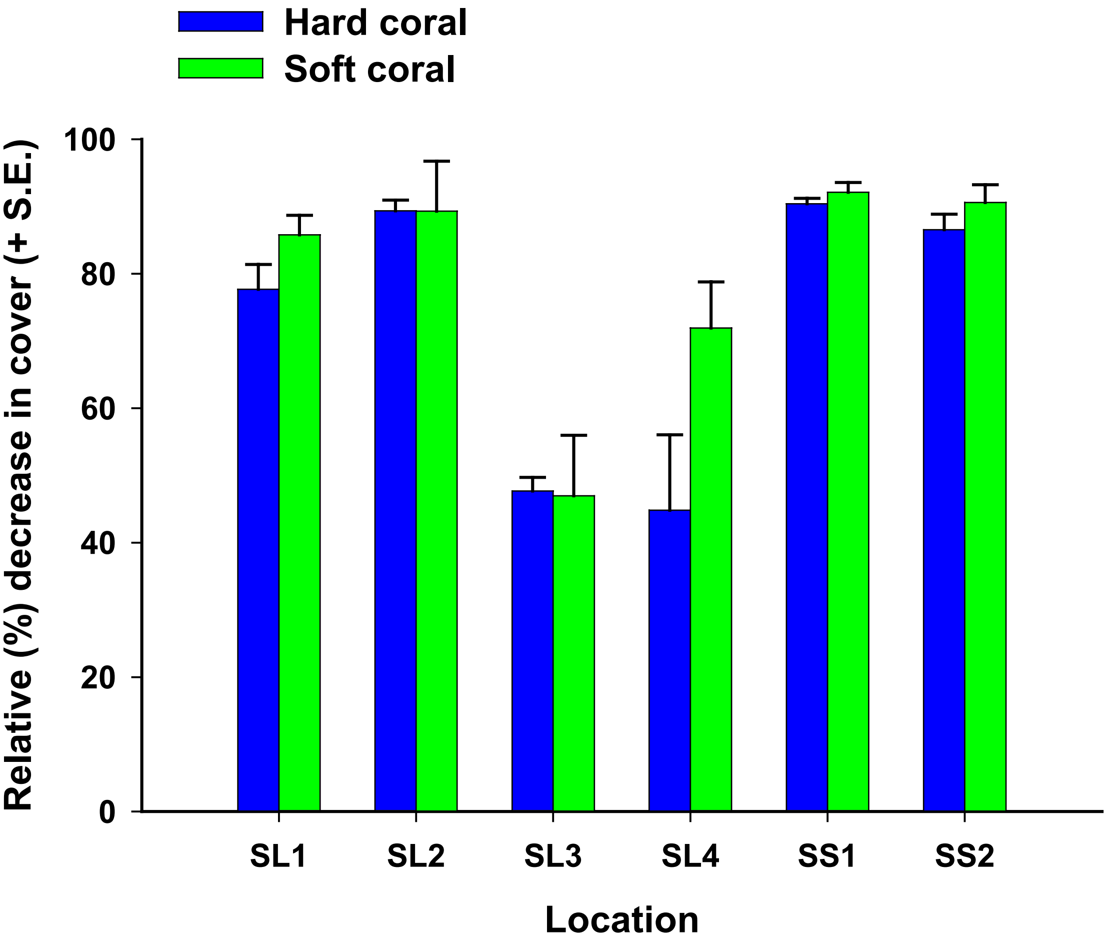

Figure 3.8 **Mortality of hard and soft coral (mean ± *s.e.*) as a result of the thermally-inducing bleaching event at Scott Reef in 1998. The decrease in overall percent cover is a comparison between November 1997 and November 1998. Each bar represents mean change in percent cover of 15 transects.**

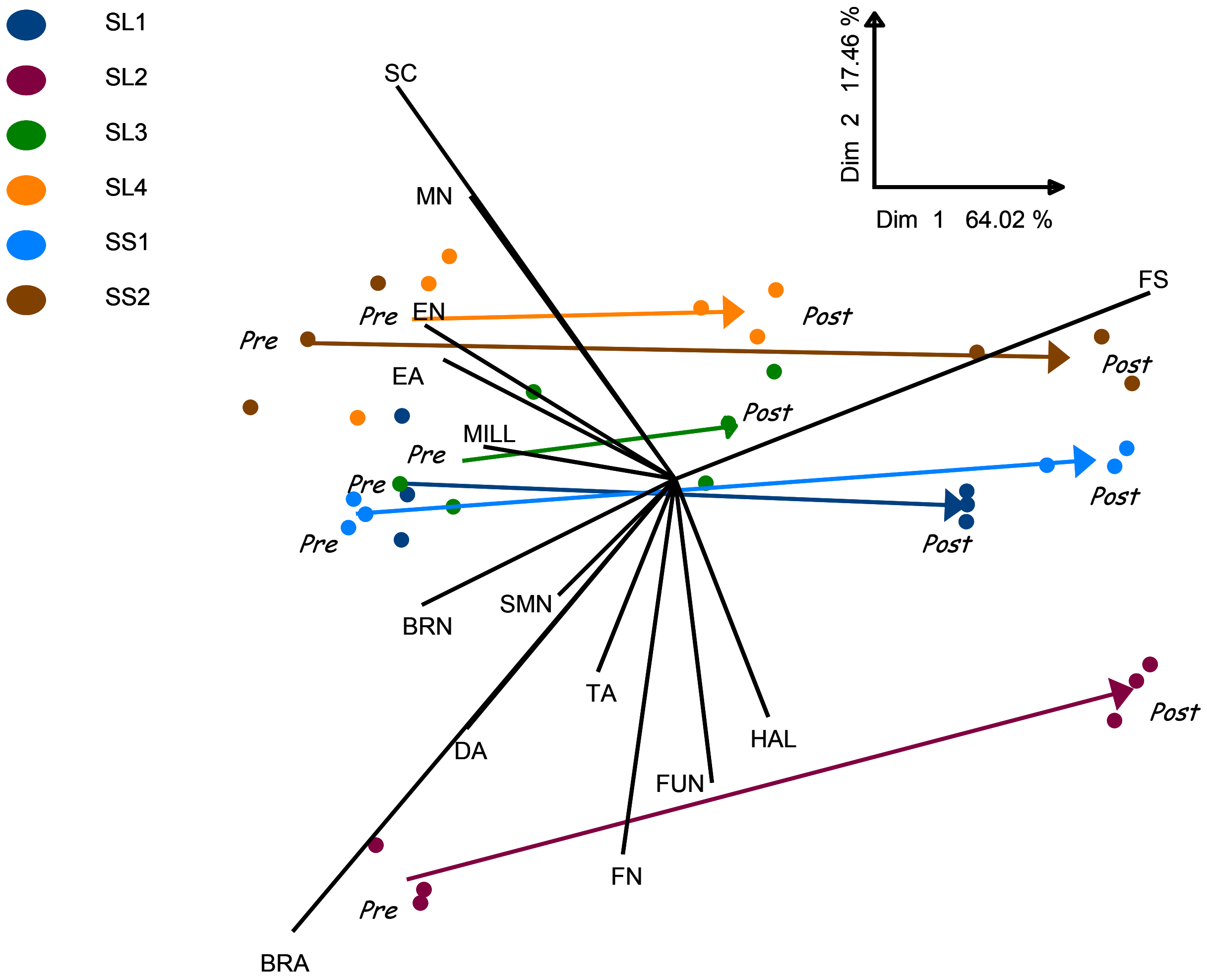

Figure 3.9 PCA bi-plot of benthic community changes, as a result a thermally-induced bleaching event at all reef slope monitoring locations at Scott Reef. Arrowed lines represent the shift in benthic communities at each location from November 1997 to November 1998. BA: Branching Acroporidae; DA: Digitate Acroporidae; TA: Tabulate Acroporidae; EA: Encrusting Acroporidae; SNA: Submassive non-Acroporidae; FNA: Foliose non-Acroporidae; BNA: Branching non-Acroporidae; ENA: Encrusting non-Acroporidae; MNA: Massive non-Acroporidae; FUN: Fungidae; SC: Soft Coral; FS: Turf and Coralline algae

Table 3.1 The mean percent cover of corals at the different habitats across the Scott Reef system and their relative decreases following the bleaching in 1998. The reef crest, lower reef crest, upper reef slope and reef slope habitats were averaged across monitoring locations at North Scott, South Scott and Seringapatam reefs. The shallow lagoon habitats were located at only North Scott.

Habitat	***Depth range (m)***	***Transect number***	***Transect length (m)***	***Mean Percent cover before bleaching (± s.e.)***	***Relative percent mortality as a result of the bleaching (± s.e.)***	***Mean Percent cover after bleaching (± s.e.)***
Shallow Lagoon	4 to 11	60	50	76.9 (± 2.4)	89.3 (± 4.8)	8.2 (± 1.9)
Reef Crest	0 to 1	18	20	42.6 (± 5.4)	83.6 (± 3.4)	6.9 (± 1.5)
Lower Reef Crest	2 to 4	18	20	48.3 (± 3.4)	85.1 (± 2.6)	7.2 (± 1.1)
Lower Reef Crest	5 to 6	18	20	58.2 (± 4.4)	79.1 (± 3.2)	6.3 (± 0.9)
Upper Reef Slope	8 to 11	105	50	49.1 (± 3.5)	74.0 (± 2.5)	7.9 (± 1.4)

Table 3.2 Mortality of the major coral groups associated with the bleaching event in 1998 averaged across monitoring locations at Scott Reef. Mean percent cover of each group before the bleaching is indicated in parentheses.

Coral group	**Mean percent mortality associated with the bleaching event**	**Mean percent cover November 1997**	**Mean percent cover November 1998**
Fungiidae	**25.0**	**1.2**	**0.9**
Massive non-*Acropora*	**54.8**	**19.1**	**10.5**
Foliose non-*Acropora*	**59.6**	**2.7**	**8.6**
Encrusting Soft Coral	**66.6**	**6.4**	**2.1**
Encrusting non-*Acropora*	**72.8**	**12.8**	**3.5**
Corymbose *Acropora*	**76.5**	**3.4**	**0.8**
Sub-massive non-*Acropora*	**76.9**	**2.5**	**0.6**
Capitate Soft Coral	**83.0**	**2.2**	**0.4**
Branching *Acropora*	**86.7**	**18.5**	**2.5**
Arborescent & Encrusting Soft Coral	**90.7**	**6.9**	**0.6**
Tabulate *Acropora*	**90.9**	**1.6**	**0.1**
Sub-massive *Acropora*	**91.4**	**5.6**	**0.5**
Branching non-*Acropora*	**94.2**	**7.9**	**0.4**
Milleporidae (fire coral)	**96.5**	**4.7**	**0.2**
Bottlebrush *Acropora*	**100.0**	**2.9**	**0.0**

Table 3.3 Comparison of mean coral abundance in three sampling periods between November 1997 and November 1998. Significantly different cells ($p < 0.05$) are shown in bold and the degrees of freedom for each cell is 32.

Taxonomic Group	**Nov '97 – Jun '98**	**Jun '98 – Nov '98**	**Nov '97 – Nov'98**
Hard Coral	**t = 20.23** **p < 0.001**	**t = 2.16** **p < 0.04**	**t = 20.39** **p < 0.001**
Family Acroporidae	**t = 18.57** **p < 0.001**	t = -1.46 p > 0.150	**t = 17.11** **p < 0.001**
Family Pocilloporidae	**t = 12.38** **p < 0.001**	t = -1.16 p > 0.25	**t = 11.22** **p < 0.001**
Family Poritidae	t = 0.948 p > 0.35	**t = 3.94** p < 0.001	**t = 4.89** **p < 0.001**
Soft Coral	**t = 8.39** **p < 0.001**	t = 2.16 p > 0.390	**t = 10.55** **p < 0.001**
Fire Coral Family Milleporidae	**t = 9.28** **p < 0.001**	t = -0.490 p > 0.960	**t = 9.23** **p < 0.001**

Chapter 4: SYSTEM-WIDE DECLINE IN CORAL COVER AND RECRUITMENT

4.1 INTRODUCTION

Coral reefs are increasingly exposed to disturbances acting over a range of spatial and temporal scales. Disturbances to coral reefs include the local effects of overfishing and sedimentation, and the regional effects of disease and declining water quality (see reviews by Knowlton 2001, Wilkinson 2002, Hughes *et al.* 2003, Bellwood *et al.* 2004). At a global scale, there is growing concern that a changing climate will affect the long-term health and resilience of coral reefs. Climate change is predicted to increase seawater temperatures and cause extensive and recurrent mass-bleaching of corals (Hoegh-Guldberg 1999, Sheppard 2003). In 1998, seawater temperature anomalies in the world's oceans affected 16% of coral reefs, many of which suffered catastrophic levels of mortality (Wilkinson 2000).

Effective management of coral reefs requires an understanding of how the scale and severity of different disturbances affect the demographic processes that underlie their replenishment and recovery. Traditionally, coral reef monitoring programmes have focussed on annual changes in percent cover of corals and other benthic organisms on reefs (see review by Connell 1997). While these studies are important in understanding yearly, and in some cases decadal changes in community structure, they provide limited understanding of the processes that underpin reef resilience (see Hughes *et al.* 2003, Smith *et al. 2005*). With increasing evidence that stock-recruitment relationships may routinely exist for many organisms at the scale of the reef (eg. corals, Hughes *et al.* 2000; fishes, Jones *et al.* 1999, Mora and Sale 2002, Underwood et al. *in press*), we need to understand how disturbances affect the supply and recruitment of larvae. In particular, at what scale and severity do disturbances dramatically reduce larval supply and recruitment? This question is becoming increasingly important for the management of coral communities, with evidence mounting that the scale of ecologically significant larval dispersal may be smaller than previously thought (Ayre and Hughes 2000, Whittaker 2004, Nishikawa and Sakai 2005, Underwood *et al.* 2007, *in press*), and that disturbances (eg. thermal bleaching, disease, declining water quality) are becoming geographically larger and more severe (Harvell *et al.* 1999, Hoegh-Guldberg 1999, Knowlton 2001). As a consequence, coral communities may be slow (or fail) to recover as severe disturbances become spatially larger than the distances over which their larvae routinely disperse.

Here I investigate how a severe mortality event affected the cover and recruitment of corals at an isolated reef system. Coral cover and rates of sexual recruitment were quantified from two years before to five years after a catastrophic thermal bleaching event that killed more than 75% of corals across an the entire reef system. My results show that to understand the resilience of reefs to disturbances requires the quantification of important demographic parameters, such as recruitment, in addition to the changes in coral cover and community structure.

4.2 METHODS

I assessed the impact of a severe thermal bleaching event on an isolated reef system by quantifying the changes in coral cover and rates of sexual recruitment. The system consists of three reefs, North Scott, South Scott and Seringapatam, which are located 270 km off the northwestern Australian coastline (Figure 4.1). The reef system is extensive, spanning 60 kilometres (north-south), and has 520 km^2 of hard substratum in depths of less than 40 m on which 233 species of hard coral from 56 genera reside (Veron 1986). Within the region, the closest reefs are the Ashmore group 240 km to the north, and the Rowley Shoals 400 km to the south. The isolation of the Scott Reef system, coupled with the lack of commercial fishing or human habitation, means it is relatively unaffected by common anthropogenic stressors to coral reefs.

To assess the long-term dynamics of benthic communities at the Scott Reef system, monitoring locations were established in 1994 at the reef slope habitat at North Scott (2), South Scott (4) and Seringapatam (1) reefs. At each location are three sites approximately 500 m apart (Figure 4.1). Each site consisted of five permanent 50 m transects, separated by approximately 10 m. Each transect followed the contour of the reef slope at approximately 9 m depth and was marked by steel rods at 10 m intervals. Monitoring sites were surveyed annually between 1995 and 1999, and in 2001 and 2004. During each survey, a 50 m tape was laid along each transect and a 30 cm wide strip of the substrata filmed using an underwater video camera. The resultant footage was analysed by pausing the video at 50 regular intervals along each transect and identifying the benthic category under each of five fixed points, giving a total of 250 points per transect. The percent cover of different families of hard coral were then calculated (see Ninio *et al*. 2003).

Surveys were also conducted at a range of other habitats to provide a more comprehensive understanding of the short-term (< year) effects of the thermal bleaching in 1998 across the Scott Reef system. At three locations (SL1, SL2, SL3), the reef crest (0 - 1 m), lower reef crest (2 - 4 m), and upper reef slope (5 - 6 m) habitats were surveyed in 1997 and 1999 (Table 4.1). At each habitat and location, six permanent 20 m transects were filmed and analysed as previously mentioned. However, during analysis the video footage was paused at 20 regular intervals. In addition, 20 randomly chosen sites were also surveyed in the shallow (4 - 15 m) lagoonal habitats at North Scott in 1999. At each site, three 50 m transects were placed haphazardly at intervals of approximately 15 m and filmed. The footage was analysed in the same manner as the 50 m reef slope transects. Changes in coral cover for the lagoonal communities following the 1998 bleaching event were calculated by estimating the area of colonies that had recently died and were covered in either turf or coralline algae.

In addition to coral cover, changes in the rates of coral recruitment were quantified annually from 1996 to 1999, and in 2002 and 2003, at the reef slope monitoring locations. At three sites at each of five locations at North and South Scott Reef, six terracotta settlement plates (110mm x 110mm x 10mm) were deployed at 50 m intervals on the reef slope (18 plates location^{-1}

year^{-1}) giving a total of 90 plates per year. The six plates at each site were spaced haphazardly, approximately 1 m apart, and attached to the reef (see Mundy 2000) two weeks (± 4 days) prior to full moon before the predicted mass coral spawning in autumn and collected eight weeks later (± 5 days). After collection, the settlement plates were bleached and the coral recruits identified to one of four taxonomic groups (Family Acroporidae, Pocilloporidae, Poritidae or Others) using a dissecting microscope (Figure 4.1). In total, 98% of the 540 plates deployed during this study were recovered.

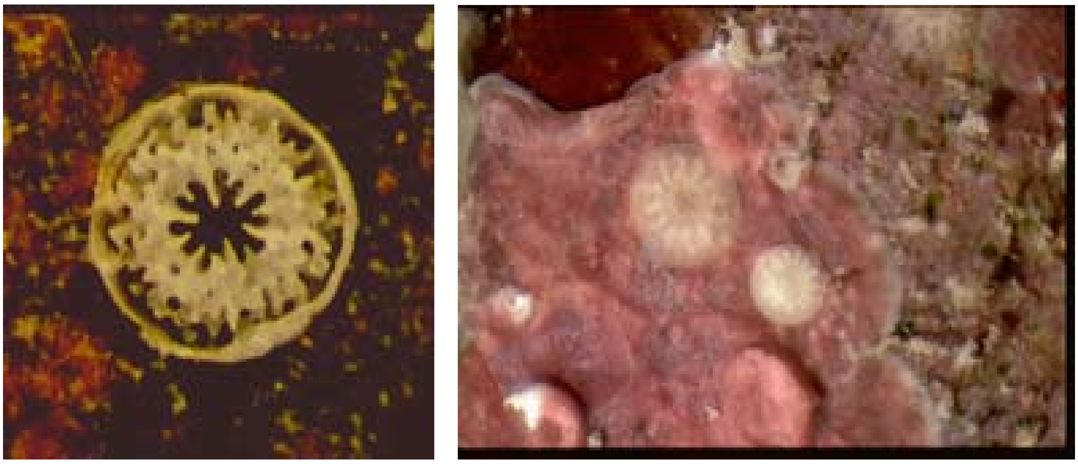

Figure 4.1 ***Acropora*** **recruits settled onto settlement plates (left: dead skeleton, right: newly settled recruits –**

Data Analysis

To compare changes in percent cover and recruitment of hard corals among locations, before and after the 1998 thermal bleaching, a set of customised contrasts were tested using linear mixed-effects models. The models were fitted using the /MIXED command and the contrasts using the /TEST command in the SPSS statistical software. The data used in the models were repeated site-level measurements of either coral cover (ie. mean of 5, 50 m transects) or recruitment (ie. mean of 6 plates) at the reef slope locations. The importance of temporal autocorrelation in the residuals was determined by fitting models both with and without first-order autoregressive correlation structure and then selecting the optimal model using Akaike Information Criteria (AIC; Burnham and Anderson 1998). All models in our analysis were fitted with an autogressive correlation structure.

The mixed-model contrasts were used to test whether the bleaching caused a significant change in mean hard coral cover and mean recruitment in the years prior to the thermal bleaching event, compared with the years following it, at each monitoring location and averaged across all locations. Additional temporal contrasts assessed whether there were significant differences in mean coral cover or recruitment, averaged across locations, between sampling years (Table 4.3). To satisfy the assumptions of the linear mixed-effects model, the recruitment data were transformed using the ln+1 function.

4.3 RESULTS

The mean cover of hard corals decreased significantly ($t = 30$, $df = 22$, $p < 0.001$, Table 4.1), from 49.1% (± 3.5 *s.e.*) prior to the bleaching to 12.9% (± 2.9 *s.e.*) six months later (Figure 4.2). Among the dominant families of hard corals at the reef slope locations, the Poritidae were least affected by the bleaching, having a relative decrease in cover of 47%, and many suffered partial- rather than whole-colony mortality (Figure 4.3). In contrast, most colonies of the other dominant families, such as the Acroporidae and Pocilloporidae, suffered whole-colony mortality and had a relative decreases in cover of more than 80%. Five years after the bleaching event, the coral communities at the Scott Reef system were slowly recovering. Mean coral cover at the reef slope locations increased significantly (t = 30, df = 22, $p < 0.001$, Table 4.2) from 12.9% (± 2.9 *s.e.*) in November 1998 to 19.8 % (± 2.0 *s.e.*) in November 2003 (Figure 4.2).

The mass mortality of hard corals caused a significant decrease in recruitment rates at all the reef slope locations across the Scott Reef system (Figure 4.2, Table 4.1). For example, rates of recruitment at SL1 fell from 168.9 (± 45.4 *s.e.*) recruits plate^{-1} prior to the bleaching, to 1.7 (± 0.5 *s.e.*) recruits plate^{-1} in the five years after. On average, there was a highly significant decrease in the annual rates of recruitment between the years before and after the bleaching of 97%, from 39.1 (± 12.6 *s.e.*) recruits plate^{-1} to 1.3 (± 0.2 *s.e.*), (t = 31.7, df = 22, $p < 0.001$; Table 4.2). However, the mean rates of recruitment in the years after the bleaching were increasing. The mean rate of recruitment across the Scott Reef system in was 0.8% (± 0.6 *s.e.*) of the pre-bleaching level in 1999, compared with 2.4% (± 0.5 *s.e.*) in 2001and 14.0% (± 2.5 *s.e.*) in 2003.

The relative decreases in the rates of recruitment were similar for all the dominant families of scleractinian corals, despite variable decreases in cover following the bleaching (Figure 4.3). The Family Acroporidae and Pocilloporidae suffered more than a 90% decrease in rates of recruitment, after a greater than 80% decrease in percent cover. Even the Family Poritidae suffered an 85% decrease in recruitment, despite a relative decrease in cover of only 47%.

4.4 DISCUSSION

The large and comparable decreases in both coral cover and recruitment following the 1998 thermal bleaching slowed the initial rates of recovery of the coral communities across the Scott Reef system. Recovery of communities devastated by catastrophic disturbances is usually facilitated by the arrival of new individuals onto the reef (Caley *et al.* 1996, Connell *et al*. 1997, Nystrom and Folke 2001). However, at the Scott Reef system the mean rate of coral recruitment in post-bleaching years was reduced by 97%, due to both the extent and severity of the disturbance and the isolation (> 240 km) of the system from unaffected reefs in the region. The comparable decreases in coral cover and recruitment following the bleaching, and the increases thereafter, provided evidence of a stock-recruitment relationship for Scott Reef, suggesting that the rates of recovery will increase with the abundance of adult corals.

While major disturbances that kill many corals on a reef are not uncommon (see reviews by Pearson 1981, Connell 1997, Karlson 1999), those of similar scale and severity to the bleaching associated mortality at Scott Reef are rare. Usually, the impacts of major disturbances are spatially patchy or species-specific. For example, crown-of-thorn starfish (*Acanthaster planci)* outbreaks tend to concentrate on reef slope communities and avoid some coral groups (Moran *et al.* 1986, Green *et al*. 1999), whereas cyclones cause most damage to branching species in exposed habitats than massive corals (Woodley *et al*. 1981, Bries *et al*. 2004, Halford *et al*. 2004). Even thermal bleaching events usually only impact a subset of reefs, habitats or species (Berkelmans and Oliver 1999, Marshall and Baird 2000, Shulman and Robertson 1996, Loya *et al*. 2001). As a consequence, adult corals from unaffected reefs or habitats can act as broodstock and replenish those areas most severely affected by a disturbance. However, the bleaching event reported here caused widespread coral mortality across all 520 km^2 of reef habitat and left few survivors to act as broodstock (Table 4.1). Given the spatial extent of the mortality at Scott Reef, a rapid recovery of the coral communities would rely heavily upon a large supply of larvae from unaffected reef systems, more than 240 km away. However, the velocity and complexity of surface currents in the region suggest larval transport times of at least 30 days between reef systems (Cresswell *et al.* 1978). Given most coral larvae are competent to settle within the first three weeks after birth (Ayre and Hughes 2000, Negri and Heyward 1999, Nishikawa *et al*. 2003, Nozawa and Harrison 2005, Miller and Mundy 2004, Wilson and Harrison 1998), it is not surprising that larval supply from unaffected reefs was insufficient to replenish the Scott Reef system. Furthermore, a recent study by Underwood (*in press*) found that for the broadcast spawning coral, *Acropora tenius*, larval supply from distant reefs (eg Rowley Shoals, Ashmore Reef) to Scott Reef is sufficient to avoid speciation but insufficient to effect reef recovery. That is, the population of *A. tenius* at Scott Reef is essentially self-seeding on ecological timescales.

Importantly, there were dramatic decreases in recruitment for all the dominant families of corals years after the bleaching, despite their different susceptibilities. In particular, the relative decreases in recruitment following the bleaching were similar (> 85%) among the dominant families, despite the Poritidae have much smaller relative decreases in cover (< 50%) than for the Acroporidae or Pocilloporidae (> 80%). This disproportionate reduction in recruitment for the Poritidae may be attributed to the decreased number and size (as a result of partial mortality) of individual colonies, causing lower per capita reproductive output (see Hall and Hughes 1996) and reduced rates of fertilisation due to lower colony densities (Oliver and Babcock 1992, Omori *et al.* 2001). Additionally, further decreases in the reproductive output of individual colonies may be due to the re-allocation of energy reserves to the repair and re-growth of injuries, rather than gamete production (Glynn 1993, Ward *et al.* 2000, Baird and Marshall 2002, Mendes and Woodley 2002). These data suggest the relationship between decreasing coral cover and recruitment may be non-linear, similar to the disproportionate increases in recruitment with an increasing percentage of gravid colonies that has been described previously (Hughes *et al.* 2000). Potentially, if the health, density and cover of corals decrease below a given critical mass, then dramatic reductions in recruitment may also occur, far above those expected. These results suggest that if coral cover on reefs around the world continue to decrease, then the potential exists for their resilience to decrease more rapidly than would otherwise be predicted.

The dramatic decline in coral recruitment following the bleaching at the Scott Reef system highlights the extent to which important demographic parameters, that underlie the resilience of reefs, can be affected by the varying levels of impact occurring on reefs around the world. The Caribbean is suffering a region-wide decline in corals, with 80% lost in the last few decades (Hughes 1994, Gardner *et al.* 2003), the Great Barrier Reef (GBR) could be suffering a similar fate (Bellwood *et al*. 2004), and as many as 30% of reefs, globally, are estimated to have been severely damaged by disturbances occurring in the last decade(s) (Wilkinson 2002). Disturbances occurring over entire regions are predicted to become more severe and frequent (eg. Indian Ocean, Sheppard 2003; GBR, Hoegh-Guldberg 1999; Caribbean, Gardner *et al.* 2003). The result would be major declines in the regional abundances of corals, leading to a disproportionate reduction in recruitment and much slower rates of recovery than previously observed. These data suggest that a regional approach to coral reef management is required, one which takes into account the scale over which the processes of disturbance and recovery occur, in order to ensure reefs are resilient to the cumulative effects of both natural and anthropogenic impacts.

Table 4.1 The percentage cover of corals at the different habitats across the Scott Reef system and their relative decreases following the bleaching in 1998. The reef crest, lower reef crest, upper reef slope and reef slope habitats were located at North Scott, South Scott and Seringapatam reefs. The shallow lagoon habitat was located at North Scott.

Habitat	Depth range (m)	Transect number	Transect length (m)	Percentage cover before bleaching (± s.e.)	Relative (%) decrease after bleaching (± s.e.)
Shallow Lagoon	4 to 11	36	50	76.9 (± 2.4)	89.3 (± 4.8)
Reef Crest	0 to 1	36	20	42.6 (± 5.4)	83.6 (± 3.4)
Lower Reef Crest	2 to 4	36	20	48.3 (± 3.4)	85.1 (± 2.6)
Upper Reef Slope	5 to 6	18	20	58.2 (± 4.4)	79.1 (± 3.2)
Reef Slope	8 to 11	105	50	49.1 (± 3.5)	74.0 (± 2.5)

Table 4.2: Temporal mixed-model contrasts comparing mean coral cover and mean recruitment between specific years. The recruitment data were transformed (ln+1).

Group	**Temporal contrast**	***d.f.***	***t-value***	***P***
Cover	*1997 versus 1998*	78	-41.1	**< 0.001**
	1998 versus 2004	93	6.3	**< 0.001**
	1999 versus 2004	89	7.6	**< 0.001**
	2001 versus 2004	78	7.2	**< 0.001**
Recruitment	*1997 versus 1998*	37	-19.7	**< 0.001**
	1998 versus 2003	42	1.8	> 0.07
	1999 versus 2003	46	8.8	**< 0.001**
	2002 versus 2003	37	9.1	**< 0.001**

Table 4.3: Mixed model contrasts comparing mean coral cover and mean recruitment in the years prior to the 1998-bleaching compared to the years after, for each monitoring location and averaged across all locations., The recruitment data were transformed (ln+1) (note: * - no analysis as a result of missing data).

	Percent Cover			**Recruitment**		
Location	*d.f.*	*t-value*	*P*	*d.f.*	*t-value*	*P*
SL1	65	-10.5	**< 0.001**	22	-28.6	**< 0.001**
SL2	65	-19.3	**< 0.001**	22	-11.6	**< 0.001**
SL3	65	-7.4	**< 0.001**	22	-12.5	**< 0.001**
SL4	65	-5.7	**< 0.001**	22	-10.6	**< 0.001**
SS1	65	-18.3	**< 0.001**	22	-7.6	**< 0.001**
SS2	69	-13.6	**< 0.001**	*		
SS3	65	-16.8	**< 0.001**	*		
ALL	65	-22.7	**< 0.001**	22	-31.7	**< 0.001**

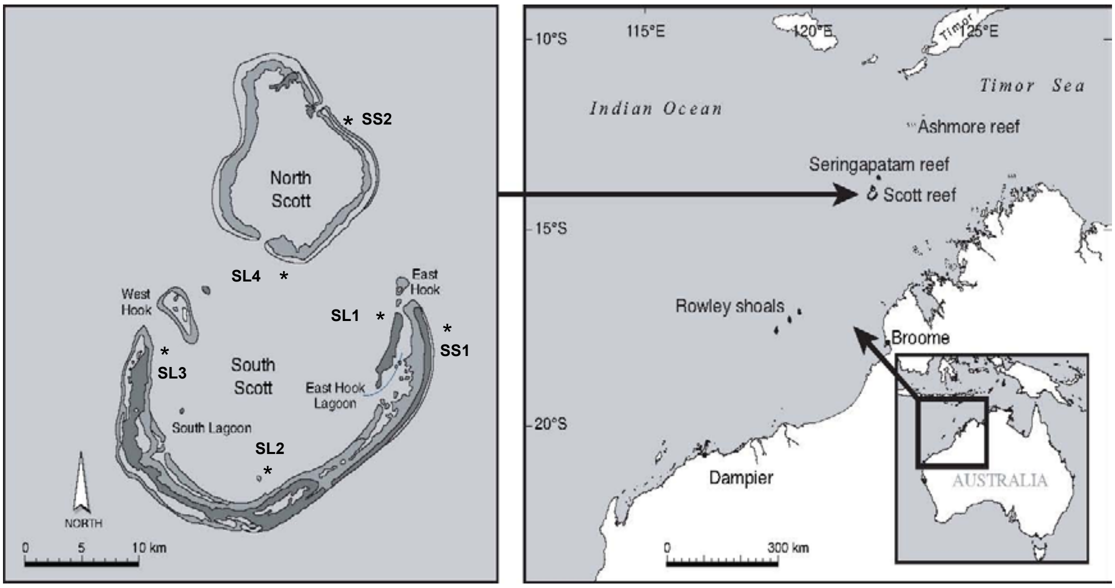

Figure 4.2: **Position of the Scott Reef system and the monitoring locations. The monitoring location at the Seringapatam Reef is on the northwest flank of the reef.**

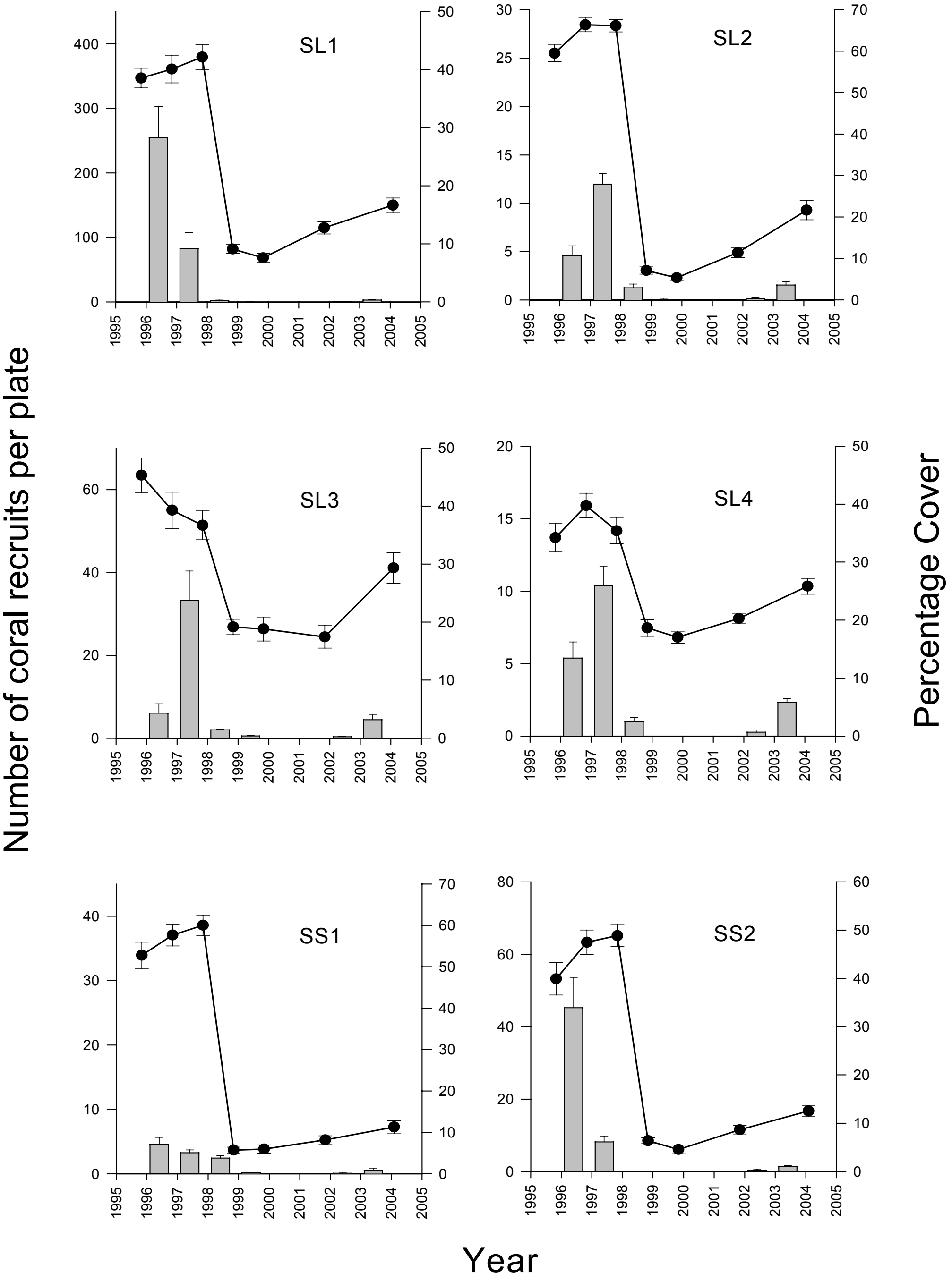

Figure 4.3: **Mean (± *s.e.*) percent cover of hard corals (line) and their rates of recruitment (bar) for sites at each monitoring location on the reef slope, from 1995 to 2004. Note that recruitment data were not collected in 2000 and 2001 for all locations. In addition, either percent cover or recruitment data exists for Location SS2 in 1998 and 1999.**

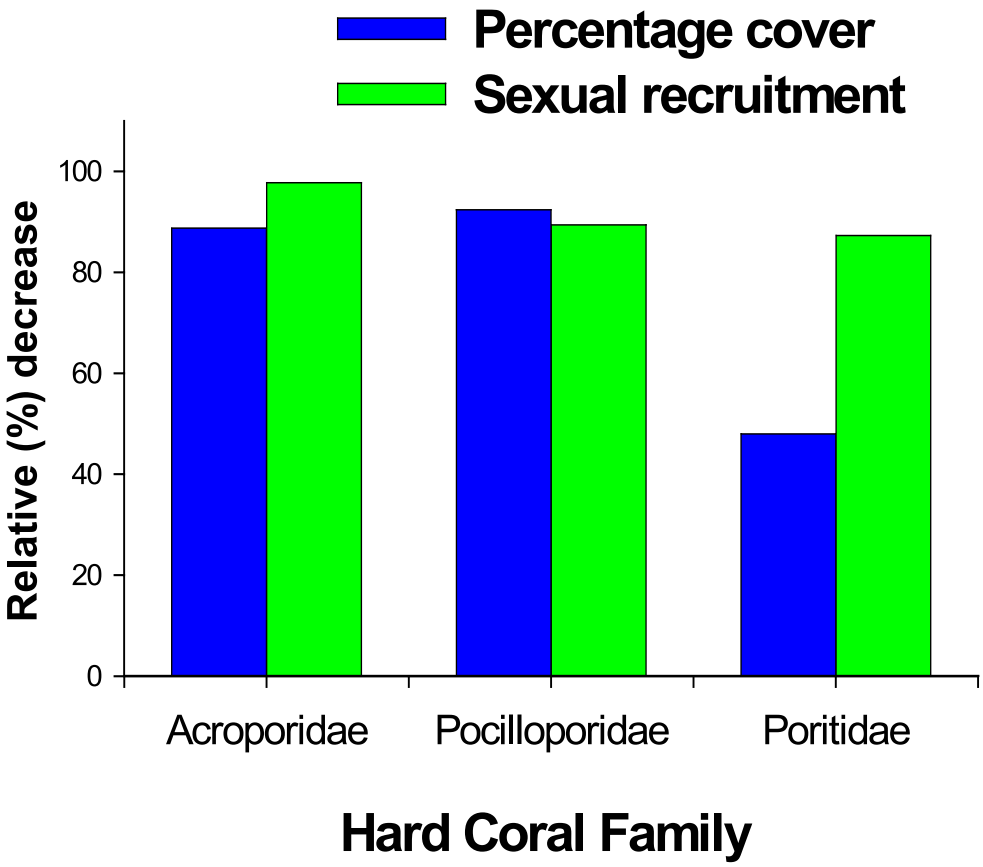

Figure 4.4: The relative decreases in the mean percent cover and rate of recruitment for three of the dominant coral families at Scott Reef, before and after the 1998 bleaching event. For example, there was a relative decrease in the percent cover of the Family Poritidae of 47%, from 10.8 % (mean cover 1995 to 1997) to 5.6 % (mean cover 1998, 1999, 2001, 2003) and an 88% relative decrease in recruitment, from 0.54 to 0.067 recruits plate^{-1} yr^{-1}.

Chapter 5: CHANGES IN POPULATION SIZE-STRUCTURE OF THREE GROUPS OF SCLERACTINIAN CORALS

5.1 INTRODUCTION

There are many reports of the catastrophic mortality of corals following mass-bleaching events that cause changes in community assemblage (e.g., Shulman and Robertson 1996, McClanahan *et al.* 2001, Aronson *et al.* 2000). The extent to which these are long-term changes, whereby there is a change in the dominant species of corals, or corals are replaced by other benthic organisms such as algae, becomes clear only after many years of monitoring of percentage cover. There are, however, currently very few long-term studies documenting community dynamics before and after mass-bleaching events. More information about the impact of disturbances such as bleaching events on coral communities, and their potential for recovery, can be obtained from changes in population structures, particularly because the life history traits of corals are so strongly influenced by their size (Hughes and Jackson 1980, Babcock 1991, Baird and Marshall 2002).

Changes in the number of colonies of different size and/or stage classes provide more information about the consequences of observed changes in percentage cover. For example, similar changes in percentage cover can result from injury to a few large adults or from the mortality of many juvenile sized colonies, but the two will have very different consequences for community dynamics in the future. Thus, changes in population structure also provide information about the potential rates of recovery following bleaching by indicating how different life history stages are affected. Recovery following disturbance is likely to be faster if colonies are injured, rather than killed, and if larger colonies of reproductive size are less affected than smaller size classes. There is some evidence that bleaching is less selective than many disturbances, causing mortality, rather than injury, across size classes (e.g., Baird and Marshall 2002, Loya *et al.* 2001, Kayanne *et al.* 2002). In addition to the severity of a bleaching event, the rates of recovery of communities of corals will vary according to scale of the disturbance at a reef and the supply of sexual recruits from adjacent reefs. Patterns of bleaching and post-bleaching mortality of corals are often spatially heterogeneous, even within species (Hoegh-Guldberg and Salvat 1995, Shulman and Robertson 1996, McField 1999, Marshall and Baird 2000, Aronson *et al.* 2000). Coral communities that escape mass-mortality make an important contribution to the recovery of the rest of the reef through the growth of the survivors and the production of sexual and asexual recruits (Glynn 1993). Populations of corals that have recovered quickly from mass-bleaching usually have a supply of recruits from sites that were less affected, or from nearby reefs (e.g., Brown and Suharsono 1990, Kayanne *et al.* 2002, Loch *et al.* 2002). If, however, a bleaching event is of such scale and severity that it affects most corals of many species on a reef, or group of reefs, then recovery is likely to take far longer. This is particularly true for reef complexes that are reproductively isolated, either being beyond the routine distances of larval dispersal or not in the direction of larval supply (Ayre and Hughes 2003).

In this study I present long-term changes in the percentage cover and population structures of three common groups of corals at an isolated reef, before and after a catastrophic mass-bleaching event. The percentage cover of corals in the Subgenus *Acropora*, Subgenus *Isopora* and Family Pocilloporidae was quantified at repeated censuses four years before and five years after mass-bleaching, and was interpreted relative to changes in the density of colonies and the proportion of different life history stages. The short- and long-term prospects of recovery are inferred from these data.

5.2 MATERIALS AND METHODS

5.2.1. Percentage cover of corals

Thirteen monitoring locations were established at Scott and Seringapatam Reefs in 1994 (see Heyward *et al.* 1997). Here I present changes in percentage cover and population structure at three representative locations at Scott Reef (L1, L2 and L3; Figure 5.1). The communities at each location are dominated by corals in the Genus *Acropora* and Family Pocilloporidae. On average, corals in these groups cover 34.3 ± 4.7% of the substrata at the three study locations, and make up almost 70% of the total hard coral cover. Each location consisted of three sites on the reef slope at approximately 9 m depth, separated by approximately 300 m. At each site were five permanent 50 m transects separated by approximately 10 m. Transects were filmed in October 1994, 1996, 1998, 2001 and 2003, and the percentage cover of benthic categories estimated using a point intercept method (*see Chapter 4 for video transect methodology*).

5.2.2. Population structure of corals

The number and size of colonies in the Subgenus *Acropora* and Family Pocilloporidae was quantified at five of the 50 m transects at each of the monitoring sites in 1996, 1998 and 2003. Along each 50 m transect, the maximum linear dimension of all colonies larger 10 cm was measured in belt transects one metre wide. Colonies less than 10 cm were measured in 25 cm belt transects, allowing for a more intensive search of smaller colonies. Colonies smaller than 5 cm were classed as juveniles, 5 to 15 cm as small adults, and greater than 15 cm as large adults. The size-structure of *Isopora* colonies was not quantified because the dominant species formed large stands and it was impossible to distinguish individuals.

5.3 RESULTS

5.3.1. Pre-bleaching percentage cover and population structure

In the years prior to the bleaching, the transects and sites within each location had very similar percentage cover of Acropora and Isopora, although this was less so for the Pocilloporidae. However, among the locations there was much greater variation in the cover of the different genera (Figure 5.2). By far the highest cover of Acropora was at Location 1, and the mean cover increased from around 14% to 23% over two years. In contrast, the mean cover of Acropora was much lower and more stable over the same period than at the other two locations, at around 5% at Location 1 and 3% at Location 3. As with the Acropora, the cover of the Isopora varied among the locations and through time. Over two years, the cover of Isopora at Location 3 increased from 22% to 27%, and from 8% to 14% at Location 2, but remained at around 2% at Location 1. The Pocilloporidae had the lowest cover that was most similar among the locations. The mean cover of Pocilloporidae ranged between approximately 0.3 and 0.7% at each of the locations over two years.

The structure of populations of *Acropora* and Pocilloporidae at each location prior to the bleaching reflected their mean percentage cover (Figure 5.3). There were approximately 5 times as many *Acropora* colonies at Location 1 and Location 2 than Pocilloporidae colonies, but less than twice as many at Location 3. For the *Acropora*, there were far more colonies at Location 1 and Location 2, having a density (10m^2) of 879 at Location 1 and 928 at Location 2, compared with 114 at Location 3. However, there were almost twice as many colonies of small adult and large adult size at Location 2 than at Location 1, resulting in the large differences in their percentage cover. For the Pocilloporidae, there were 157 colonies at Location 1 ($10m^2$) and 173 at Location 2, but only 72 at Location 3.

Despite the differences in the density of *Acropora* and Pocilloporidae colonies among the locations, the relative abundances of life history stages were similar, particularly for the Pocilloporidae (Figure 5.3). For the *Acropora* at all locations, between approximately 50 and 70% of colonies were juveniles, 15 and 40% were small adults, and 10 and 20% were large adults. For the Pocilloporidae, between 35 and 45% of colonies at all locations were juveniles, between 40 and 50% small adults, and between 10 and 15% were large adults.

5.3.2. Post-bleaching percent cover and population structure

The bleaching caused catastrophic mortality of corals in all three groups of coral across all transects, sites and locations at Scott Reef, resulting in >85% relative decrease in cover at each location six months later. Percentage cover at all locations had decreased from between 4 and 23% to < 0.3% in the *Acropora*, from between 2 and 27% to < 0.15% in the *Isopora*, and between 0.4 and 0.6% to < 0.1% in the Pocilloporidae (Figure 5.2). There was a corresponding decrease in the density of colonies, with the number of *Acropora* and Pocilloporidae decreasing by more than 90% at all locations, apart from an 85% decrease in *Acropora* at Location 1 and a 77% decrease in Pocilloporidae at Location 3 (Figure 5.3). However, the decreases in the proportion of life history stages varied among the locations, and the mortality of colonies was independent of their size.

Five years after the bleaching, there was only limited recovery at all locations, particularly for the Isopora. On average, the percentage cover of *Acropora* and Pocilloporidae at all locations had increased to around 30% of their pre-bleaching levels, but to only 6% for the *Isopora*. For each group of corals there were similar increases in cover among the locations, but there was some evidence that recovery was faster at locations with the highest cover remaining after the bleaching, and that with increasing cover came increasing rates of recovery. Location 1 and Location 2 for the *Acropora*, and Location 1 for the Pocilloporidae, had the highest remaining cover after the bleaching and the highest cover five years later. Additionally, as the percentage cover at each location increased, so did the annual rates of recovery. For example, at all locations the increases in percentage cover of *Acropora* and Pocilloporidae three years after the bleaching in 2001 were followed by similar or greater relative increases two years later in 2003 (Figure 5.2).

The density of colonies five years after the bleaching varied among the locations, relative to their pre-bleaching value (Figure 5.3). For the *Acropora*, the number of colonies at Location 1 and Location 2 were less than half those prior to the bleaching, but there were 30% more at Location 3; for the Pocilloporidae, there was a similar number at Location 1 and Location 3, and 45% more at Location 2. There was no clear pattern of change in the structures of the populations of *Acropora* or Pocilloporidae at any of the locations as they recovered, with no obvious increases in the proportion of colonies of juvenile or small adult size. However, at the locations where the density of colonies was similar or greater than before the bleaching, the number of large adult colonies was less than half of the pre-bleaching number, explaining the lack of recovery of percentage cover. Apart from these differences, the relative proportion of colonies of different life history stages was similar among all the censuses.

5.4 DISCUSSION

The bleaching of corals at Scott Reef resulted in the mass-mortality of *Acropora*, *Isopora* and Pocilloporidae across all locations, from which there was limited recovery five years later. Many other studies at Pacific and Indo-Pacific reefs have also documented dramatic declines in the cover of these corals following their bleaching (Brown and Suharsono 1990, Marshall and Baird 2000, Loya *et al.* 2001, Kayanne *et al.* 2002, Loch *et al.* 2002). Importantly, the patterns of post-bleaching mortality at Scott Reef displayed very little spatial variation, with the decreases in percentage cover being similar at all transects, sites and locations.

Despite being among the most susceptible coral to bleaching, the *Acropora*, *Isopora* and Pocilloporidae are often the first to recover and species may quickly occupy space that becomes available following bleaching (Hoegh-Guldberg and Salvat 1995, Baird and Marshall 2002, McClanahan 2004). In particular, brooding corals such as the *Isopora* and Pocilloporidae may be successful at colonising available substrata after bleaching events because they tend to reproduce sooner and more regularly than spawning corals (Hoegh-Guldberg and Salvat 1995, Glynn 1993). Conversely, because they are the most susceptible, there are examples where species of these corals have become locally extirpated following catastrophic bleaching events (e.g., Brown and Suharsono 1990, McClanahan 2000, Sheppard *et al.* 2000, Loya *et al.* 2001), suggesting there is a critical threshold of cover below which recovery is far slower, or not possible (Glynn 1993).

Five years after the bleaching event at Scott Reef there was only limited recovery, with the percentage cover of *Acropora* and Pocilloporidae having increased to around 30% of their pre-bleaching levels, and the *Isopora* to around 6% of their pre-bleaching levels. However, percentage cover provides limited information about future recovery if new recruits and juveniles make an insignificant contribution to cover. Increases in the number of juvenile colonies and small adults at Scott Reef at the final census, particularly for the Pocilloporidae, suggest future increases in percentage cover will follow in the absence of disturbance. The slow recovery of corals at all locations at Scott Reef system can be attributed to the scale and severity of the bleaching event, and to their relative isolation from other unaffected reefs.

The potential recovery of coral communities is largely determined by the size of the survivors and the rates of sexual and asexual recruitment to the available substrata, which are affected by the scale and severity of the bleaching event. At Scott Reef, the bleaching caused similar levels of mortality at all spatial scales and there were no sites or locations with a high level of coral cover remaining. Additionally, the bleaching was of such severity that it resulted in the mortality of colonies of all life history stages, rather than just injuring corals or disproportionately removing smaller size classes and leaving adults. The lack of selectivity displayed by bleaching in its affects on the *Acropora*, *Isopora* and Pocilloporidae has been documented previously, and will greatly slow their rates of recovery (Baird and Marshall 2002, Loya *et al.* 2001).

In addition to the scale and severity of the bleaching event, the slow recovery of corals at Scott Reef can be attributed to their isolation from other reef systems. Population structures and observations at the study sites provided no evidence of cohorts of sexual larvae recruiting from adjacent reefs not affected by the bleaching. The closest reefs to the north and south are more than 240 km away and larvae are unlikely to routinely travel these distances following spawning events, based on larval ecology and oceanographic data for the region. The brooded larvae of *Isopora* and Pocilloporidae probably disperse over much shorter distances than those of the spawning *Acropora* (Harrison and Wallace 1990, Ayre and Hughes 2000). Large-scale water movements in the region of north-western Australia suggest that even if larvae of spawning corals travelled directly between Scott and the nearest reefs, it would take them more than 25 days (Creswell *et al.* 1978). This is a minimum dispersal time that is approaching the upper optimal competency period for larvae (e.g., Heyward and Negri 1999), so the routine recruitment of a large number of larvae to Scott Reef from the adjacent reef systems is unlikely to occur.

Changes in percentage cover and population structures suggest that the coral communities at Scott Reef will continue to recover slowly in the absence of major disturbance, or at increasing rates, despite their isolation. Scott Reef has a good potential for recovery because the available substrata that was created following the bleaching has not been occupied by competitors such as algae or sponges that could exclude coral recruits and cause a longer term phase-shifts in community assemblage (e.g., Shulman and Robertson 1996, Ostrander *et al.* 2000, McClanahan *et al.* 2001, Aronson *et al.* 2002). In such cases, the effects of acute bleaching are often compounded by additional chronic stresses, such as over fishing, sedimentation, and nutrient inputs. At Scott reef, macroalgae and even turfing algae are rare, and its isolation means it is free of many chronic disturbances that some nearshore reefs experience. Much of the available substrata at Scott has been colonised by crustose coralline algae that induces settlement of coral larvae, of which some species can potentially increase post-recruitment survival of larvae (Raimondi and Morse 2000, Harrington *et al.* 2004). Thus, despite apparently having a strong stock-relationship, recovery of coral cover at Scott Reef is likely to occur, albeit over decades, in the absence of other major disturbances.

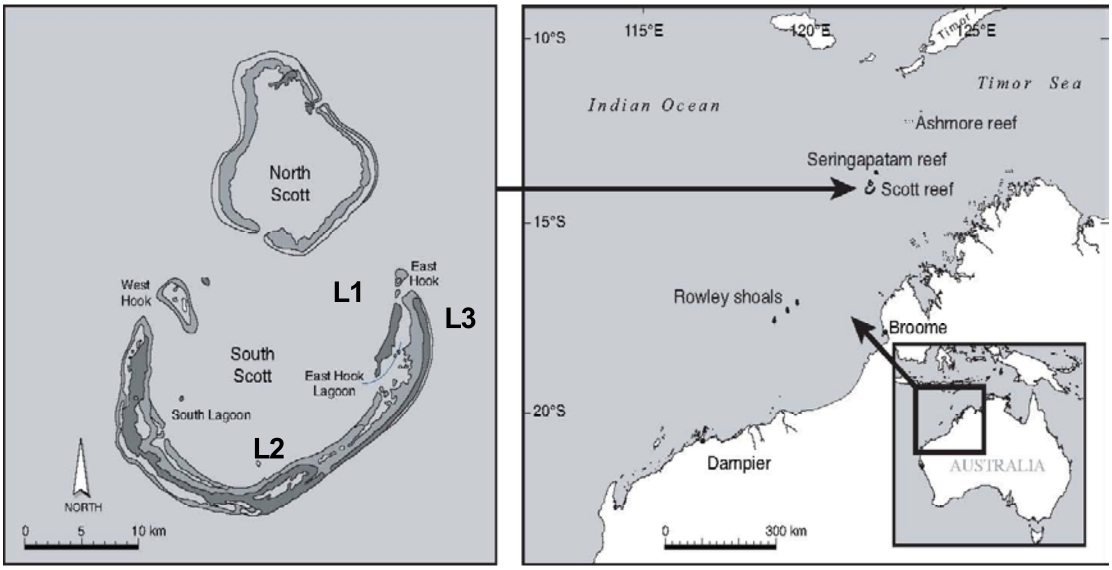

Figure 5.1 **Position of Scott Reef and the three study locations (L) off north-western Australia. Changes at the coral communities at each of the three locations are representative of those observed at an additional 11 locations at North Scott and Seringapatam Reefs.**

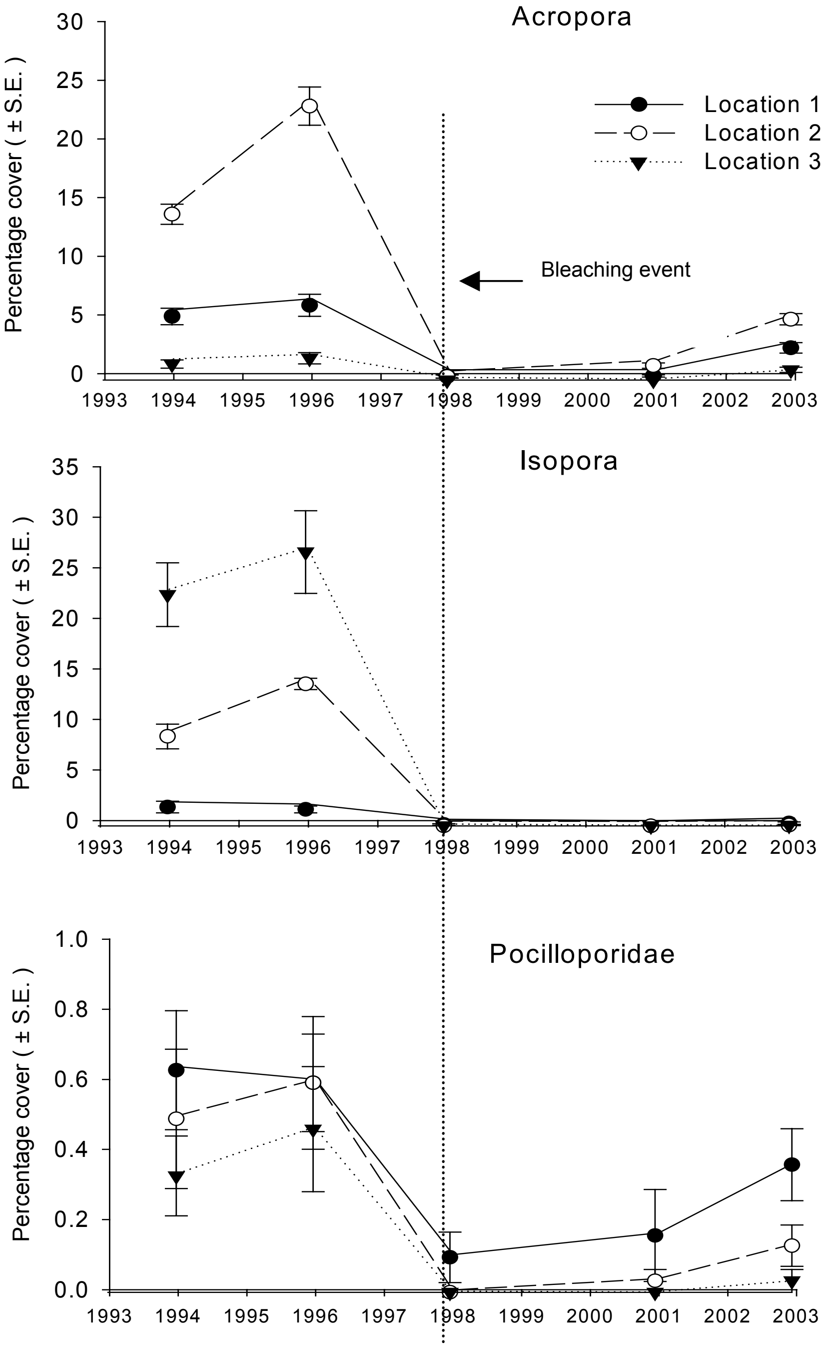

Figure 5.2 **Changes in the percentage cover of Acropora, Isopora and Pocilloporidae between surveys conducted in October each year.**

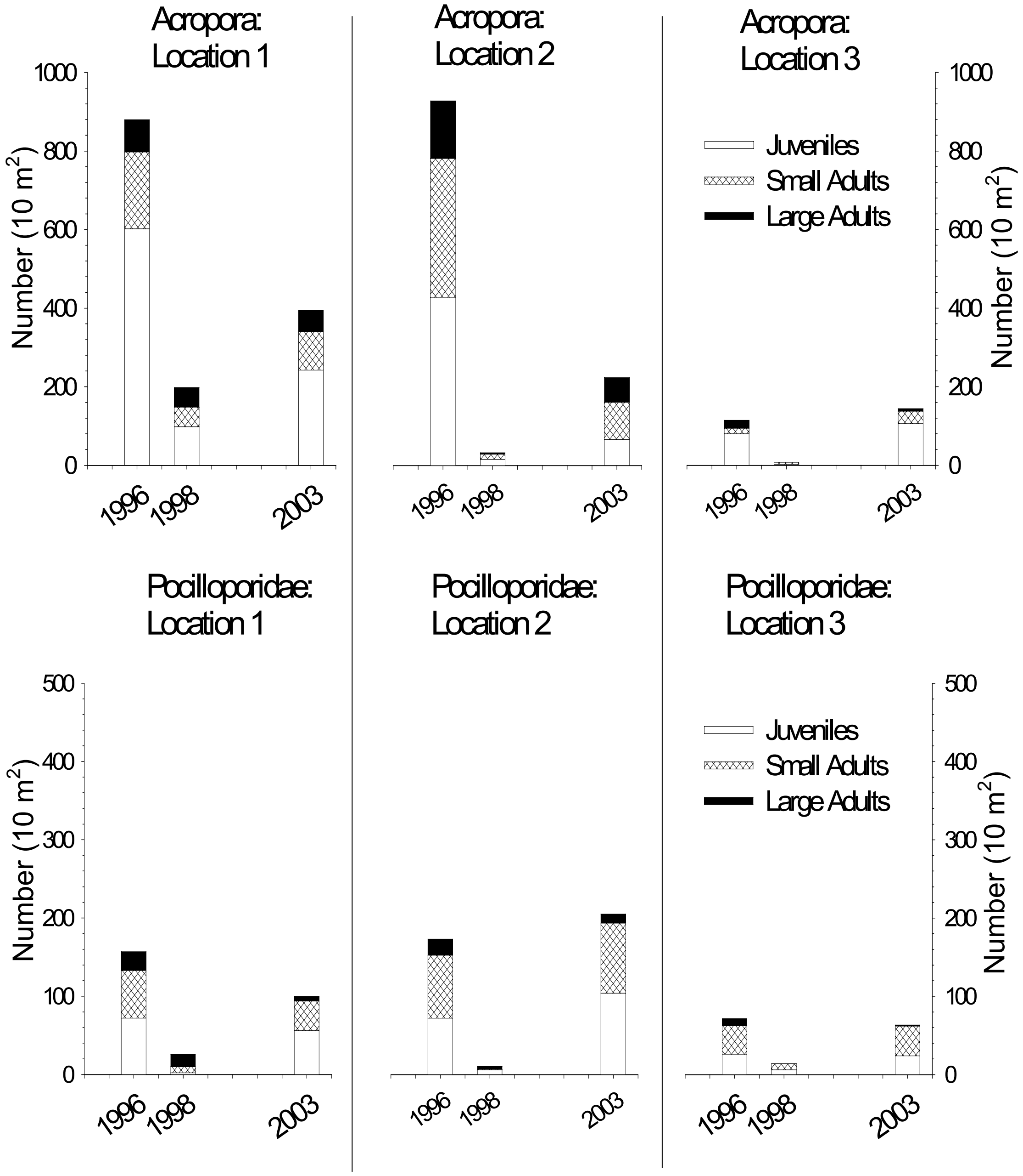

Figure 5.3 Changes in the population structure of Acropora and Pocilloporidae between surveys conducted in October each year.

Chapter 6: LONG-TERM DYNAMICS OF AN ISOLATED CORAL REEF: EFFECTS OF A SEVERE BLEACHING EVENT

6.1 INTRODUCTION

Predicted changes in the world's climate have lead scientists to question the resilience of coral reefs should the frequency and severity of bleaching events continue to increase (Hoegh-Guldberg 1999, Sheppard 2003). Coral bleaching describes the expulsion zooxanthellae and/or pigments by the coral host (Yonge 1931, Hoegh-Guldberg 1989), and is most commonly a consequence of thermal stress. Thermal stress is largely due to elevated water temperatures, but solar irradiance, weather conditions and current flow have also been implicated in bleaching (Brown *et al.* 1994, McField 1999, Nakamura and van Woesik 2001, Gleason 1993, Aronson 2002, Kayanne *et al.* 2002). Regardless of the causes, mass-bleaching events can result in significant coral mortality and major changes in the structure of benthic communities.

Patterns of susceptibility for different coral taxa have been identified in a variety of studies, but can vary among locations and regions (e.g. Hoegh-Guldberg and Slavat 1995, Marshall and Baird 2002, Loya *et al.* 2001). Generally, the hydrocoral, Milliporidae, and species of Pocilloporidae and Acroporidae are the fastest, and most likely to bleach, and also have the highest rates of mortality; the Poritidae and Faviidae are less likely to bleach and die, and *Genera* such as the *Turbinara*, *Galaxea* rarely bleach. These differing susceptibilities mean the relative abundance of coral taxa can change dramatically after a mass-bleaching event, and taxa that were previously dominant my become rare or absent (McClanahan 2000, Loya *et al.* 2001, Aronson *et al.* 2002). In severe events, many of the most abundant species of corals can die, causing a dramatic reduction in coral cover and a corresponding increase in the cover of other benthic organisms such as algae or sponges (Brown and Suharsono 1990, Mumby *et al.* 2001, Loya *et al.* 2001). With predictive models indicating that bleaching episodes are likely to increase in severity and scale (Hoegh-Guldberg 1999, Sheppard 2003), there is much speculation that coral reefs will undergo long-term phase-shifts to a more degraded state.

An understanding of the resilience of coral reefs to mass-bleaching events requires long-term, large-scale, studies of changes in community structure before and after the event, because patterns of bleaching, mortality, and recovery, frequently vary in space and time (Coles and Brown 2003). However, there are relatively few long-term studies documenting the recovery of corals reefs following mass-bleaching, particularly for the catastrophic bleaching events that occurred during 1998, and in many of the studies that have been conducted the rates of recovery were confounded by additional stresses. Previous studies into the effects of bleaching were often performed at reefs subjected to stresses resulting from terrestrial inputs, such freshwater runoff (Baird and Marshall 2002, Berkelmans and Oliver 1999), sedimentation (Aronson 2000), eutrophication, or a combination of factors (Shulman and Robertson 1996, Ostrander *et al.* 2000, Sweatman *et al.* 2000). Terrestrial inputs, or other anthropogenic stresses such as overfishing, will compound the effects of mass-bleaching and potentially reduce the numbers of sexual recruits that are so important for the recovery of coral communities (Bellwood *et al.* 2004).

In this study, changes in the structure of benthic communities at an isolated group of reefs were quantified over nine years; four years before and five years after a catastrophic bleaching event. The isolation of the reefs means they are comparatively free of anthropogenic pressures (e.g. sedimentation, eutrophication, commercial fishing), and no other large-scale disturbances occurred during the period of investigation. Community dynamics are discussed and I suggest these results provide an insight into the fate of reefs, globally, if the frequency, scale and severity of bleaching events increase.

6.2 MATERIAL AND METHODS

6.2.1. Long-term monitoring

Six long-term monitoring locations were established in October 1994 (Figure 6.1). Each monitoring location of consisted three sites of 5, 50 m transects following a nine metre depth contour on the reef slope. The three monitoring sites, at each location, covered approximately 1 km of continuous reef. Each transect was permanently marked using combination of star-pickets and 10 mm reinforcing bar, hammered into the reef at 10 m intervals. During each survey in 1994, ’95, ’96, ’97, ’98, ’99, ’01 and ‘03 a fibreglass tape was laid between the permanent markers along each transect. All benthos on each transect were recorded using a hand-held underwater video camera. Video was undertaken with a diver swimming at a slow speed along the upslope of the transect tape, holding the video camera perpendicular to, and 30 cm above, the reef substratum.

The video footage of each transect was analysed to determine the percentage cover of coral and other benthic categories, using a point sampling technique (after Carleton and Done 1995). The video footage of each transect was paused 40 times at regular intervals, and the organism or substratum type beneath five fixed points on the video monitor assigned to a benthic categories. Corals were identified to the greatest taxonomic level achievable by the observer.

6.2.2 Data analysis

To assess the temporal trends in major groups of corals in the years prior to the bleaching ('94–'97), and in the years following it ('98-'03) a series of customised contrasts were tested using mixed-effects models. The models were fitted using the /MIXED command and the contrasts using the /TEST command in SPSS (v12) statistical software. The data used in the models were repeated site-level measurements (ie. mean percentage cover of 5, 50 m transects) of either *Soft Coral*, *Hard Coral*, *Family Acroporidae*, *Family Poritidae* or *Family Pocilloporidae*. To satisfy model assumptions percent cover data for *Families Acroporidae*, *Pocilloporidae*, and *Soft Coral* were transformed using a square root function prior to fitting the model, while *Hard Coral* and *Family Poritidae* remained untransformed. The importance of temporal autocorrelation in the residuals was determined by fitting models both with and without first-order autoregressive correlation structure and then selecting the optimal model using Akaike Information Criteria (AIC; Burnham and Anderson 1998). For each coral group, I assessed whether the temporal trend in the pre-bleaching years or post-bleaching years was linear, quadratic or cubic. If no temporal trend existed for a coral group, then there was no significant change in the percentage cover for that group within the time period tested (ie pre- or post-bleaching years). Where a significant temporal trend existed, it is possible that the trend was a combination of two trends. For example, have a linear and quadratic temporal trend component, which I would refer to as a linear quadratic trend.

A principal component analysis (PCA) of transformed (square root) data was used to compare the changes in the structure of benthic communities during censuses conducted between 1994 and after 2003 (S-Plus, Statistical Sciences 1999). Comparisons are made between communities at each location; using 12 benthic groups (see Figure 6.5 for groups). Free space represented a combination of turf algae, crustose coralline algae and bare rock categories as there were difficult to distinguish on the video transects. I encompassed a polygon around each year's data points. Vectors representing the benthic groups, and arrows representing the mean direction of change in benthic groups, were superimposed on each PCA bi-plot.

6.3 RESULTS

6.3.1. Changes in percent cover of hard and soft corals

The mean cover of hard and soft corals at Scott Reef increased from 1994 to 1997 and then decreased dramatically as a result of the mass bleaching in 1998. In the six years following the bleaching hard and soft corals increased slowly (Figure 6.2). In 1994, the cover of hard corals ranged between approximately 30% and 60% (mean = 42.8 ± 4.6% *s.e.*) at all monitoring locations across Scott Reef, and increased linearly of 1.76 (± 1.3% s.e.) p.a. to 1997 (contrasts d.f. = 82, t = 4.6, p < 0.001). By comparison, the cover of soft corals in 1994 was much lower and more variable among the sites and years, ranging between <1% and 20% (mean = 9.0 ± 0.4% s.e.; Figure 6.2). Between 1994 and 1997, cover of soft corals increased linearly at 1.13 (± 0.49%) p.a. (contrasts d.f = 82, t = 2.29, p < 0.03) over all locations at Scott Reef. In 1998, the thermal stress caused a dramatic reduction in the cover of hard and soft corals across all monitoring locations at Scott Reef; with between 45% and 90% of all hard corals (mean 73.4 ± 4.52%; d.f = 40, t = 41.1, p < 0.001) and between 50% and 94% of soft corals dying (mean 80.3 ± 4.0%, d.f. = 18, t = 14.2, p < 0.001).

Six years after the bleaching there had been a significant increase in cover for some taxa at Scott Reef. The percent cover of hard corals between 1998 and 2003, increased significantly at a linear quadratic rate (df = 40, t = -6.03, p < 0.001). That is, the cover of hard corals increased by 2.11 ± 0.62 % in the first three years after the bleaching and 6.43 ± 1.07 % in the next three years (Figure 6.3). In contrast, the mean cover of soft corals showed no significant increase in the six years following the bleaching (1998 vs 2003; t = -1.65, df = 18, p > 0.11; Table 6.2). As a result, soft coral cover remains very low at all locations at Scott Reef with a mean of 3.06 ± 1.25%.

6.3.2. Changes in coral cover at location level

The extent of hard coral mortality at individual locations was a strong indicator of post-disturbance recovery with a strong linear relationship between the rates of mortality in 1998 and subsequent recovery (r^2 = 0.76, p < 0.001; Figure 6.4A). Coral communities (ie. SL2, SS1, SS2) that suffered high mortality rates (> 80%) showed recovery rates of less than 30% over the six years following the bleaching event. Alternatively, communities (eg SL3, SL4) that had less that a < 50% die-off, have increased to > 50% of their pre-bleaching cover by 2003. This strong linear relationship between initial mortality and subsequent recovery for hard coral is not as clear for soft coral (r^2 = 0.32, p < 0.03; Figure 6.4B).

6.3.3. Changes in percent cover of different coral families

The dominant families of corals in the years prior to the bleaching were the Acroporidae (25%), Poritidae (10%) and Pocilloporidae (4%). Over the years prior to the bleaching ('94 – 97'), Family Acroporidae increased linearly by 1.76 ± 0.62% p.a. (Table 6.2; $t = 5.8$, $df = 82$, $p < 0.001$). There was little change in the cover of the Portitidae prior to the bleaching, while cover of the Pocilloporidae decreased between 1994 and 1997 (Table 6.2). The cover of Family Pocilloporidae fell from a high in 1995 of 4.86 ± 0.85% to 3.28 ± 0.68% in 1998.

All of these dominant families of hard coral were affected by the bleaching, but the relative decreases in cover six months after the bleaching varied greatly. The Acroporidae were worst affected with a decrease in mean cover of 88%, from 27.39 ± 4.97% to 3.29 ± 1.48% (Figure 6.3). Similarly, there was a 90% decrease in the mean cover of Pocilloporidae, decreasing from 3.28 ± 0.68% to 0.31 ± 0.14%. Of all the families, the Poritidae were least affected, having a relative decrease in mean cover across all locations of 55% after the bleaching. The mean cover of the Poritidae decreased from 9.82 ± 2.00% to 4.41 ± 1.14%, six months after the bleaching.

The recovery of individual coral families was highly variable in the six years following the 1998 event. The Family Acroporidae has shown a significant increase in cover from 3.3 ± 0.8% following the die-off to 5.1 ± 1.1% in 2003 ($df = 23$, $t = -3.70$, $p < 0.01$). This recovery of the Acroporidae has been accelerating since the mortality event (linear quadratic trend; Figure 6.4, Table 6.2). The Poritidae, also increased their cover significantly ($df = 23$, $t = -3.59$, $p < 0.002$), rising from 4.4 ±

0.6% to 6.3 ± 1.0% in the six years after the bleaching. Most of this increase in Portidae cover occurred between 1999 and 2001 (see cubic trend, Table 6.2; Figure 6.4). Pocilloporidae showed a significant increase in cover in the six years following the bleaching rising from 0.31 ± 0.1% to 1.4 ± 0.4% (Figure 6.4; df = 32, t = -2.646, $p < 0.001$). This recovery of Pocilloporidae, in the six years following the bleaching event, has been accelerating with most of the increase in cover occurring between 2001 and 2003 (linear quadratic trend; Table 6.2; Figure 6.4).

6.3.4. Changes in community structure

The variable susceptibility of the different families, and the overall decrease in the cover of hard corals following the bleaching, caused dramatic changes in the community structure of scleractinian corals at Scott Reef. Six years after the bleaching these changes largely remain. Among the hard corals, the most obvious changes were the reduction in the relative abundance of Acroporidae and the increased relative abundance of the Poritidae. Prior to the bleaching, the Acroporidae composed between approximately 57%, which decreased to 30% after the die-off. In contrast, the contribution of the Portidae increased from 20% to 38% following the bleaching. Six years after the bleaching, the Poritidae remained the dominant family of hard coral constituting 32% of the overall hard coral community.

In addition to the changes in the community structure of the hard corals, the bleaching caused major changes in overall benthic community. Between 1994 and 1997, the contribution of hard and soft coral to the benthic community increased, as coral taxa replaced turf and coralline algae groups (FS, Figure 6.5). In response to the thermal induced bleaching in 1998 most fauna possessing symbiotic algae were killed and replaced by turf and coralline algae. This die-off caused major shifts in the structure of Scott Reef's benthic community. For example, in 1994 turf and coralline algae constituted only 36% of the substratum and a result of the coral die-off this increased to 84% as a result of the 1998 bleaching event. Six years later it is still 76% of the overall benthic cover. It is important to note throughout the study, no macroalgae was found at any locations, with the exception of *Halimeda spp.*. In the first four years (1998 – 2001) following the die-off the benthic communities remained dominated by turf and coralline algal groups (FS). However, between 2001 and 2003 there were shifts towards the pre-bleaching communities at all locations, with algal communities being replaced by an array of mostly branched hard coral species (Figure 6.5).

6.4 DISCUSSION

The mass-bleaching at the Scott Reef system was a major disturbance that decreased coral cover at all reefs. However, coral reefs have historically been resilient to even major disturbances (Grigg and Dollar 1990, Pandolfi *et al.* 2003), which can promote diversity and structural complexity (Connell 1978, Karlson 1999). Today, however, the frequency, severity and types of disturbances to coral communities are increasing, and their rates of recovery are slowing (Wilkinson 1999, Nyström *et al.* 2000, Hughes *et al.* 2003). In the worst instances, coral reefs are undergoing phase shifts to a more degraded state, whereby benthic organisms other than corals become dominant (Ostrander *et al.* 2000, McClanahan *et al.* 2001, Aronson *et al.* 2002). Long-term phase shifts usually occur on reefs that are exposed to anthropogenic stressors, such as the reduced abundances of herbivores, and/or decreased water quality, whereas the Scott Reef system is free of most anthropogenic stressors and benthic organisms that can exclude or outcompete corals did not come to occupy the available substrata following the bleaching.

The bleaching dramatically altered the structure of benthic communities across the Scott Reef system, of which the most obvious changes were that the Acroporidae is no longer the spatial dominant coral and the increased cover of turfing and coralline algae following comparable decreases of all other benthic groups. However, the turfing algae was largely replaced by coralline algae within a year of the bleaching, which provided a suitable substrata for recolonisation by the benthic organisms worst affected by the bleaching. After almost six years, the hard corals had returned to approximately 40% of their pre-bleaching cover and the community was returning to its previous structure, with evidence of an increasing rate of recovery in the later years, and I would expect the recovery to continue in the absence of major disturbances.

The coral communities across the Scott Reef system were recovering from the bleaching, but at individual sites the rates of recovery varied according to the level of mortality; sites that had the smallest relative decreases in cover (as a result of the 1998 bleaching) had the fastest rates of recovery, particularly for the hard corals. These data suggest that the increases in cover within six years of the bleaching were largely driven by the asexual growth of survivors, rather than the recruitment and growth of new individuals (e.g. Brown and Suharsono 1990, Kayanne *et al.* 2002), and following the bleaching there was a 97% reduction in sexual recruitment across the Scott Reef system (Chapter 4). Nevertheless, in the final years of this study the rates of recruitment and the abundance of juvenile corals were increasing, even at the worst affected sites. The short-term (years) increases in coral cover following severe disturbances may be largely driven by the growth of survivors at the sites least affected, particularly for isolated coral reefs, from which recruits are produced that supplement the recovery of an entire system (Connell 1997, Karlson 1999). Consequently, the corals at sites that best survive severe disturbances are most likely to be valuable broodstock, and require the highest levels of protection.

All hard corals were affected by the bleaching, but the susceptibility and resilience of the different families were evident in their short- and longer-term changes in cover. The Poritidae were least susceptible to the elevated water temperatures, and because many colonies suffered partial- rather than whole-colony mortality, their relative decreases in cover were much less than for the Acroporidae and Pocilloporidae (see also Brown and Suharsono 1990, Loya *et al.* 2001, McClanahan *et al.* 2001). The re-growth of survivors resulted in the Poritidae initially having the most rapid increases in cover, but more than three years after the bleaching there was little change in the cover of Poritidae and rapid increases in the cover of the Acroporidae and Pocilloporidae. Families such as the Acroporidae and Pocilloporidae tend to have the highest mortality after bleaching, but their recovery can accelerate due to high rates of recruitment and rapid growth (Glynn 1993, Halford *et al.* 2005). Given their increasing rates of recruitment (Chapter 4) and rapid growth, the Acroporidae are expected to again become the dominant coral across the Scott Reef system within a relatively short period, baring any further disturbances, reflecting the extent to which the patterns of recovery of groups of hard coral can vary through time.

As with the most susceptible families of hard corals, there were dramatic decreases in the cover of soft corals after the bleaching, but the rates of recovery of the soft corals had not increased nearly as rapidly in the final years of this study. By far the most abundant (> 80% cover) species of soft coral at Scott Reef were in the Family Alcyoniidae, which tend to grow slowly and maintain populations through asexual propagation, rather than sexual recruitment (Benayahu and Loya 1987, McFadden 1991, Fabricius 1995). But, there was limited potential for recovery by asexual propagation because the bleaching killed many colonies, and within six years cover had not increased significantly. The high rates of mortality of the Alcyoniidae, and their slow growth and low rates of sexual recruitment, suggest populations are particularly vulnerable to predicted increases in sea-water temperatures, which may be reflected by a decreasing contribution to communities on coral reefs.

This study documented almost ten years of change in the benthic communities at the Scott Reef system, which included a major disturbance in the form of elevated sea-water temperatures. The temperature anomalies caused the mass-mortality of hard and soft corals across three reefs to a depth of 20 m, and almost complete failure in the recruitment of hard corals (Chapter 4). Yet, despite the severity of the bleaching and the isolation of the Scott Reef system, within six years the hard corals had returned to approximately 40% of their pre-bleaching cover and the benthic communities were returning to their previous structure. I attribute this resilience to the lack of many anthropogenic stressors that reduce the population growth rates of corals and promote the growth of competitors (but see Ostrander *et al.* 2000). These results provide evidence of the resilience of coral communities to extreme, but infrequent (decades) disturbances, and highlight the extent to which human activities are compromising this resilience elsewhere.

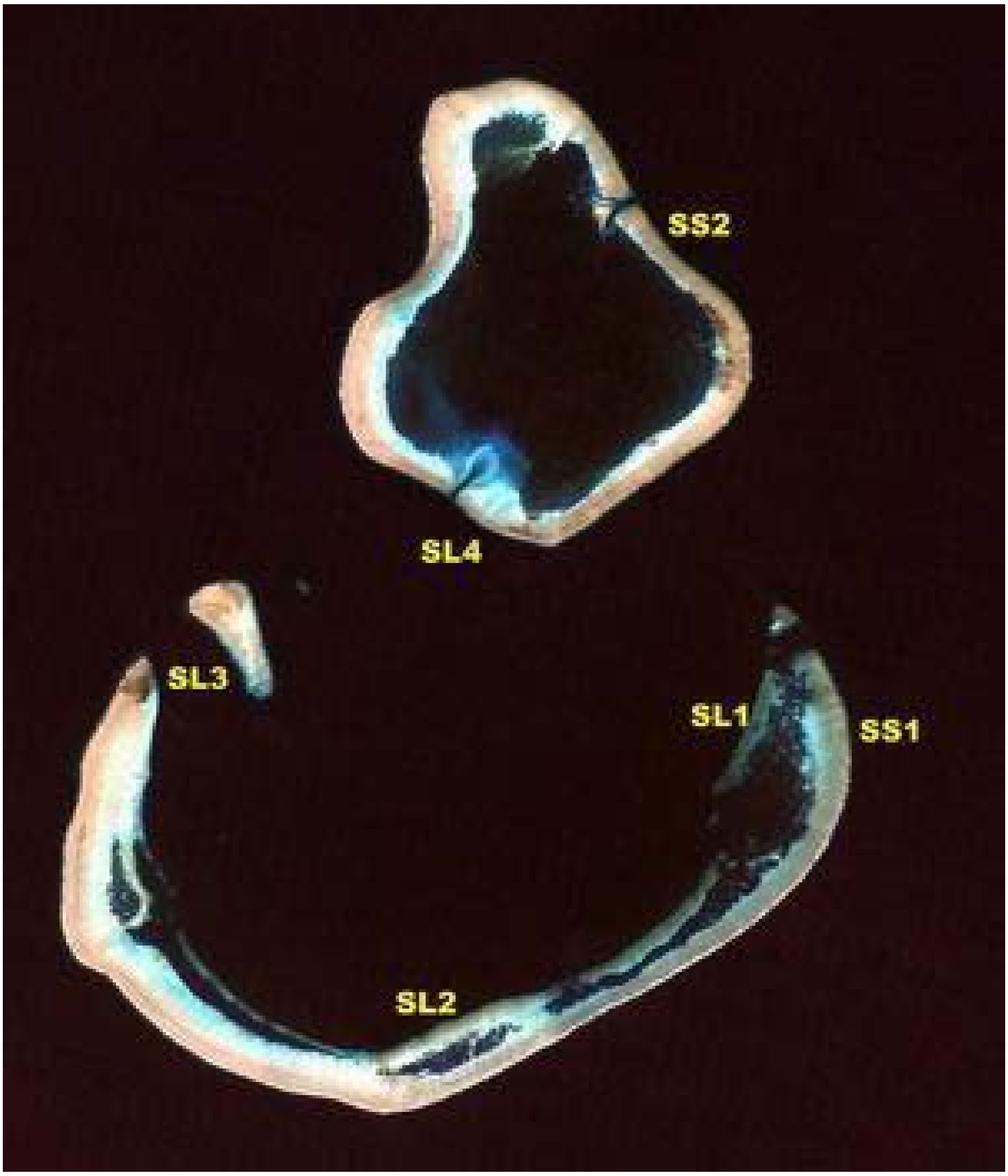

Figure 6.1 Location of monitoring locations at Scott Reef

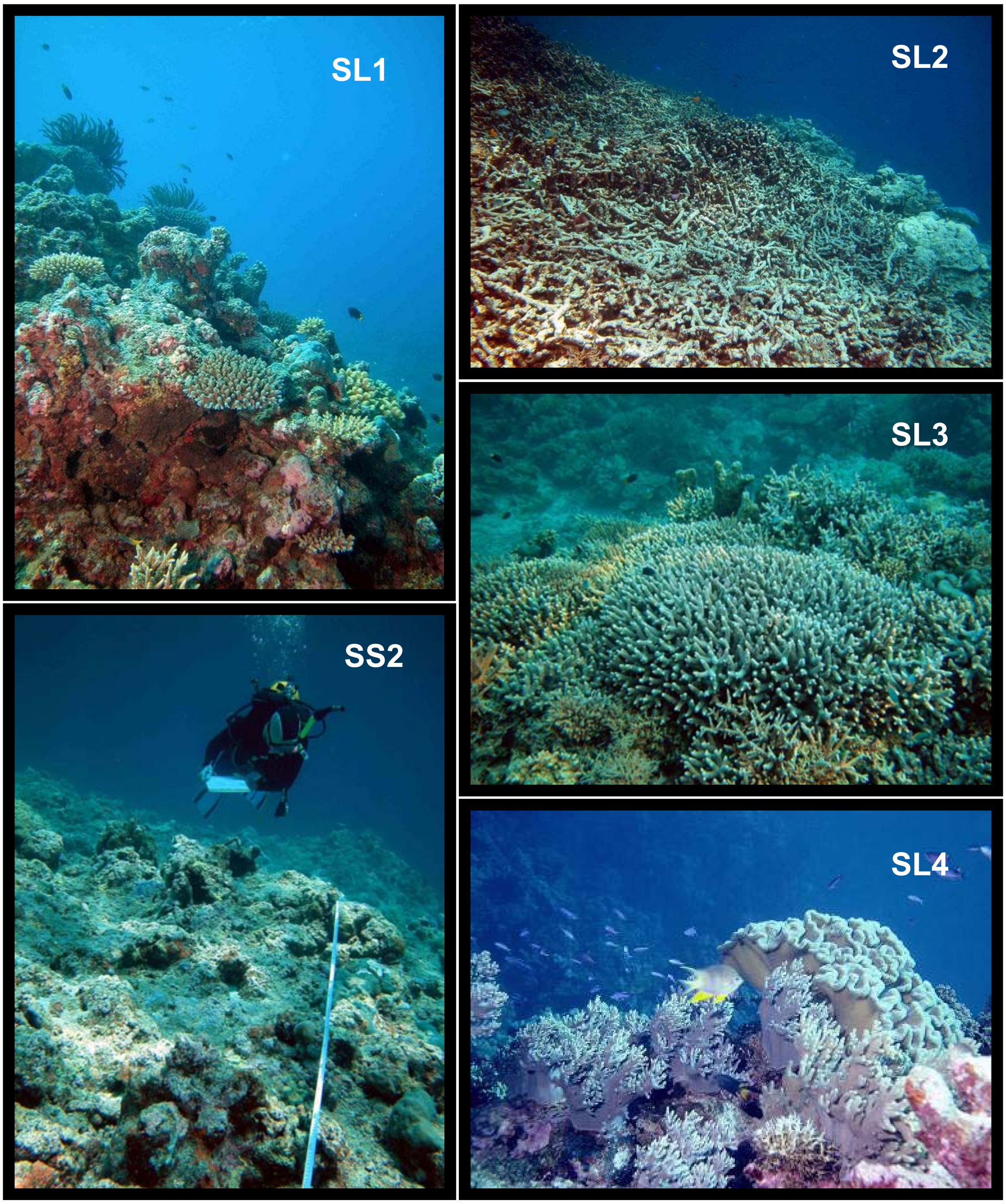

Figure 6.2 **Representative image of each monitoring location at Scott Reef in 2003, almost six years after the bleaching event.**

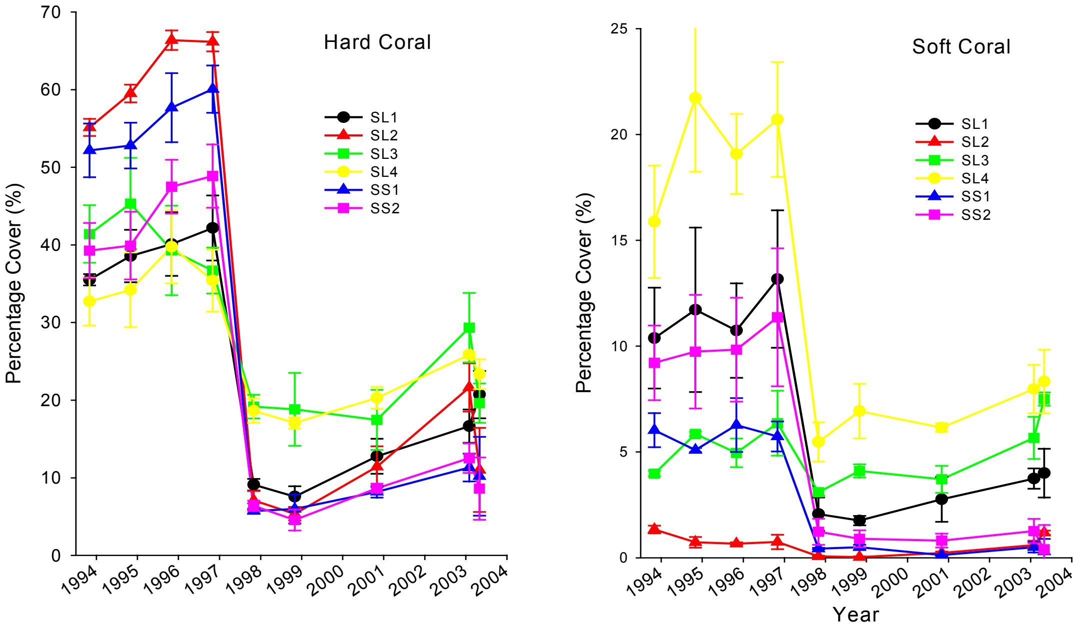

Figure 6.2 **Percent coverage of hard and soft coral (mean ± s.e.) at all monitoring locations. Each monitoring location is represented by 15, 50 metre permanent transects.**

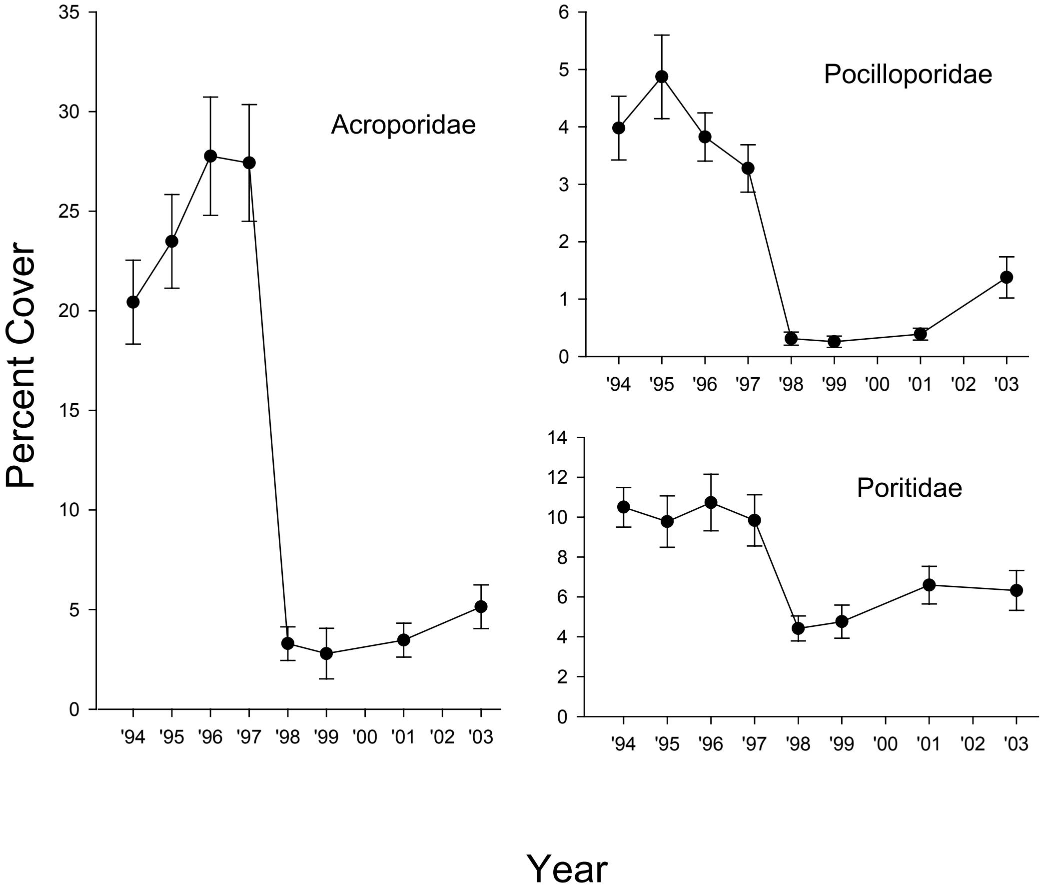

Figure 6.3 **Percent coverage (mean ± *s.e.*) for major families of scleractinian coral; Acroporidae, Pocilloporidae and Poritidae average across all monitoring sites between 1994 and 2003.**

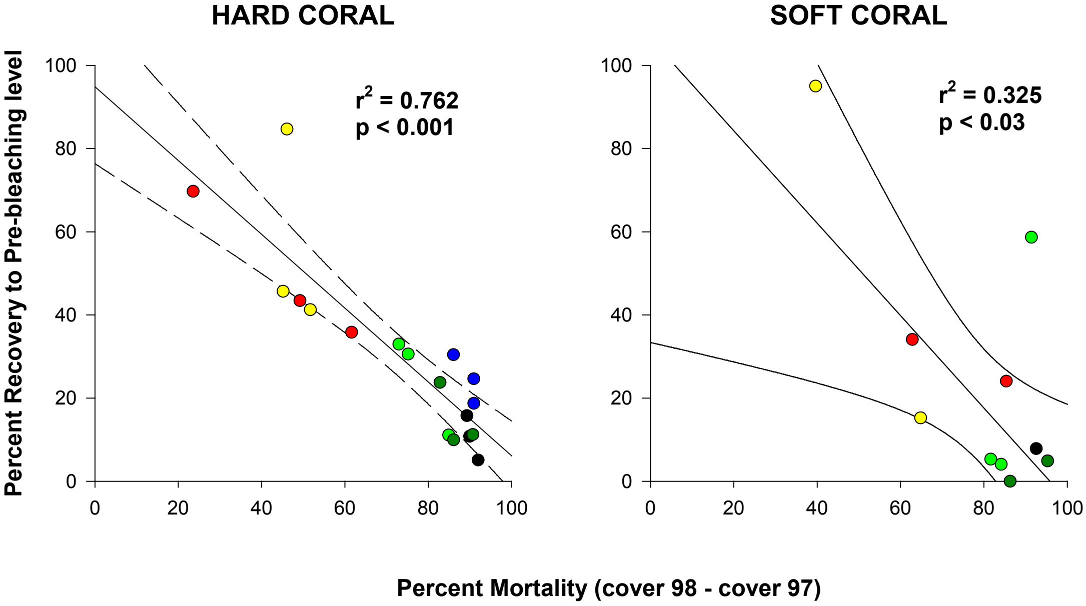

Figure 6.4 **The relationship between percent recovery to pre-bleaching levels of individual monitoring locations (ie 1997 vs 2003) and percent mortality suffered as a result of the 1998 bleaching event at Scott Reef, for hard coral and soft coral. Each point represents the mean of an individual monitoring site (ie 5, 50 metre permanent transects). Dots represent; light green, SL1; blue, SL2; yellow, SL3; red, SL4; black, SS1; dark green, SS2.**

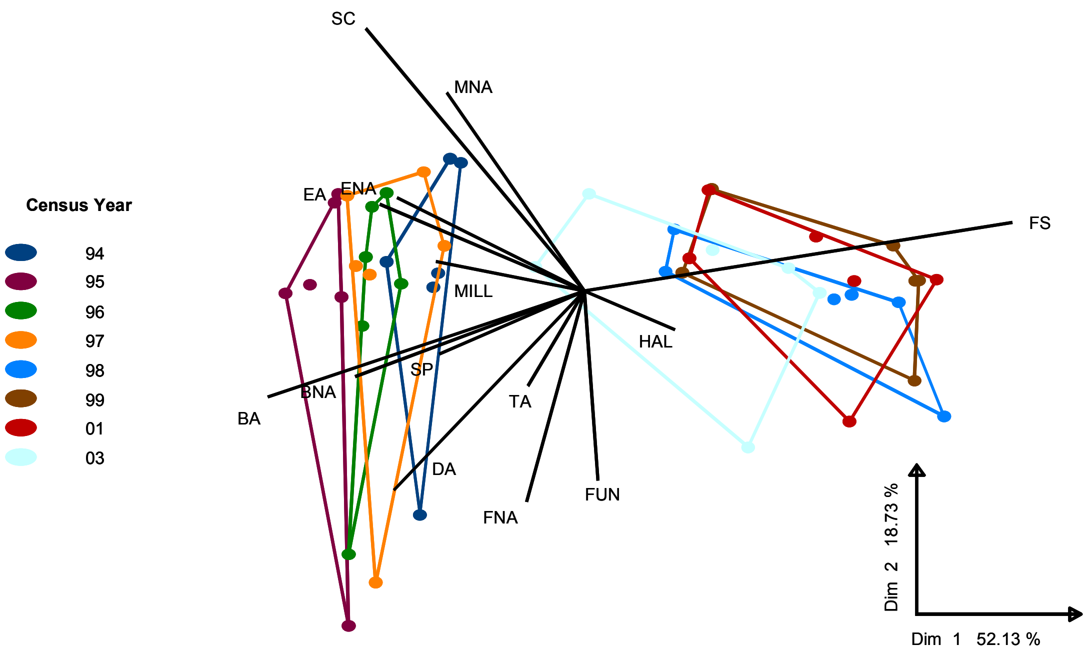

Figure 6.5 **PCA bi-plot of benthic community changes over ten years (eight visits) at Scott Reef. Each point represents a single monitoring location at a particular census. Individual years are colour coded and have been encapsulated in a convex hull. Codes are; BA: Branching Acroporidae; DA: Digitate Acroporidae; TA: Tabulate Acxroporidae; EA: Encrusting Acroporidae; SNA: Submassive non-Acroporidae; FNA: Foliose non-Acroporidae; BNA: Branching non-Acroporidae; ENA: Encrusting non-Acroporidae; MNA: Massive non-Acroporidae; FUN: Fungidae; SC: Soft Coral; FS: Free Space (turf and coralline algae)**

Table 6.1 Temporal trends in major groups of corals in the years prior to the thermal induced bleaching event (1994 – 1997). Bold cells represent significant trends at 0.05 significance level.

	d.f.	Linear	Quadratic	Cubic
Hard Coral	82	**t = 4.57, p < 0.001**	T = -1.26, p > 0.21	t = -1.14, p > 0.25
Soft Coral	82	**t = 2.29, p < 0.03**	T = -0.25, p > 0.70	t = 1.60, p > 0.11
Acroporidae	82	**t = 5.80, p > 0.001**	T = -1.87, p > 0.65	t = -1.16, p > 0.20
Poritidae	82	t = -0.99, p < 0.32	T = 0.08, p > 0.93	t = -1.64 p >0.11
Pocilloporidae	82	**t = -2.20, p < 0.03**	**T = -2.56, p < 0.02**	t = 1.53, p > 0.13

Table 6.2 Temporal trends in major groups of corals in the six years following the 1998 bleaching event (1998-2003). Bold cells represent significant trends at 0.05 significance level.

	d.f.	Linear	Quadratic	Cubic
Hard Coral	82	**t = 6.48, p < 0.001**	**t = 3.56, p < 0.01**	t = -0.6, p > 0.95
Soft Coral	82	t = 1.46, p > 0.14	t = 0.32, p > 0.75	t = 1.06, p > 0.29
Acroporidae	82	**t = 4.87, p <0.001**	**t = 4.24, p < 0.001**	t = -1.04, p > 0.20
Poritidae	82	**t = 4.87, p < 0.01**	t = -0.64, p > 0.50	**t = -2.77 p <0.01**
Pocilloporidae	82	**t = 6.60, p < 0.001**	**t = 3.82, p < 0.001**	t = 0.158, p > 0.87

Chapter 7: SURFACE CURRENTS SUGGEST REPRODUCTIVE ISOLATION OF SCOTT REEF

7.1 INTRODUCTION

The life-cycle of scleractinian corals has a larval phase, during which the larvae are passively transported within the water column (Harrison and Wallace 1990). Broadcast spawning corals have a minimum development period of 2 – 5 days before they are competent to settle and usually settle and metamorphose within 10 – 14 days after birth (Heyward and Negri 1999, Miller and Mundy 2005). However, laboratory-based studies, preventing coral larvae from settling, have shown that larvae of some species can remain competent for up to 105 days (Wilson and Harrison 1998, Nozawa and Harrison 2005). Research using gel electrophoresis indicates that the vast majority of coral larvae recruit to their parental reef (Ayre and Hughes 2000, Whittaker 2004) implying larvae settle within days of spawning, rather than weeks or months. Populations of coral are now thought to have a much stronger stock-recruitment relationship than was initially thought, which has important consequences for population genetics and the recovery of coral communities following major disturbances (Hughes *et al.* 2000). Recent work by Underwood *et al.* (*in press*) in northwest Australia has shown successful 'seeding' of coral larvae between Scott Reef and Rowley Shoals, on ecological timescales, is extremely rare. As a result, they concluded that isolated reef systems of northwest Australia are likely to be self-seeding.

The issue of successful larval dispersal is very important when severe or catastrophic disturbances kill the majority of resident corals on a reef (Connell 1997, Chapter 3). For example, a coral bleaching event in 1998 at Scott Reef killed over 75% of all corals down to a depth of 20 metres across all habitats (Chapter 3) and the extent of this mortality means recovery must be driven by colonisation of new sexual recruits rather than the growth of survivors. Given the isolation of Scott Reef system, having an understanding of potential larval transport times in the region can give us a better understanding of recovery potential of Scott Reef.

Here I indirectly assess the potential transport times of coral larvae among three reef systems in northwestern Australia, using satellite drogues. The three systems I assess are Scott Reef (North, South and Seringapatam Reefs) which was dramatically affect by the 1998 bleaching; Ashmore Reef (Ashmore, Cartier and Herbernia Reefs) 240 km to the north of Scott Reef and Rowley Shoals (Mermaid, Clerke and Imperiuse Reefs), 220 km to the south of Scott Reef which were unaffected by the 1998 bleaching. From these data and knowledge of the competency periods of coral larvae, I make inferences about the potential extent of larval connectivity among the reef systems, genetic diversity of resident populations and potential recovery times following major disturbances.

7.2 MATERIAL AND METHODS

Lagrangian surface drifters were deployed off the coast of northwest Australia to determine near-surface movement of the water column and the potential for larval transport from among three reef-systems; Ashmore Reefs, Scott Reefs and the Rowley Shoals close to the time of the predicted time of the multi-species spawning in spring and autumn. I used ‘Davis’ type near-surface drifters that float in the upper one meter of the water column. The drifters consisted of a central core and eight arms connecting four vertical sails, each are approximately 1 m^2 (Figure 7.1). The sails and the body of the drifter sat below the water column, and a small antenna extended above the water column; there was little influence of wind or waves on the movement of the drifters. Each drifter contained an onboard GPS that recorded its location every hour, and locations were transmitted via the CLS Argos satellite system to a base station. Each drifter had a maximum life of approximately 3 - 4 months. Three drifters were deployed during 2003 and 2004, one at each of Scott, Ashmore and Mermaid (Rowley Shoals) Reef systems (Table 7.1).

7.3 RESULTS

The three surface current drifters deployed during 2003 and 2004 in northwest Australia showed transport times between isolated reef systems of approximately 25 days. Interestingly, the direction of these surface currents reverses through the year. Surface currents flowed in a southerly direction during April to June and then reverse, travelling in a northerly direction from July to October.

The first drifter was released from Scott Reef in September 2003, a month before the predicted mass spawning in October 2003 and followed a southern trajectory for approximately 2 days, and then drifted north, northeast, for approximately three weeks (Figure 7.2). While travelling north, there is evidence that the drifter encountered a surface eddy after approximately two weeks, before then continuing north. The drifter was recovered approximately 28 kilometres east of Ashmore Reef on 15th October, 2003. The total distance covered by the drifter was 585 kilometres, over 22 days at an average speed of 26.5 kilometres per day.

The second drifter, which was released from Ashmore Reef in April 2004, travelled rapidly (51 km day^{-1}) in a westerly direction into the Indian Ocean for approximately one week, before changing direction to the southeast for five days with velocities between 8.6 and 26 km day^{-1}(Figure 7.3). It then travelled south for eight days, passing Seringapatam Reef on May 3rd and drifting within 25 km of Scott Reef on the May 4th, 28 days after release. The drifter continued in a southwesterly direction, roughly parallel to the edge of the continental shelf. On May 22nd, the drifter entered an anticlockwise eddy, where it remained until June 10th. The drifter then travelled south-southwest during June, passing on the western side of the Rowley Shoals, within approximately 31 km of Mermaid Reef, 15 km from Clerke Reef and within 5 km of Imperieuse Reef on July 6th, 91 days after release. The drifter then reversed direction, travelling in a northerly direction for 32 days before transmission ceased. At this time the drogue was 110 km south west of Scott Reef, having been released 124 days previously. Overall the drifter travelled a total of 2458 km, at a mean velocity of 19.9 kilometres per day.

A third drifter was released from Rowley Shoals, on April 8th 2004 (Figure 7.4). Over the following five days, the drifter tracked anticlockwise around the southern edge of Mermaid Reef. While around Mermaid Reef, the drifter moved no more than 11 km from the edge of the reef. From the north edge of Mermaid Reef, the drifter travelled west-northwest for 10 days and west for three days, before returning to a west-northwest course until it stop transmitting on April 29th, 21 days after release. The total distance travelled was 661km, at an estimated drift speed of 31 km day^{-1}.

7.4 DISCUSSION

Based on the passive transport times larvae disperse would take at least one month to travel between isolated reef systems of Australia's northwest assuming they escape the tidal influence of their natal reef prior to settlement. Similar tracks for current drifters have been report by Cresswell *et al.* (1993) but at even slower speeds than report here. These potential dispersal times are longer the optimal competency periods and similar to the upper competency periods of most coral larvae (e.g., Wilson and Harrison 1998, Nishikawa *et al.* 2003, Miller and Mundy 2003, Nozawa and Harrison 2005), and the large decrease in survival beyond one month in laboratory experiments (e.g., Baird 2004, Nishikawa et al. 2003, Nozawa et al. 2006) are probably higher in natural conditions. As a result, for the offshore reef systems of northwestern Australia we predict that larvae routinely disperse within their natal reef, periodically between reefs with a system and rarely between the reef systems on ecological timeframes. A recent study by Underwood *et al.* (*in press*) assessing population genetics of *Acropora tenius* using micro-satellites support this conclusion. They found that *A. tenius* larvae recruited within 10 kilometres of their natal reef location and that movement between reef systems of Australia's northwest for this species was extremely rare. The transport times between systems are likely to explain the Underwood et al (*in press*) findings. The passive transport times between reefs of the northwest and the population genetics of *A. tenius* both provide support for the postulation that low recruitment rates at Scott Reef following the 1998 bleaching event were a result low broodstock numbers and very few larvae arriving from unaffected reefs to the south (Rowley Shoals) or north (Ashmore), (Chapter 6).

The reproductive isolation of these remote coral reefs can have profound implications for recovery following catastrophic mortality. As a result of the mass mortality of corals at Scott Reef, there is likely to be limited genetic variation among the survivors and a high incidence of inbreeding (Ayre and Hughes 2000). Electrophoresis studies of five species of hard corals along the Great Barrier Reef indicated large heterozygote deficiencies that can be attributed to inbreeding. Many of the populations of corals were considered to be largely self-seeded at the scale of the reef, but with sufficient gene flow to prevent fixed genetic differences among reefs. Whether the isolation of the groups of reefs off northwest Australia is sufficient to cause fixed genetic differences needs further investigation. However, the potential for decreased genetic diversity and increased levels of inbreeding among coral surviving catastrophic mortality events may reduce their ability to cope with future change in environmental conditions.

The different trajectories shown by each drifter highlights the complexity of the surface circulation in the Scott Reef region of northwestern Australia and the need for further replication. The drifter data confirms the seasonality of the prevailing surface currents in the vicinity of Scott and Ashmore Reefs, with a southward drift occurring during September to January, and a northward drift occurring during March to August (Cresswell *et al.*1978). The mass-spawning of corals occurs at Scott Reef during autumn and spring each year (see Chapter 2), coinciding with the change in the direction of the currents around Scott Reef. Coral larvae that disperse beyond Scott Reef are likely to be transported north during spring and south during autumn. However, a much larger number of corals participate in the autumn spawning, so there is likely to higher rates of gene flow southward of Scott Reef.

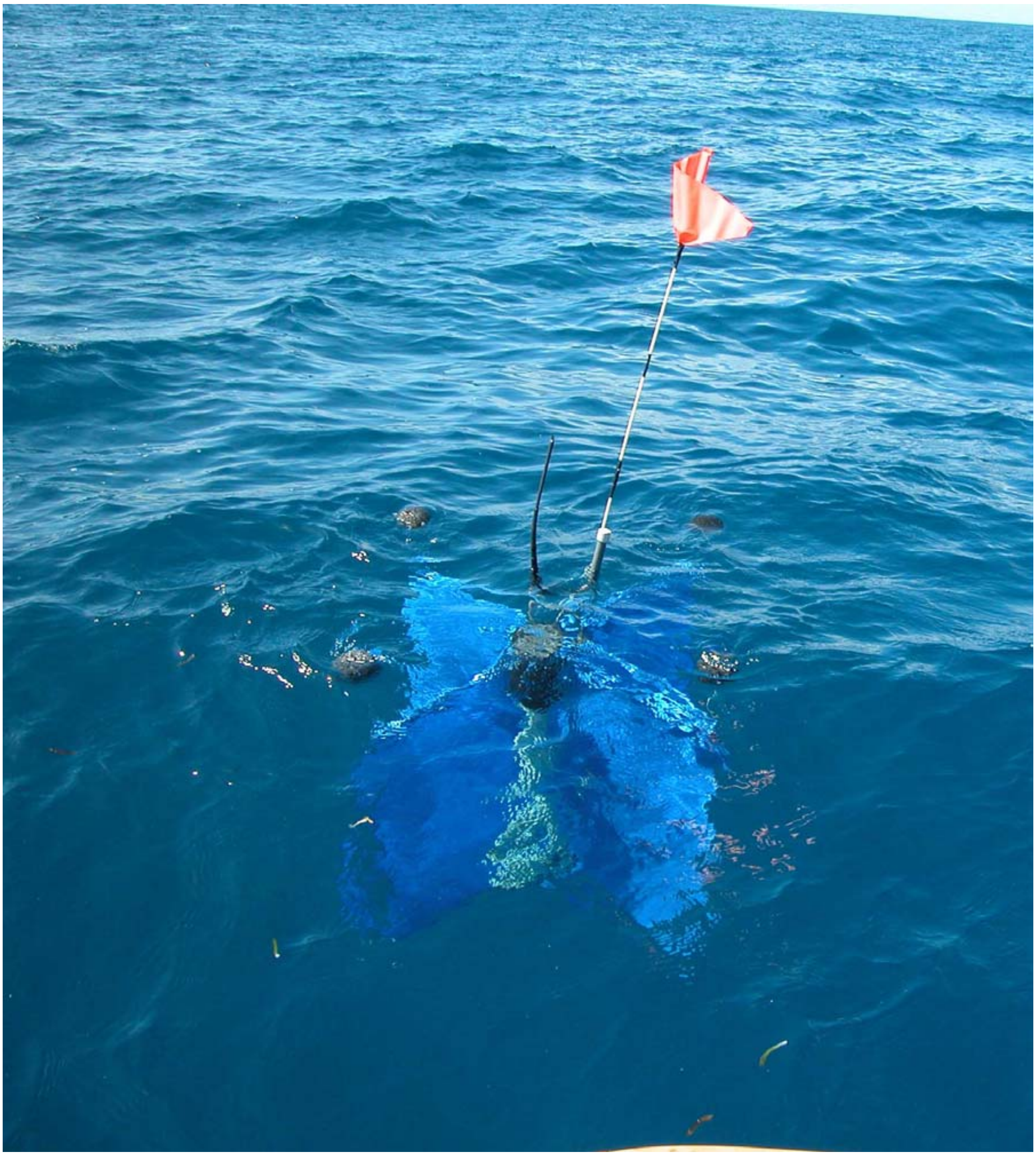

Figure 7.1 **Davis type near-surface drifter released at Scott Reef in August 2003.**

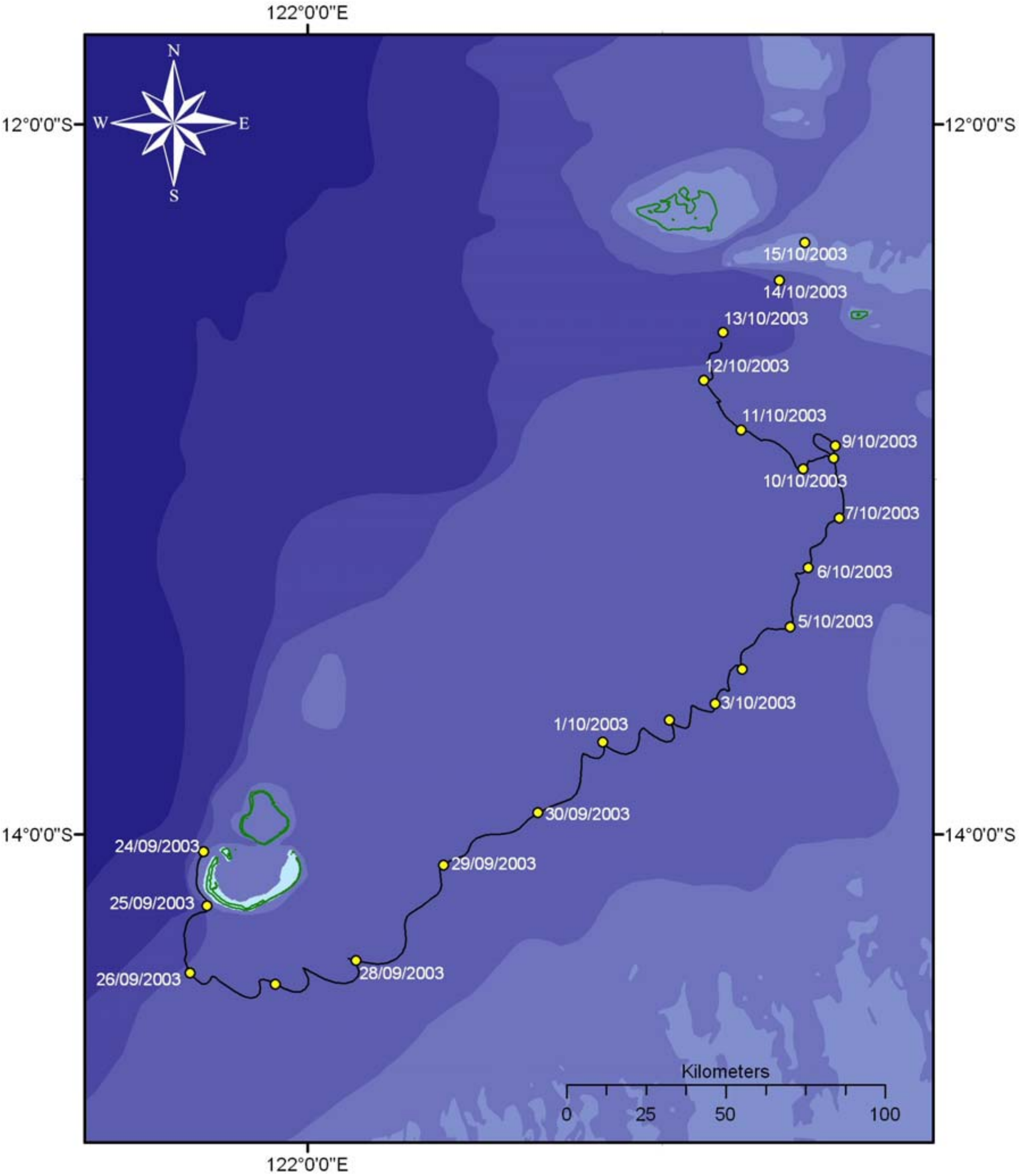

Figure 7.2 Trajectory of surface drifter deployed from Scott Reef, September 2003. Yellow dots indicate date.

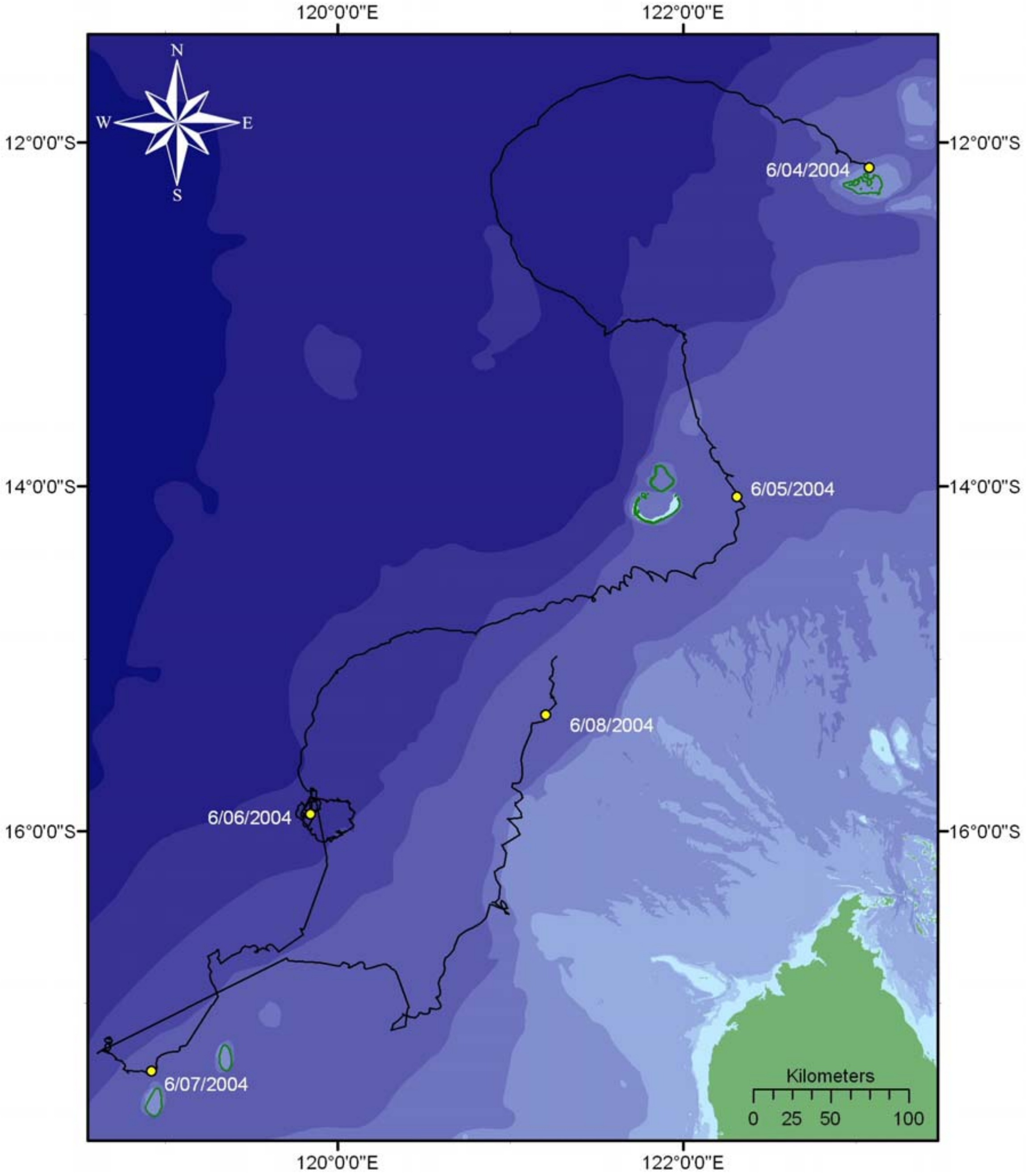

Figure 7.3 Trajectory of surface drifter deployed from Ashmore Reef, April 2004. Yellow dots indicate date.

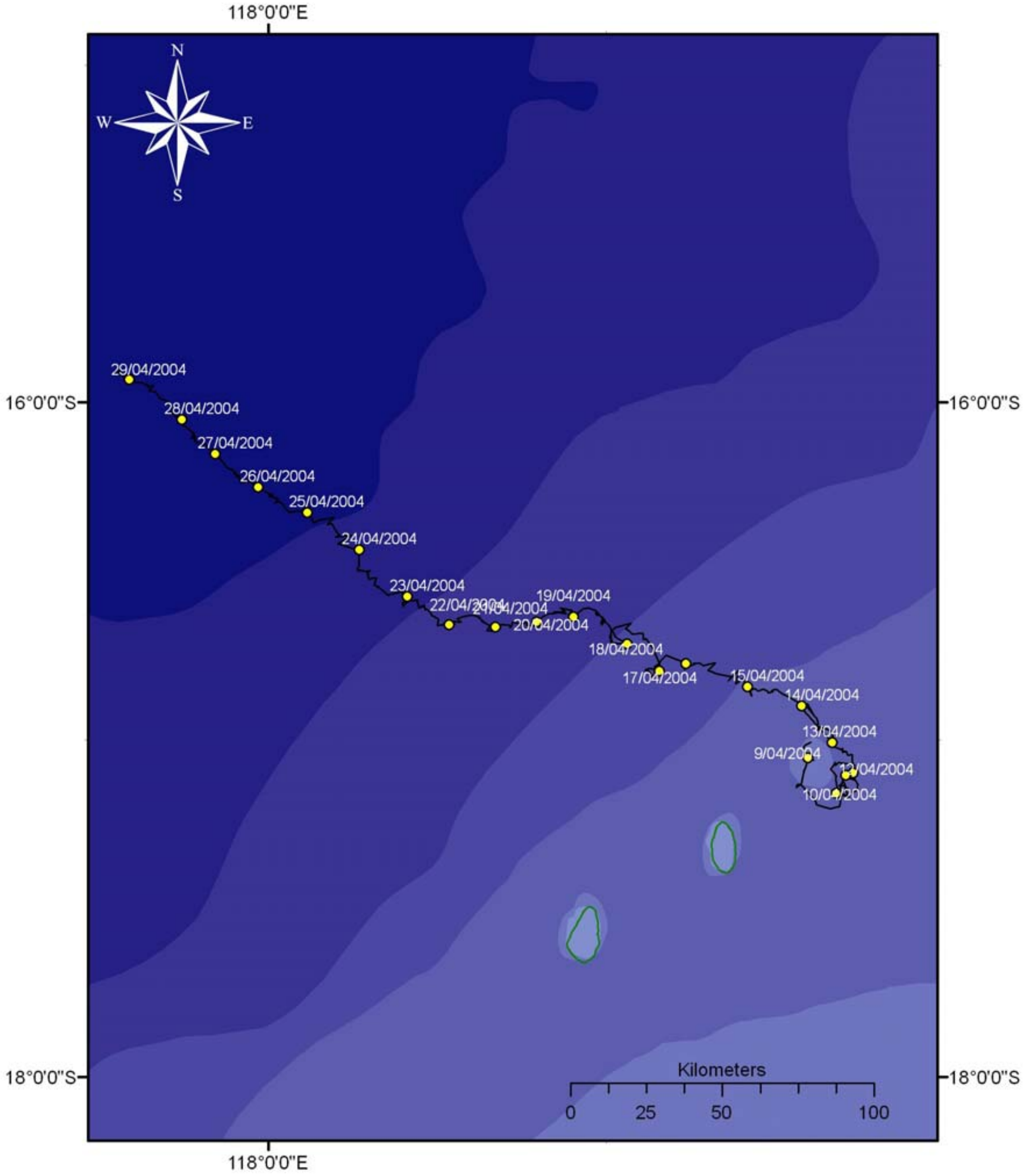

Figure 7.4 Trajectory of surface drifter deployed from Mermaid Reef, April 2004. Yellow dots indicate date.

Table 7.1 Far-field lagrangian drifter deployment summary

Deployment Reef	**Position**	**Date Deployed**
Scott Reef	S 14º 00.131’ E 121º 45.376’	23/09/03
Ashmore Reef	S 12º 08.72’ E 123º 04.74’	06/04/04
Mermaid Reef (Rowley Shoals)	S 17º 00.42’ E 119º 36.36’	08/04/04

Chapter 8: GENERAL DISCUSSION

This thesis has significantly extended our knowledge of the short- and long-term affects of thermal-induced bleaching on coral communities. It provides important data on the direct impacts of a severe bleaching event during the actual period of elevated temperatures and in the months and years following it. I assessed the recovery of coral communities in the five years following the disturbance, including the changes in recruitment, benthic cover and population size-structures. Overall, this thesis provides a key dataset to further our understanding of the impacts of severe bleaching events on coral communities and the process of replenishment and recovery, for which an overview is provided below.

Reproductive output of scleractinian corals is highly seasonal (Harrison and Wallace 1990). For broadcast spawning corals, this seasonality can be confined to just a few nights a year when a multi-species spawning event can occur. The actual timing of this event varies greatly between geographical locations. For example, most corals spawn on the west coast in autumn, whereas those on the east coast spawn in late spring to summer. In Chapter 2, I showed that the coral communities at Scott Reef, a low latitude reef of Western Australia, had evidence of two annual multi-species spawning events, one occurring in autumn and one in spring. In addition, there was a pulse of new coral recruits associated with each of these spawning events. However, by far, the dominant pulse of coral recruits was in autumn. As a consequence, I was able to initiate a long-term study on coral recruitment at Scott Reef (Chapter 4).

In 1994, I initiated a monitoring program at numerous locations at Scott Reef. A thermal-induced bleaching event in 1998 caused major changes to the local reef communities. All reef habitats (< 15 m) were severely affected by the bleaching;

almost 100% of hard and soft corals bleached, and their rates of mortality were between 74% and 89%, depending on the habitat (Chapter 3). Three surveys between November 1997 and November 1998 revealed extreme rates of mortality (50 - 95%) for all zooxanthellate taxa. One of the most interesting findings was that some taxa (eg. Family Poritidae, soft corals) had high levels of mortality after water temperatures had returned to normal. This is the first account of delayed mortality responses and indicates that secondary impacts (eg. pathogens, starvation) affect species differently. Given the severe mortality of corals at Scott Reef in 1998, I would have expected the recovery of their coral communities to be very slow.

To assess the recovery and resilience of coral communities at the Scott Reef system, I investigated how a severe mortality event affected the coral recruitment rates (Chapter 4). I found that rates of coral recruitment in the years following the bleaching were reduced by 97%, due to both the extent and severity of the disturbance and the isolation (> 240 km) of the system (Chapter 7). My results suggest that rates of coral recruitment at Scott Reef will increase with increasing local abundance of adult corals. The dramatic reduction in coral cover as a result of the 1998 thermal bleaching and the subsequent fall in recruitment rates provided further evidence that recovery of Scott Reef coral populations and communities was likely to take decades.

While data on percent cover of taxa provides useful information on changes in community structure, they tell us little about affects on process of change (Hughes and Jackson 1980, Babcock 1991, Baird and Marshall 2002). Changes in the number of colonies of different size classes provide more information about the consequences of observed changes in the percentage cover. In Chapter 5, I assessed changes in population size-structure of three important taxa and show that the bleaching event affected all life stages (ie juvenile, small adults and large adults) of corals. In addition, the number of juvenile corals in the families Acroporidae and Pocilloporidae five years after the bleaching were unexpectedly high, given the very low rates of recruitment. These data suggest that survival of few new recruits, that are likely to be locally derived, is relatively high and recovery is occurring, and would be expected to increase as the juvenile corals grow into adults.

In Chapter 6, I showed that almost six years after a catastrophic bleaching event, percentage cover of hard corals had returned to approximately 40% of their pre-bleaching cover and the community was returning to its previous structure, with evidence of an increasing rate of recovery in the later years. In fact, coral communities at some monitoring sites had almost returned to their pre-bleaching precent cover by 2003. It likely that the survival and growth rates of corals at the Scott Reef system is relatively high. As a consequence, the coral communities are recovering, and at a faster rate than would be predicted, based in the severity of the bleaching event and the reduction in coral recruitment rates. I attribute this recovery to the lack of many anthropogenic stressors that reduce the population growth rates of corals and promote the growth of competitors (but see Ostrander *et al.* 2000). These results provide evidence of the resilience of coral communities to extreme, but infrequent (decades) disturbances, and highlight the extent to which human activities are compromising this resilience elsewhere.

REFERENCES

Aronson RB, Precht WF, Macintyre IG, Murdoch TJT (2000) Coral bleach-out in Belize. *Nature* 405:36

Aronson RB, Precht WF, Toscano MA, Koltes KH (2002) The 1998 bleaching event and its aftermath on a coral reef in Belize. *Marine Biology* 141:435-447

Ayre DJ, Hughes TP (2000) Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. *Evolution* 54:1590-1605

Ayre DJ, Hughes TP (2003) Climate change, genotypic diversity and gene flow of reef-building corals. *Ecology Letters* 7:273-278

Babcock RC, Bull GD, Harrison PL, Heyward AJ, Oliver JK, Wallace CC, Willis BL (1986) Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef. *Marine Biology* 90:379-394

Babcock RC (1991) Comparative Demography of Three Species of Scleractinian Corals Using Age- And Size-Dependent Classifications. *Ecological Monographs* 61:225-244

Babcock RC, Wills BL, Simpson CJ (1994) Mass spawning of corals on a high latitude coral reef. *Coral Reefs* 13:161-169

Baird AH (2001). The ecology of coral larvae: settlement patterns, habitat selection and the length of the larval phase. *PhD Thesis, James Cook University*.

Baird AH, Marshall PA (1998) Mass bleaching of corals on the Great Barrier Reef. *Coral Reefs* 17:376

Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series* 237:133-141

Baker AC, Starger CJ, McClanahan TR, Glynn PW (2004) Corals' adaptive response to climate change. *Nature* 430:741

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* 429:827-833

Benayahu Y, Loya Y (1987) Long-term recruitment of soft corals (Octocorallina: Alcyonacea) on artificial substrata at Eilat (Red Sea). *Marine Ecology Progress Series* 38:161-167

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

Berkelmans R, Willis BL (1999) Seasonal and local spatial patterns in the upper thermal limits of corals on the inshore Central Great Barrier Reef. *Coral Reefs* 18:219-228

Bird J, Steinberg C, Brinkman R, McAllister F (2004) *The physical environment of Scott Reef: 2004.* Australian Institute of Marine Science, Australia.

Bries JM, Debrot AO, Meyer DL (2004) Damage to the leeward reefs of Curacao and Bonaire, Netherlands Antilles from a rare storm event: Hurricane Lenny, November 1999. *Coral Reefs* 23:297-307

Brown BE, Suharsono (1990) Damage and recovery of coral reefs affected by El Ninio related seawater warming in the Thousand Islands, Indonesia. *Coral Reefs* 8:163-170

Brown BE, Dunne RP, Scoffin TP, Le Tissier MA (1994) Solar damage in intertidal corals. *Marine Ecology Progress Series* 105:219-230

Brown BE, Dunne H, Chansang H (1996) Coral bleaching relative to elevated seawater temperature in the Andaman Sea (Indian Ocean) over the last 50 years. *Coral Reefs* 15:151-152

Brown BE, Downs CA, Dunne RP, Gibb SW (2002) Exploring the basis of thermotolerance in the reef coral *Goniastrea aspera*. *Marine Ecology Progress Series* 242:119-129

Burnham KP, Anderson DR (1998) *Model selection and inference: a practical information-theoretic approach.* Springer-Verlag, New York.

Bythell JC (1988) A total nitrogen and carbon budget for the elkhorn coral *Acropora palmata* (Lamarck). *Proceedings of the 6th International Coral Reef Symposium, Townsville, Australia* 2:535-540

Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the Local Dynamics of Open Marine Populations. *Annual Review of Ecology & Systematics* 27:477-500

Carleton JH, Done TJ (1995) Quantitative video sampling of coral reef benthos: large-scale application. *Coral Reefs* 14:35-46

Coles SL, Brown BE (2003) Coral bleaching - capacity for acclimatization and adaptation. *Advances in Marine Biology* 46:183-223

Connell JH (1978) Disturbance in Tropical Rainforests and Coral Reefs. *Science* 199:1302-1310

Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16:S101-S113

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs* 67:461-488

Cresswell G, Frische A, Peterson J, Quadfasel D (1978) Circulation in the Timor Sea. *Journal of Geophysical Research* 98:14379-14389

Dai CF, Soong K, Fan TY (1992) Sexual reproduction of corla in the northern and southern Taiwan. *Proceeding of the 7th International Coral Reef Symposium, Guam* 1: 448-455

De'ath G, Moran PJ (1998) Factors affecting the behaviour of crown-of-thorns starfish (*Acanthaster planci* L.) on the Great Barrier Reef: 2: Feeding preferences. *Journal of Experimental Marine Biology & Ecology* 220:107-126

Done TJ, Potts DC (1992) Influences of habitat and natural disturbances on contributions of massive *Porites* corals to reef communities. *Marine Biology* 114:479-493

Dove SG, Takabayashi M, Hoegh-Guldberg O (1995) Isolation and partial characterization of the pink and blue pigments of pocilloporid and acroporid corals. *Biological Bulletin* 187:288-297

Fabricius KE (1995) Slow population turnover in the soft coral genera *Sinularia* and *Sarcophyton* on mid- and outer-shelf reefs on the Great Barrier Reef. *Marine Ecology Progress Series* 126:145-152

Fabricius KE, Mieog JC, Colin PL, Idip D, Van Oppen MJH (2004) Identity and diversity of coral endosymbionts (zooxanthellae) from three Palauan reefs with contrasting bleaching, temperature and shading histories. *Molecular Ecology* 13:2445-2458

Fagerstrom JA, Rougerie F (1994) 1994 Coral bleaching event, Society Islands, French Polynesia. *Marine Pollution Bulletin* 29:34-35

Fitt WK, Warner ME (1995) Bleaching patterns of four species of Caribbean reef corals. *Biological Bulletin* 187:298-307

Fujioka Y (1999) Destruction and recovery of hermatypic coral communities after the mass bleaching event at Ishigaki Island. *Galaxea* 4: 51-63

Gardner TA, Cote IM, Gill JA, Grant JA, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:956-960

Gleason MG (1993) Effects of disturbance on coral communities- Bleaching in Moorea, French-Polynesia. *Coral Reefs* 12:193-201

Glynn PW (1984) Widespread coral mortality and the 1982-83 El Nino warming event. *Environmental Conservation* 11:133-146

Glynn PW (1991) Coral reef bleaching in the 1980s and possible connections with global warming. *Trends in Ecology & Evolution* 6:175-179

Glynn PW (1993) Coral reef bleaching: Ecological perspectives. *Coral Reefs* 12:1-17

Glynn PW, Colley SB, Ting JH, Mate JL, Guzman HM (2000) Reef coral reproduction in the eastern Pacific: Costa Rica, Panama and Galapagos

Islands (Ecuador). IV. Agariciidae, recruitment and recovery of *Pavona varians* and *Pavona sp.a*. *Marine Biology* 136:785-805

Green AL, Birkeland CE, Randall RH, 1999. Twenty years of disturbance and change in Fagatele Bay National Marine Sanctuary, American Samoa. *Pacific Science* 53:376-400

Grigg RW, Dollar SJ (1990) In: Dubinsky.Z (ed) *Ecosystems of the World: Coral Reefs*. Elsevier Publishers, New York pp 439-452

Grigg RW (1994) Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Marine Ecology Progress Series* 103:25-34

Guest JR, Chou LM, Baird AH, Goh BPL (2002) Multispecific, synchronous coral spawning in Singapore. Coral Reefs 21: 422-423

Guest JR, Baird AH, Goh BPL, Chou LM (2005) Reproductive seasonality in an equatorial assemblage of scleractinian corals. Coral Reefs 24: 112-116

Halford A, Cheal AJ, Ryan D, Williams DMcB (2004) Resilience to large-scale disturbances in coral and fish assemblages on the Great Barrier Reef. *Ecology* 85:1892-1905

Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: Comparative studies of reef-building corals. *Ecology* 77:950-963

Harrington L, Fabricius K, De'ath G, Negri AP (2004) Recognition and Selection of Settlement Substrata determine Post-settlement survival in corals. *Ecology* 85:3428-3437

Harrison PL Wallace CC (1990) Reproduction, dispersal, and recruitment of scleratinian corals. In: Dubinsky.Z (ed) *Ecosystems of the World: Coral Reefs*. Elsevier Publishers, New York. pp 133-207

Harriott VJ (1985) Mortality rates of scleractinian corals before and during a mass bleaching event. *Marine Ecology Progress Series* 21:81-88

Harvell CD, Kim K, Burkholder JM, Colwell RR, Epstein PR, Grimes DJ, Hofmann EE, Lipp EK, Osterhaus ADME, Overstreet RM, Porter JW, Smith GW, Vasta GR 1999. Emerging marine diseases: climate links and anthropogenic factors. *Science* 285:1505-1510

Heyward AJ, Collins JD (1985) Growth and sexual reproduction in the scleractinian coral *Montipora digitata* (Dana). *Australian Journal of Marine and Freshwater Research* 36:441-446

Heyward AJ, Halford A, Smith L, Williams DMcB (1997) Coral reefs of north west Australia: Baseline monitoring of an oceanic reef ecosystem. *Proceedings of the 8th International Coral Reef Symposium, Panama* 1:289-294

Heyward AJ, Negri AP (1999) Natural inducers for coral larval metamorphosis. *Coral Reefs* 188:273-279

Highsmith RC (1982) Reproduction by Fragmentation in Corals. *Marine Ecology Progress Series* 7:207-226

Hoegh-Guldberg O, Smith GJ (1989) The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* (Esper) and *Seriatopora hystrix* (Dana). *Journal of Experimental Marine Biology & Ecology* 129:279-303

Hoegh-Guldberg O, Salvat B (1995) Periodic mass-bleaching and elevated sea temperatures: bleaching of outer reef slope communities in Moorea, French Polynesia. *Marine Ecology Progress Series* 121:181-190

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine & Freshwater Research* 50:839-866

Hughes TP, Jackson JBC (1980) Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. *Science* 209:713-715

Hughes TP, Ayre D, Connell JH (1992) The evolutionary ecology of corals. *Trends in Ecology & Evolution* 7:292-295.

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

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwaskyj NA, Prachett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity and larval recruits. *Ecology* 81:2241-2249

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystroem M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate Change, Human Impacts, and the Resilience of Coral Reefs. *Science* 301:929-933

Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. *Nature* 402:802-804

Karlson RH, Cornell HV (1999) Integration of Local and Regional Perspectives on the Species Richness of Coral Assemblages. *American Zoologist* 39:104-112

Karlson RH (1999). *Dynamics of Coral Communities*. Kluwer Academic Publishers, Netherlands.

Kayanne H, Harii S, Ide Y, Akimoto F (2002) Recovery of coral populations after the 1998 bleaching on Shiraho Reef, in the southern Ryukyus, NW Pacific. *Marine Ecology Progress Series* 239:93-103

Knowlton N (2001) The future of coral reefs. *Proceedings of the National Academy of Sciences* 98:5419-5425

Kojis BL (1986) Sexual reproduction in *Acropora* (*Isopora*) (Colenterata : Scleractinia). I. A. cuneata and A. Palifera on Heron Island, Great Barrier Reef. Marine Biology

Muscatine L, McCloskey LR, Marian RE (1981) Estimating the Daily Contribution of Carbon from Zooxanthellae to Coral Animal Respiration *Limnology and Oceanography* 26: 601-611

Levitan DR, Petersen C (1995) Sperm limitation in the sea. *Trends in Ecology & Evolution* 10:228-231

Loch K, Loch W, Schuhmacher H, See WR (2002) Coral Recruitment and Regeneration on a Maldivian Reef 21 Months after the Coral Bleaching Event of 1998. *Marine Ecology* 23:219-236

Loya Y (1976) Recolonization of Red Sea Corals Affected by Natural Catastrophes and Man-Made Perturbations. *Ecology* 57:278-289

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecology Letters* 4:122-131

Mangubhai S, Harrison PL (2006) Seasonal patterns of coral reproduction on equatorial reefs in Mombassa, Kenya. Proc 10th Int Coral Reef Symp: 106-114

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

McClanahan TR (2000) Bleaching damage and recovery potential of Maldivian coral reefs. *Marine Pollution Bulletin* 40:587-597

McClanahan TR, Muthiga NA, 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

McClanahan TR (2004) The relationship between bleaching and mortality of common corals. *Marine Biology* 144:1239-1245

McClanahan TR, Baird AH, Marshall PA, Toscano MA (2004) Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Marine Pollution Bulletin* 48: 327-335

McFadden CS (1991) A comparative demographic analysis of clonal reproduction in a temperate soft coral. *Ecology* 72:1849-1866

McField M (1999) Coral Response During and After Mass Bleaching in Belize. *Bulletin of Marine Science* 64:155-172

McWilliams JP, Cote IM, Gill JA, Sutherland WJ, Watkinson AR (2005) Accelerating impacts of temperature-induced coral bleaching in the Caribbean. *Ecology* 86:2055-2060

Mendes JM, Woodley JD (2002) Effect of the 1995-1996 bleaching event on polyp tissue depth, growth, reproduction and skeletal band formation in *Montastraea annularis. Marine Ecology Progress Series* 235:93-102

Michalek-Wagner K, Willis BL (2001) Impacts of bleaching on the soft coral *Lobophytum compactum* 1. Fecundity, fertilization and offspring viability. *Coral Reefs* 19:231-239

Miller KJ, Mundy CN (2005) *In situ* fertilisation success in the scleractinian coral *Goniastrea favulus*. *Coral Reefs* 24:313-317

Mora C, Sale PF (2002) Are populations of coral reef fish open or closed? *Trends in Ecology & Evolution* 17:422-428

Moran PJ, Bradbury RH, Reichelt RE (1988) Distribution of recent outbreaks of the crown-of-thorns starfish (*Acanthaster planci*) along the Great Barrier Reef: 1985-1986. *Coral Reefs* 7:125-137

Mumby PJ, Chisholm JRM, Edwards AJ, Clark CD, Roark EB, Andrefouet S, Jaubert J (2001) Unprecedented bleaching-induced mortality in *Porites spp*. at Rangiroa Atoll, French Polynesia. *Marine Biology* 139:183-189

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

Nakamura T, van WoesikR (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Marine Ecology Progress Series* 212:301-304

Negri AP, Heyward AH (1999) Natural inducers for coral larval metamorphosis. Coral Reefs 18: 273-279

Ninio R, Meekan MG (2002) Spatial patterns in benthic communtities and the dynamics of a mosaic ecosystem on the Great Barrier Reef, Australia. *Coral Reefs* 211:95-103

Ninio R, Delean S, Osborne K, Sweatman H (2003) Estimating cover of benthic organisms from underwater video images: Variability associated with multiple observers. *Marine Ecology Progress Series* 265:107-116

Nishikawa A, Sakai K 2003. Genetic Variation and Gene Flow of Broadcast Spawning and Planula Brooding Coral, *Goniastrea aspera* (Scleractinia) in the Ryukyu Archipelago, Southern Japan. *Zoological Science* 20:1031-1038

Nozawa Y, Harrison PL (2005) Temporal settlement patterns of larvae of the broadcast spawning reef coral *Favites chinensis* and the broadcast spawning and brooding reef coral *Goniastrea aspera* from Okinawa, Japan. *Coral Reefs* 24:274-282

Nystrom M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends in Ecology & Evolution* 15:413-417

Nystrom M, Folke C (2001) Spatial Resilience of Coral Reefs. *Ecosystems* 4:406-417

Ogden JC, Ogden NB (2003) The coral reefs of the San Blas Islands: Revisited after 20 years. Rosientiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, pp 267-272 In: Ginsburg RN (ed) *Proceedings of Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History*.

Oliver JK, Babcock RC, Harrison PL, Willis BL (1988) Geographic extent of mass coral spawning: Clues to ultimate causal factors. *Proceedings of the 5th International Coral Reef Symposium, Townsville* 2:803-810

Oliver J, Babcock R (1992) Aspects of the fertilization ecology of broadcast spawning corals: Sperm dilution effects and in situ measurements of fertilization. *Biological Bulletin* 183:409-417

Omori M, Fukami H, Kobinata H, Hatta M (2001) Significant drop of fertilization of *Acropora* corals in 1999: An after-effect of heavy coral bleaching? *Limnology & Oceanography* 46:704-706

Ostrander GK, Armstrong KM, Knobbe ET, Gerace D, Scully EP (2000) Rapid transition in the structure of a coral reef community: The effects of coral bleaching and physical disturbance. *Proceedings of the National Academy of Sciences* 97:5297-5302

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke R, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955-958

Pearson R (1981) Recovery and Recolonization of Coral Reefs. *Marine Ecology Progress Series* 4:105-122

Raimondi PT, Morse ANC (2000) The consequences of complex larval behavior in a coral. *Ecology* 81:3193-3211

Rowan R, Knowlton N, Baker A, Jara J (1997) Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* 388:265-269

Rowan R (2004) Coral bleaching: Thermal adaptation in reef coral symbionts. *Nature* 430:742

Salih A, Larkum A, Cox G, Kuhl M, Hoegh-Guldberg O (2000) Fluorescent pigments in corals are photoprotective. Nature 408:850-853

Sano M (2000) Stability of reef fish assemblages: Responses to coral recovery after catastrophic predation by *Acanthaster planci*. Marine Ecology Progress Series 198:121-130

Sheppard CRC, Wilson SC, Salm RV, Dixon D (2000) Reefs and coral communities of the Arabian Gulf and Arabian Sea. In: McClanahan TR, Sheppard CRC, Obura DO (eds) *Coral Reefs of the Indian Ocean: their ecology and conservation*. Oxford University Press, New York, p 257-293

Sheppard CRC (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature* 425:294-297

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

Shimoike K, Hayashibara T, Kimura T, Omori M (1992) Obversations of split spawning in Acropora spp. at Akjima Island, Okinawa. *Proceeding of the 7th International Coral Reef Symposium, Guam* 1: 484-488

Simpson CJ (1988) *Ecology of the scleractinian corals in the Dampier Archipelago, Western Australia.* Environmental Protection Authority Technical Series.

Simpson CJ, Pearce AF, Walker DI (1991) Mass spawning of corals on Western Australian reefs and comparisons with the Great Barrier Reef. *Proceedings of the Royal Society of Western Australia* 5:85-91

Smith LD, Hughes TP (1999) An experimental assessment of survival, re-attachment and fecundity of coral fragments. *Journal of Experimental Marine Biology & Ecology* 235:147-164

Smith LD, Devlin M, Haynes D, Gilmour JP (2005) A demographic approach to monitoring the health of coral reefs. *Marine Pollution Bulletin* 51:399-407

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

Szmant-Froelich A, Yevich, P Pilson MEQ (1980). Gametogensis and early development of the temperate coral *Astrangia danae* (Anthozoa: Scleractinian). *Biological Bulletin* 158: 257-269.

Vogt HP (1995) Coral reefs in Saudi Arabia: 3.5 years after the Gulf War oil spill. Coral Reefs 14:271-273

Wallace CC (1985) Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. Marine Biology 88:217-233

Wallace CC (1999) Staghorns of the World. CSIRO Publishing, Australia.

Ward S, Harrison P, Hoegh-Guldberg O (2000) Coral bleaching reduces reproduction of scleractinian corals and increases susceptibility to future stress. *Proceedings 9th International Coral Reef Symposium, Bali, Indonesia.* 2:1123-1128

Underwood JN, **Smith LD**, van Oppen MJH and Gilmour JP (2007) Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. Molecular Ecology 16: 771-784

Underwood JN, **Smith LD**, van Oppen MJH and Gilmour JP (*in press*) Genetic connectivity in a broadcast spawning coral *Acropora tenius* between isolated reef systems of northwestern Australia. *Ecology Letters* 16: 771-784

Whittaker K (2004) Non-random mating and population genetic subdivision of two broadcasting corals at Ningaloo Reef, Western Australia. *Marine Biology* 144:593-603

Wilkinson CR (1999) Global and local threats to coral reef functioning and existence: review and predictions. *Marine & Freshwater Research* 50:867-878

Wilkinson CR (2000) *Status of Coral Reefs of the World: 2000*. Australian Institute of Marine Science, Townsville, Australia.

Wilkinson CR (2002) *Status of coral reefs of the world: 2002*. Australian Institute of Marine Science, Townsville, Queensland

Willis BL, Babcock RC, Harrison PL, Oliver JK (1985) Patterns in the Mass Spawning of Corals on the Great Barrier Reef from 1981 to 1984. *Proceedings of the 5th International Coral Reef Congress* 4:343-348

Wilson JR, Harrison PL (1998) Settlement-competency periods of larvae of three species of scleractinian corals. *Marine Biology* 131:339-345

Woodley JD, Chornesky EA, Clifford P, Jackson JC, Kaufman LS, Knowlton N, Lang JC, Pearson M, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe V, Wahle C, Wulff JL, Curtis A, Dallmeyer M, Jupp B, Koehl M, Neigel J, Sides E (1981) Hurricane Allen's Impact on Jamaican Coral Reefs. *Science* 214:749-755

APPENDIX 1

Publications during the course of my PHD candidature;

1. **Smith LD**, Hughes TP (1999). An experimental assessment of survival, re-attachment and fecundity of coral fragments. *Journal of Experimental Marine Biology & Ecology* 235:147-164.

2. Babcock R, **Smith LD** (2002). Effects of sedimentation on coral settlement, survivorship and demography. *Proceedings of the 9th International Coral Reef Symposium, Bali* 1:245-248.

3. Heyward AJ., **Smith LD**, Rees M and SN Field (2002). Enhancement of coral recruitment by in situ mass culture of coral larvae. *Marine Ecology Progress Series* 230:113-118.

4. Negri AP, **Smith LD**, Webster NS and AJ Heyward (2002). Understanding ship-grounding impacts on a coral reef: potential effects of anti-foulant paint contamination on coral recruitment. *Marine Pollution Bulletin* 44:111-117.

5. **Smith LD**, Negri AP, Philipp E, Webster NS, Heyward AJ (2003). The effects of antifoulant-paint-contaminated sediments on coral recruits and branchlets. *Marine Biology* 143:651-657.

6. Webster NS, **Smith LD**, Heyward AJ, Watts, JEM, Webb RI, Blackall LL, Negri AP (2004). Metamorphosis of a Scleractinian Coral in Response to Microbial Biofilms. *Applied and Environmental Microbiology* 70:1213-1221.

7. **Smith LD**, Rees M, Colquhoun J, Heyward AP (2005). Survey of the beche-de-mer and *Trochus* populations at Ashmore Reef: baseline survey. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory* Supplement 1:177-184.

8. **Smith LD**, Devlin M, Haynes D, Gilmour JP (2005). A demographic approach to monitoring the health of coral reefs. *Marine Pollution Bulletin* 51:399-407.

9. **Smith LD**, Gilmour JP, Heyward AJ (2006) Mass-bleaching, mortality and slow recovery of three common groups of scleractinian corals at an isolated reef. *Proc 10th Int Coral Reef Symp* 651-656

10. Gilmour JP, Baird AH, Pratchett MP, **Smith LD** (2006) The maintenance of populations of the mushroom coral *Fungia fungites* under different disturbance regimes: Sexual versus asexual recruitment. *Proc 10th Int Coral Reef Symp* 351-358

10. Gilmour JP, **Smith LD** (2006). Category 5 cyclone at Scott Reef, northwestern Australia. *Coral Reefs 25: 200*

11. Underwood JN, **Smith LD**, van Oppen MJH and Gilmour JP (2007) Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. Molecular Ecology 16: 771-784

12. Underwood JN, **Smith LD**, van Oppen MJH and Gilmour JP (*in press*) Genetic connectivity in a broadcast spawning coral *Acropora tenius* between isolated reef systems of northwestern Australia. *Ecology Letters* 16: 771-784

13. **Smith LD**, Gilmour JP, Heyward AP (*in press*). System-wide decline in coral cover and recruitment following a catastrophic bleaching at an isolated group of reefs. *Coral Reefs*

APPENDIX 2

BIANNUAL SPAWNING, RAPID LARVAL DEVELOPMENT AND EVIDENCE OF SELF-SEEDING FOR CORALS AT AN ISOLATED SYSTEM OF REEFS

This chapter is currently in review in *Coral Reefs*. It is essentially a combination of Chapters Two and Seven.

ABSTRACT

Some of the most important demographic parameters underlying the resilience of coral communities are determined by their patterns of reproduction. In this study, a variety of methods were used to investigate the patterns of spawning, larval development and dispersal for corals at an isolated reef system off far-north Western Australia. Two short and distinct periods of gamete maturation and multi-specific spawning occurred during spring and autumn each year, in contrast to the single mass spawning described on most other reefs around Australia. The subsequent rates of embryogenesis and larval development were among the fastest described for corals, with pre-competency periods of approximately three days. Within three days of spawning, slicks of spawn and current drifters had dispersed < 5 km, and < 10 km after six days, while the times taken for drifters to travel between adjacent (> 240 km) reef systems were similar or greater than the upper competency periods of most coral larvae. Thus, under similar conditions the entire reef system, and to some extent the reefs within the system, are largely self-seeded; rates of immigration from other systems are insufficient to rapidly increase the recovery of communities within years of a major disturbance. These results have implications for the management of similar reef systems and highlight the need for replicate areas of protection both within and among similar reefs.

NTRODUCTION

Among the most important and least understood aspects of the life histories of corals are their patterns of reproduction (gametogenesis, spawning, dispersal and recruitment). Although most corals are known to broadcast spawn their gametes for external fertilization (Harrison and Wallace 1990), the proportion spawning during different months within a year, the *in situ* rates of larval development, and the distances over which the larvae disperse, are largely unknown for most reefs around the world. Yet, knowing when corals spawn and the degree of connectivity among their communities is critical for effective management of coral reefs and the design of marine protected areas (Caley et al. 1996, Gains et al. 2003).

Many species of Indo-Pacific corals participate in mass spawning or multi-specific spawning events that involve the synchronous release of their gametes over a few nights each year (see Harrison and Wallace 1990, Guest et al. 2002, Baird et al. 2000, Carroll et al. 2006, Mangubhai and Harrison 2006, Nozawa et al. 2006). On reefs around Australia, most of the initial research into the reproduction of broadcast-spawning corals was conducted on the Great Barrier Reef where many corals spawn their gametes over a few consecutive nights each year (Babcock et al. 1986), and synchronous spawning was subsequently reported for reefs off Western Australia (Simpson 1991, Babcock et al. 1994). Further studies had identified more species participating in mass spawning events, but also differences in the times of spawning on in- and offshore reefs and the tendency for ‘split-spawning’ to occur over consecutive months during some years (Willis et al. 1985, Simpson 1991). In addition, quantification of cycles of gametogenesis in an increasing number of colonies and species provided evidence of spawning at times other than during the main nights of mass spawning, over a more protracted period, and more than once a year (e.g., Wallace 1985, Stobart et al. 1992, Wolstenholme 2004).

In addition to knowing when corals spawn, estimating the distances over which their larvae routinely disperse is critical to the management of coral communities because dispersal distances provide insights into patterns of connectivity within and among reefs. Dispersal distances are influenced by larval competency periods, reef structure, oceanographic conditions, and larval behavior. In most laboratory experiments, larvae are generally competent to settle between three and six days after spawning, whereas upper competency periods are generally between two and ten weeks (Wilson and Harrison 1998, Gilmour 1999, Miller and Mundy 2003, Nishikaswa et al. 2003, Baird 2004, Nozawa et al. 2006). Because coral larvae are poor swimmers, dispersal during their competency period is determined by the direction and speed of currents, which are influenced by factors such as reef topography, winds and waves (e.g., Willis and Oliver 1988, 1990), all of which vary with depth. Larvae generally remain close to the surface between approximately 12 and 72 hours after spawning, depending on weather conditions, and then disperse through deeper waters until they are competent to settle and suitable substrata are available (e.g., Bull 1985, Willis and Oliver 1988, Raimondi and Morse 2000). Current speeds are usually faster near the surface and slowest adjacent to the substrata, so most dispersal is likely to occur prior to larvae settling out of the water column, after which dispersal may be limited to the exploration of microhabitats until a suitable site of attachment is found.

Coral larvae clearly disperse among distant reefs over evolutionary times, but management strategies aimed at maintaining community resilience to an increasing variety of disturbances require estimates of the routine distances of dispersal and recruitment over ecological times scales (< decades). Routine distances of dispersal cannot be determined directly, but have been inferred from different data and methods, such as rates of larval settlement (e.g., Wilson and Harrison 1998, Baird 2004), following slicks of spawn and using plankton tows (e.g., Bull 1985, Willis and Oliver 1988), hydrodynamic models (e.g., Black 1993), genetics (e.g., Ayre and Hughes 2000, Underwood et al. 2007) and patterns of recruitment (e.g., Fisk and Harriot 1990, Hughes et al. 1999). Most methods suggest that larvae remain on their natal reef or disperse to adjacent reefs up to tens of kilometers away over their pre-competency periods, but that dispersal varies among different reefs and conditions. In this study, a combination of methods was used to investigate the patterns of reproduction and dispersal for mass spawning corals at an isolated reef system. Firstly, the times and extent of mass spawning were determined by quantifying cycles of oogenesis, the numbers of species spawning, and the rates of larval recruitment, around two potential seasons of spawning (Spring / Autumn) on Indo-Pacific reefs. Secondly, the pre-competency periods of larvae were determined by quantifying the *in situ* rates of embryogenesis and larvae development, and by conducting settlement experiments. Finally, the extent to which reefs and reef systems within the region are self-seeded was inferred by deploying short- and far-field current drifters at the times of coral spawning.

METHODS

This research was conducted at the Scott system of reefs (S14° 04', E121°46'), located approximately 260 km off the coastline of north-western Australia. The various components of this research were conducted at one or more of six locations across Scott Reef (Fig. 1).

Annual cycles of oogenesis

Oogenic cycles were quantified for the hermaphroditic spawning corals *Acropora hyacinthus* and *A. spicifera*, which are abundant at Scott Reef and have a wide geographic distribution (Wallace 1999). Colonies of each species at two sites at Location 3 (Fig. 1) were sampled at intervals of between three and five months over almost four years. During most sampling trips, two branches (> 8 cm) were collected from the central region of 20 colonies of each species, and the presence of pigmented (pink/red) eggs within polyps recorded. Samples were fixed in a solution of 10% formalin and seawater and then processed according to Wallace (1985). At least 10 polyps from each branch were dissected and viewed under a binocular microscope. If eggs were present, their sizes within five polyps were recorded as being small (100 to 300 μm), medium (300 to 500 μm) or large (500 to 700 μm).

In addition to quantifying the oogenic cycles of two species, replicate colonies of a range of species were sampled haphazardly during all trips to determine whether they had large and pigmented eggs, from which inferences about the times of spawning were drawn (Harrison et al. 1984, Guest et al. 2005). Species observed to participate in multi-specific spawning events were also recorded.

Larval recruitment

During two of the years in which the cycles of gametogenesis were studied, the rates of coral recruitment were quantified at three sites at each of the six locations (Fig. 1), following the spawning between six and 10 nights after the full moon in Autumn (March / April) and Spring (October / November). In addition to these predicted times of mass spawning, settlement plates were deployed during four other months over the two year period to quantify background rates of recruitment. At each location, three groups of five terracotta settlement plates (110 x 110 x 10mm) were attached (see Mundy 2000) haphazardly to the substrata, with each group spaced at 50 m intervals along the reef slope. Settlement plates were deployed three weeks (± 4 d) prior to the predicted dates of mass spawning and collected seven weeks later (± 5 d). After collection, the settlement plates were bleached and the number of *Acropora* recruits recorded using a dissecting microscope.

Rates of embryogenesis and larval development

To determine the *in situ* rates of embryogenesis and larval development, samples were collected from within and around two slicks originating from the reefs at locations 3 and 5 during one year (Fig. 1). From two to 10 hours after the time of mass spawning, 5 L samples (n = 16) were collected from the centre and edge (< 1 m) of each slick at the surface (< 0.5 m) and a depth of 2 m. Each 5 L sample was collected using a vacuum pump and concentrated to 1 L, from which four 100 ml sub-samples were taken. These were immediately transported to the laboratory and sub-sampled further by transferring each of three, 2 ml replicates to a haemocytometer. The developmental stages of most embryos and larvae were quantified immediately using a dissection microscope, or for a few sub-samples at a later time from photographs.

At approximately 17 hours after the spawning, the slicks had become putrid and were no longer sampled. However, there was a high density of embryos in the water column, which were subsequently sampled along the reef edge near location 3 (Fig. 1) using a plankton net attached to an underwater scooter. The plankton net was 1.5 m long, its mouth 0.5 m in diameter, and mesh size 100 µm, and samples were collected in a 500 ml jar at the cod end. Three replicate tows (500 m) were conducted at the surface, 5 m and 10 m depths, at 1 (17 hours), 2 (41 hours) 3 (67 hours) and 4 (91 hours) days after the spawning. Very few larvae were collected in tows four days after spawning, which was confirmed by 12 additional tows at two other locations, and three additional tows at Location 3 five days after spawning.

The larvae collected in plankton tows two days after spawning were combined and added to sterile six-well (12 ml) culture plates (Heyward and Negri 1999) that evening. Ten larvae were added to each well in four plates (n = 240), which contained a chip of crustose coralline algae (5 x 5 mm). The numbers of larvae that had settled after 12 and 24 hours were quantified using a dissection microscope. Settled larvae were divided between those actively exploring the bottom of the container and those that had attached aborally or were in various stages of metamorphosis. Because the numbers of larvae collected in plankton tows decreased so dramatically more than two days after the spawning, no further settlement studies could be conducted.

Local and regional current movements

To infer the dispersal distances of larvae during their pre-competency period, slicks of spawn and current drifters were tracked from Locations 3 and 5 (Fig. 1). Four surface drifters tracked the movement of the surface waters up to four days after the spawning, and their dispersal was influenced by wind and waves in addition to currents. The surface drifters consisted of a square float (20 x 20 x 5 cm) with ballast submerged to 0.15 m and an attached GPS. Additionally, two sub-surface drifters were used to track current movements in the top 1 m of the water column up to one week after spawning, and their dispersal was far less influenced by wind and wave action. The sub-surface drifters consisted of a cylinder (1 x 0.1 m) and 4 material sails that were submerged in the water and radiate out from the cylinder by 0.5 m. During this period, water temperatures were quantified using data loggers at 9 m depth and at the surface using digital thermometers, while wind speeds and directions were quantified using a portable weather station.

The sub-surface drifters were also used to track the long-distance movement of currents between Scott Reef and the closest reef systems in the region, Ashmore Reef 250 km to the north east and the Rowley Shoals 400 km to the south west (Fig. 1). Over three years, seven sub-surface drifters were deployed from one of the reef systems around the time of mass spawning during Spring or Autumn, and their position logged via the Argos satellite network.

RESULTS

Oogenesis, spawning and recruitment

Cycles of gametogenesis and observations of gamete release indicated two spawning events each year at Scott Reef, of which the primary mass spawning occurred during Autumn (March / April) and the secondary spawning during Spring (October / November) (Table 1). At the end of November or in mid-December, small (≤ 300 μm) eggs were found in colonies of *A. spicifera* or *A. hyacinthus*. In January, medium (300 to 500 μm) sized eggs were present in more than 75% of colonies of both species, and a higher proportion had large (≥ 500 μm) eggs in early March. Colonies of both species, and 54 other species, were observed to spawn or have pigmented eggs in late March or early April during one or more years (Table

2). Within these species, between 45% and 95% of the colonies that were randomly sampled had pigmented eggs. However, during the second year of the study, spawning was apparently split between March and April due to the early full moon, and in late March large eggs were present in 40% of *A. spicifera* colonies but absent from all other colonies of *A. spicifera* and *A. hyacinthus*.

Eggs were not seen in colonies of *A. spicifera* or *A. hyacinthus* during May, but small eggs were visible in between 20% and 60% of colonies of both species in August. In October, large eggs were present in between 40% and 65% of colonies of both species, and during late October or early November colonies were observed to spawn. Colonies of 24 other species of corals were observed to spawn or have pigmented eggs in October or November during one or more years, and between 10 and 80% of the colonies within each species had pigmented eggs. There was no evidence of any species spawning exclusively during October or November (Table 2).

The patterns of oogenesis and spawning over two years were supported by the rates of recruitment of *Acropora* at 18 sites across the Scott Reef system. Numerous recruits were on settlement plates at all sites following the spawning in Autumn and Spring, but there were consistently between ten and twenty times more following that in Autumn (Fig. 2). On average (± 95% C.I.), there were 36.2 (± 13.7) recruits plate^{-1} yr^{-1} following the spawning in Autumn, compared with 3.4 (± 0.8) following that in Spring. Background rates of recruitment of *Acropora* in the four deployments of settlement plates during times other than the two spawning periods ranged between 0.08 (± 0.15) and 0.2 (± 0.5) recruits plate^{-1} yr^{-1}.

Rates of embryogenesis and larval development

Slicks of spawn were sampled on the main night of spawning in Autumn, eight nights after the full moon in March, at sites where 85% (by cover) of the corals belonged to the *Acropora* and Faviidae. Most colonies had released their gametes between approximately 19.30 and 21.00, and within two hours slicks had formed on the surface; the two largest slicks were sampled through time. Two hours after spawning, more than 50% of eggs had undergone cleavage (Fig. 3 a), but after five hours the slicks had begun to disperse and the centre of both contained a high density of eggs and embryos that were not viable and were decomposing. At this time, most live embryos were around the edges of both slicks where the densities were much lower. After approximately seven hours, more than 80% of the embryos had developed beyond the 16-cell stage, and after ten hours more than 80% had reached the dish or blastula stages (Fig. 3 a). At 17 hours after spawning, the slicks were breaking apart and becoming putrid, and there were few live embryos or larvae in the centre or at the edge of each slick, nor in additional samples (n = 12) collected from beside (< 5 m) or underneath (< 2 m) either slick. However, there were numerous embryos throughout the water column adjacent to the reef crest, of which approximately half collected in plankton tows had reached the dish or blastula stage, while the remainder had reached the larval stage (Fig. 3 b). The numbers of embryos and larvae were most abundant at ≤ 2 m, but there was considerable variation among the depths and among the replicate tows conducted at each depth (Fig. 3 b).

On the second day (41 hours), only larvae were collected in the plankton tows, of which approximately 40% were motile and actively swimming (Fig. 3 b). As with the previous census, the numbers in each stage varied among depths, but with considerable variation among tows, and there was no clear pattern to the distribution of larvae in different stages of development with depth. For example, larvae were not more abundant at shallow depths and motile larvae were not more abundant closer to the substrata (≥ 5 m). Over the following days, all the larvae collected in plankton tows were motile and their numbers decreased dramatically (Fig. 3 b). On the third day (67 hours), the total number of larvae was < 2% of those collected in the preceding day, and on the forth day (67 hours) only five larvae were obtained from the tows collected at all depths. On the forth day, few larvae (n = 11) were found in additional tows (n = 12) at two other locations, as with additional tows (n = 3) conducted at the main sampling location on the fifth day after spawning.

Larvae (n = 240) collected in tows on the second day (41 hours) after spawning were added to experimental containers that evening, and by the next morning (62 hours) the mean percentage (± 95% C.I.) that were actively exploring the bottom of the containers was 31% (± 11), and 28% (± 5) had settled and attached to either the container or the crustose coralline algae. By the evening (72 hours), 29% (± 7) of larvae were exploring the bottom of the containers and 57% (± 9) had attached or commenced metamorphosis.

8.1.1 Physical conditions and current movements during spawning

The movement of the two slicks of spawn and six current drifters following the spawning indicated that larvae remained within 5 to 10 km of their site of origin during their pre-competency period. The spawning occurred during neap tides when the winds speeds were less than 5 knots and the water temperature at the study sites reached 32.6ºC at the surface (< 1 m) and 30.8ºC at 9 m depth. Within three days of the spawning, the two slicks that were sampled and the current drifters that were deployed all traveled less than 5 km and in similar directions. Between three and six days after the spawning the slicks had broken apart and the tidal amplitude was increasing, but the dispersal of drifters had remained at less than 10 km.

Based on the movement of the sub-surface drifters following spawning, larvae would take at least four days to escape the tidal influence of Scott Reef and approximately one or more months to travel among the nearest reef systems in the region. Of the seven drifters released outside the tidal influence of the reef systems around the times of spawning, two traveled in a westerly direction and two traveled for two months without reaching the vicinity (< 50 km) of another reef system (Fig. 4). Two of the seven drifters traveled from one reef system to within 50 km of another and a third traveled in a southerly direction among the reefs at the Rowley Shoals (Fig. 4).

Based on these data, larvae will take at least one month to travel between Scott Reef and the Ashmore reef system 250 km to the north, and at least two months to travel between Scott Reef and the Rowley Shoals system 400 km to the south west.

The path of the drifters indicated a seasonal reversal of the surface circulation in the region during the middle of the year, from a predominately southerly and westerly drift to a northerly drift. The path of one drifter reversed during July, and those deployed during April or May traveled in a southerly direction, compared with a northerly direction between August and September (Fig. 4). The two drifters that had a strong westerly drift were both deployed during April.

DISCUSSION

Times of mass spawning

Coral communities at Scott Reef participated in two short and distinct periods of multi-specific spawning each year, in contrast to the single mass spawning previously documented on most reefs around Australia (Harrison and Wallace 1990, Simpson 1991, Babcock et al. 1994). Although the spawning in Spring at Scott Reef was minor compared with the mass spawning during Autumn, both involved many colonies, species and genera, as opposed to the cases of secondary spawning that have been reported on the Great Barrier Reef (e.g., Stobart et al. 1992, Wolstenholme 2004). The times of spawning at Scott Reef were the same as those reported for at least 11 species of *Acropora* at either of two other Western Australian reefs

(Rosser and Gilmour 2007), and coincide with the mass spawning events previously reported on the east and west coasts of Australia. More than one multi-specific spawning event within a year has also been reported on other reefs around the world, such as those adjacent to Papua New Guinea (Oliver et al. 1988), Singapore (Guest 2005), and Kenya (Mangubhi and Harrison 2006). The patterns of spawning at Scott Reef most resemble those at reefs off Singapore, whereby a second multi-specific spawning occurs at least three months after the primary spawning, although a larger proportion of colonies and species apparently participate in the secondary spawning at Scott Reef.

For the two spawning periods each year at Scott Reef, the total percentage of randomly sampled *Acropora spicifera* or *A. hyacinthus* colonies with ripe eggs exceeded 100%, indicating the potential for colonies to have two annual gametogenic cycles. Most spawning corals have been documented to have only one annual gametogenic cycle, although instances of two cycles being initiated and only one maturing have been reported (Harrison and Wallace 1990). Alternately, some corals during some years have two gametogenic cycles that fully mature (Oliver et al. 1988, Stobart et al. 1992, Guest et al. 2005; Mangubhai and Harrison 2006). Favorable conditions are probably required for two annual gametogenic cycles, and could be provided by the warmer waters at low-latitude reefs, although prolonged periods of warm water can obviously stress corals. The water temperatures around Scott Reef are warmer than on most Australian reefs, but more variable than on equatorial reefs, having two annual increases and decreases around the times of mass-spawning (Fig. 5) that could provide important cues for cycles of reproduction. However, determining the extent to which individuals and species participate in one or two spawning events each year requires further quantification of gametogenic cycles over several years and under a range of environmental conditions.

Larval development and pre-competency periods

Larvae were competent to settle at Scott Reef three days after spawning, which is sooner than has been documented in most studies (but see Miller and Mundy 2003, Nozawa and Harrison 2005). Most studies have documented pre-competency periods of four to six days, although the period may be defined by the time at which larvae metamorphosed into a polyp, rather than when larvae settle out of the water column and actively explore or attach to the substrata. The short pre-competency period for larvae at Scott Reef may also be related to their being collected *in situ* two days after spawning, and therefore developing in warmer water than in laboratory experiments at higher latitudes (Nozawa and Harrison 2002).

The rates of development and the settlement of larvae three days after spawning corresponded to a dramatic decrease in the numbers collected in plankton tows, although most sampling was only conducted at a single location and up to five days after spawning. Thus, the decreases in larvae four days after spawning could be due to their having already settled, or their being carried away with no subsequent influx of larvae with the sampling area or period. Nevertheless, the dispersal of the larvae during this period was probably limited (see below), and their decreased abundance corresponded to the pre-competence period in settlement experiments. The extent to which these results can be extrapolated to other spawning events or reefs remains to be determined, but they provide evidence of rapid *in situ* rates of development and the short periods over which larvae may disperse while on a reef, before settling out of the water column and exploring the substrata.

Distances of larval dispersal

During their pre-competency period, many of the larvae that originated from the study location may have dispersed no more than 5 to 10 km before settling. The slicks of spawn and surface drogues traveled in similar directions, and in the calm conditions their dispersal was primarily influenced by neap tides. Approximately one day after the spawning there were few live embryos or larvae associated with slicks, similar to the findings of Oliver and Willis (1987), but in contrast to those of Willis and Oliver (1998). The death and decomposition of embryos and larvae in the dense slicks was probably related to the high water temperatures and the light winds. Wind speeds initially have a major influence on slick dispersal, with strong winds rapidly dispersing larvae horizontally and vertically, whereas in light winds larvae tend to remain closer to their site of origin and in the surface layer for longer (Bull 1985, Willis and Oliver 1988). In contrast, most viable larvae at Scott Reef had dispersed below the surface layer within a day of the spawning, but there was no evidence of larvae at deeper depths being in a more advanced developmental stage. However, there was considerable variation among replicate tows and the distribution of larvae was extremely patchy, as has been reported in other studies that employed greater spatial and temporal replication (Bull 1985, Willis and Oliver 1990).

Larvae produced in different weather conditions or from different areas at Scott Reef may regularly disperse further than the short distances indicated here, potentially among the adjacent reefs within the system (North Scott, South Scott, Seringapatam). The weather conditions described here are typical of those during the main spawning in Autumn, but also similar to those during the Spring spawning, with the exception of wind directions. In addition to water temperatures peaking at around the time of spawning in Spring and Autumn, wind speeds are also at their weakest (Fig. 5). However, in conditions of lower water temperatures and higher winds speeds, larvae may be slower to develop and disperse further than indicated in this study. Variation in winds and the topographical features of a reef clearly influence the patterns of flow at different depths, and therefore the distances of which larvae disperse (Willis and Oliver 1990, Oliver et al. 1992). Nevertheless, inferences of larval dispersal from these data are supported by genetic analyses of coral populations at Scott Reef, which indicate that larvae from the brooding coral *Seriatopora hystrix* routinely disperse over distances of less than a few hundred meters, and those from the spawning coral *Acropora tenuis* over distances of less than 10 km (Underwood et al. 2007, Underwood et al. in review).

Regardless of the distances over which larvae disperse within Scott Reef, the entire system is largely self-seeded. Among a mosaic of reefs, such as the Great Barrier Reef, larvae may regularly disperse among adjacent reefs within a region (Willis and Oliver 1988, Ayre and Hughes 2000), but Scott Reef and the other reef systems in the region are far more isolated. Of the current drifters released from one of the reef systems off northwestern Australia, half had not reached another system within two months or had drifted west off the continental shelf. Of the drifters that traveled between the systems, those released around the time of the primary spawning in Autumn traveled in a southerly direction, whereas those released around the time of spawning in Spring traveled in a predominately northerly direction, reflecting the change in the flow of currents around the middle of the year (Creswell 1993, Holloway and Nye 1985). Based on these data, larvae would take at least one month to travel between Scott Reef and Ashmore Reef 250 km to the north, and at least two months to travel between Scott Reef and the Rowley Shoals 400 km to the south, assuming they escaped the tidal influence of their natal reef prior to settlement. Similar tracks for current drifters have been reported in other studies (e.g. Creswell et al 1993), but at even slower speeds and with a higher proportion being carried off the continental shelf to the west. These dispersal times are longer than the optimal competency periods and similar to the upper competency periods of most coral larvae (e.g., Wilson and Harrison 1998, Nishikawa et al. 2003, Miller and Mundy 2003, Nozawa and Harrison 2005), and the large decreases in survival beyond one month in laboratory studies (e.g. Baird 2004, Nishikawa et al. 2003, Nozawa et al. 2006) are probably larger in natural conditions. Thus, for the off-shore reef systems of northwestern Australia within an ecological time frame, we predict that larvae routinely disperse among locations on their natal reef, periodically among reefs within a system, and rarely between the systems. A lack of large and regular input of larvae from outside these isolated reef systems has important implications for the management of their coral communities (Ayre and Hughes 2003). Areas within each reef need to be protected from impacts to facilitate the recovery of other communities, as a single area within one of a few reefs will not be sufficient to facilitate the recovery of the whole.

REFERENCES

Ayre, DJ, Hughes TP (2000) Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. Evolution 54: 1590-1605

Ayre DJ, Hughes TP (2003) Climate change, genotypic diversity and gene flow of reef-building corals. Ecol Lett 7: 273-278

Babcock RC, Bull GD, Harrison PL, Heyward AJ, Oliver JK, Wallace CC, Willis BL (1986) Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef. Mar Biol 90: 379-394

Babcock RC, Wills BL, Simpson CJ (1994) Mass spawning of corals on a high latitude coral reef. Coral Reefs 13: 161-169

Baird, A H (2004) The ecology of coral larvae: settlement patterns, habitat selection and the length of the larval phase. J Proc Royal Soc NSW 137 Parts 1-2: 43

Baird AH, Marshall PA, Wolstenholme JK (2000) Latitudinal variation in the reproduction of *Acropora* in the Coral Sea. Proc 9th Int Coral Reef Symp 1: 385-389

Black KP (1993) The relative importance of local retention and inter-reef dispersal of neutrally buoyant material on coral reefs. Coral Reefs12: 43-53

Bull GD (1985) Distribution and abundance of coral plankton. Coral Reefs 4: 197-200

Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the Local Dynamics of Open Marine Populations. Ann Rev Ecol Syst 27: 477-500

Carroll A, Harrison P, Adjeroud M (2006) Sexual reproduction of *Acropora* reef corals at Moorea, French Polynesia. Coral Reefs 25: 93-97

Creswell G, Frische A, Peterson J, Quadfasel D (1993) Circulation in the Timor Sea. J Geophys Res 98:14379-14389

Fisk DA, Harriott VJ (1990) Spatial and temporal variation in coral recruitment on the Great Barrier Reef: Implications for dispersal hypotheses. Mar Biol 107: 485-490

Gaines S.D., Gaylord B. & Largier J.L. (2003) Avoiding current oversights in marine reserve design. *Ecol. App.*, 13, S32-S46

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

Guest JR, Chou LM, Baird AH, Goh BPL (2002) Multispecific, synchronous coral spawning in Singapore. Coral Reefs 21: 422-423

Guest JR, Baird AH, Goh BPL, Chou LM (2005) Reproductive seasonality in an equatorial assemblage of scleractinian corals. Coral Reefs 24: 112-116

Harrison PL, Babcock RC, Bull GD, Oliver JK, Wallace CC, Willis BL (1984) Mass spawning in tropical reef corals. Science 223: 1187-1188

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) Ecosystems of the world, Vol 25: Coral Reefs. Elsevier Science Publishers, Amsterdam, pp133-207

Heyward AJ, Negri AP (1999) Natural inducers for coral larval metamorphosis. Coral Reefs 18: 273-279

Holloway PE, Nye HC (1985) Leeuwin Current and wind distributions of the southern part of the Australian North West Shelf between January 1982 and July 1983. Mar Freshwater Res 36:123-137

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. Nature 397: 59-63

Mangubhai S, Harrison PL (2006) Seasonal patterns of coral reproduction on equatorial reefs in Mombassa, Kenya. Proc 10th Int Coral Reef Symp: 106-114

Miller K, Mundy C (2003) Rapid settlement in broadcast spawning corals: implications for larval dispersal. Coral Reefs 22: 99-106

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

Nishikawa A, Katoh M, Sakai K (2003) Larval settlement rates and gene flow of broadcast-spawning (*Acropora tenuis*) and planula-brooding (*Stylophora pistillata*) corals. Mar Ecol Prog Ser 256: 87-97

Nozawa Y, Harrison PL (2002) Larval settlement patterns, dispersal potential, and the effect of temperature on settlement of larvae of the reef coral, *Platygyra daedalea*, from the Great Barrier Reef. In: Proceedings of the 9th international coral reef symposium, Bali, vol 1, pp 409–415

Nozawa Y, Harrison PL (2005) Temporal settlement patterns of larvae of the broadcast spawning reef coral *Favites chinensis* and the broadcast spawning and brooding reef coral *Goniastrea aspera* from Okinawa, Japan. Coral Reefs 24: 274-282

Nozawa Y, Tokeshi M, Satoshi N (2006) Reproduction and recruitment of scleractinian corals in a high-latitude coral community, Amakusa, southwestern Japan. Mar Biol 149: 1047-1058

Oliver JK and Willis BL (1987) Coral-spawning slicks in the Great Barrier Reef: preliminary observations. Mar Biol 94: 521-529

Oliver JK, Babcock RC, Harrison PL, Willis BL (1988) Geographic extent of mass coral spawning: Clues to ultimate causal factors. Proc 6th Int Coral Reef Symp: 803-810

Oliver JK, King BA, Willis BL, Babcock BC, Wolanski E (1992) Dispersal of coral larvae from a lagoonal reef-II. Comparisons between model predictions and observed concentrations. Cont Shelf Res 12: 873-889

Raimondi PT, Morse ANC (2000) The consequences of complex larval behavior in a coral. Ecology 81:3193-3211

Rosser NL (2005) Reproductive seasonality and biannual spawning of *Acropora* on two north-west Australian reefs. Honours thesis, Murdoch University, p125

Simpson CJ (1991) Mass spawning of corals on Western Australian reefs and comparisons with the Great Barrier Reef. J R Soc West Aust 74: 85-91

Smith LD, Gilmour JP, Heyward AJ (2007) Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. Coral Reefs (in press)

Stobart B, Babcock RC, Willis BL (1992) Biannual spawning of three species of scleractinian coral from the Great Barrier Reef. Proc 7th Int Coral Reef Symp 1: 494-499

Underwood JN, Smith LD, Van Oppen MJH, Gilmour JP (2007) Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. Molecular Ecology 16:771-784

Underwood JN, Smith LD, Van Oppen MJH, Gilmour JP (in review). Ecologically relevant dispersal of a brooding and a broadcast spawning coral on isolated reefs: implications for managing community resilience. In review at Ecology Letters

Wallace CC (1985) Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. Mar Biol 88: 217-233

Wallace CC (1999) Staghorn corals of the world. A revision of the coral genus *Acropora* (Scleractinia; Astrocoeniina; Acroporidae) worldwide, with emphasis on morphology, phylogeny and biogeography. CSIRO publishing, Australia

Willis BL, Babcock RC, Harrison PL, Oliver JK (1985) Patterns in the mass spawning of corals on the Great Barrier Reef from 1981 to 1984. Proc 5th Int Coral Reef Symp 4: 343-348

Willis BL, Oliver JK (1988) Inter-reef dispersal of coral larvae following the annual mass spawning on the Great Barrier Reef. Proc 6th Int Coral Reef Symp 2: 853-859

Willis BL, Oliver JK (1990) Direct tracking of coral larvae: Implications for dispersal studies of planktonic larvae in topographically complex environments. Ophelia 31: 145-162

Wilson JR, Harrison PL (1998) Settlement-competency periods of larvae of three species of scleractinian corals. Mar Biol 131: 339-345

Wolstenholme JK (2004) Temporal reproductive isolation and gametic compatibility are evolutionary mechanisms in the *Acropora humilis* species group (Cnidaria; Scleractinia). Mar Biol 144: 567-582

Table 1. The percentage of eggs in different developmental stages within colonies (n = 20) of *Acropora hyacinthus* and *A. spicifera*.

Year	Month	Day	Species	% with eggs	Modal size of eggs (µm)	Size range of eggs (µm)
Year 1	August	5	*A. spicifera*	65	200	200 - 400
			A. hyacinthus	60	200	100 - 300
	October	15	*A. spicifera*	65	600	500 - 700
			A. hyacinthus	55	700	500 - 700
Year 2	January	28	*A. spicifera*	100	400	400 - 600
			A. hyacinthus	80	400	400 - 500
	March	29	*A. spicifera*	40	700	600 - 700
			A. hyacinthus	0		
	May	21	*A. spicifera*	0		
			A. hyacinthus	0		
	August	1	*A. spicifera*	60	200	100 - 300
			A. hyacinthus	20	200	150 - 200
	October	29	*A. spicifera*	55	600	500 - 600
			A. hyacinthus	40	600	550 - 600
Year 3	March	10	*A. spicifera*	95	600	600 - 700
			A. hyacinthus	90	700	500 - 700
	May	5	*A. spicifera*	0		
			A. hyacinthus	0		
	August	24	*A. spicifera*	50	200	100 - 300
			A. hyacinthus	50	100	100 - 200
	December	15	*A. hyacinthus*	55	200	200 - 300
			A. spicifera	60	200	100 - 200
Year 4	March	4	*A. spicifera*	100	700	600 - 700
			A. hyacinthus	80	600	550 - 600
	November	24	*A. spicifera*	50	200	100 - 300
			A. hyacinthus	35	100	100 - 200

Table 2. **Species observed to spawn or have pigmented eggs during one or more years in Autumn (March / April), and Autumn and Spring (October / November). In each sample, more than 3 colonies of each species were investigated, and for each species between 20 and 95% of colonies were observed or inferred to participate in the spawning in Autumn or Spring.**

Autumn		Autumn and Spring
Acropora	*abrolhosensis*	
	acuminata	
	anthoceris	
	aspera	X
	cerealis	X
	cytherea	X
	digitifera	
	elseyi	
	formosa	
	florida	X
	gemmifera	X
	grandis	
	horrida	
	humilis	X
	hyacinthus	X
	intermedia	X
	indonesia	
	listeri	
	loisettea	
	microphthalma	
	millepora	X
	monticulosa	X
	muricata	X
	nana	X
	nasuta	
	nobilis	
	polystoma	X
	pulchra	
	robusta	X
	samoensis	X
	secale	
	selago	X

	specifera	**X**
	subulata	**X**
	tenuis	**X**
	valida	
Diploastrea	*heliopora*	**X**
Echinopora	*lamellosa*	
Favites	*abdita*	**X**
	chinensis	
	flexuosa	
	halicora	
Fungia	*fungites*	
	horrida	
Galaxea	*fascicularis*	
Goniastrea	*aspera*	
	edwadsi	
	favulus	
	minuta	**X**
	retiformis	**X**
Leptoria	*phrygia*	**X**
Lobophyllia	*hemprichii*	
Mycedium	*elephantotus*	
Porites	*sp.*	

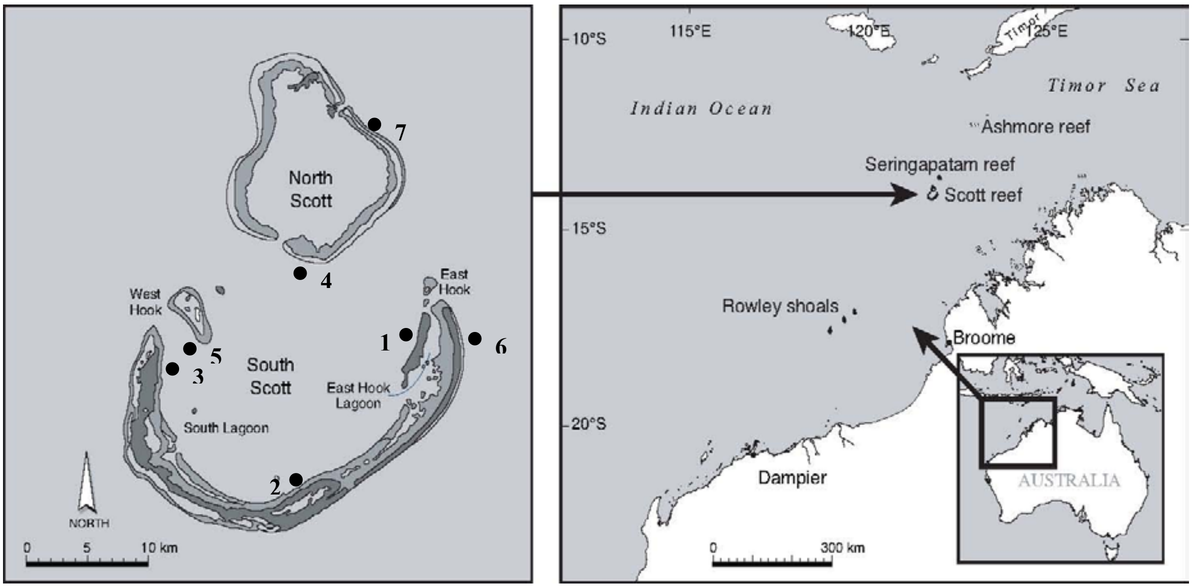

Figure 1. Position of Scott Reef and the study locations off north-western Australia.

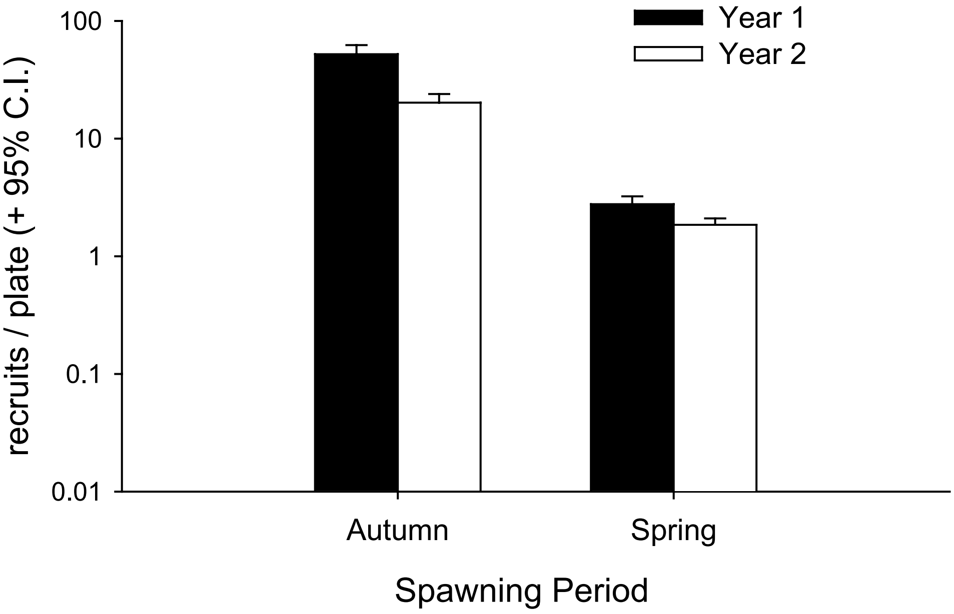

Figure 2. **Mean number of *Acropora* recruits on settlement plates over two consecutive years following mass spawning during Autumn (March / April) and Spring (October / November).**

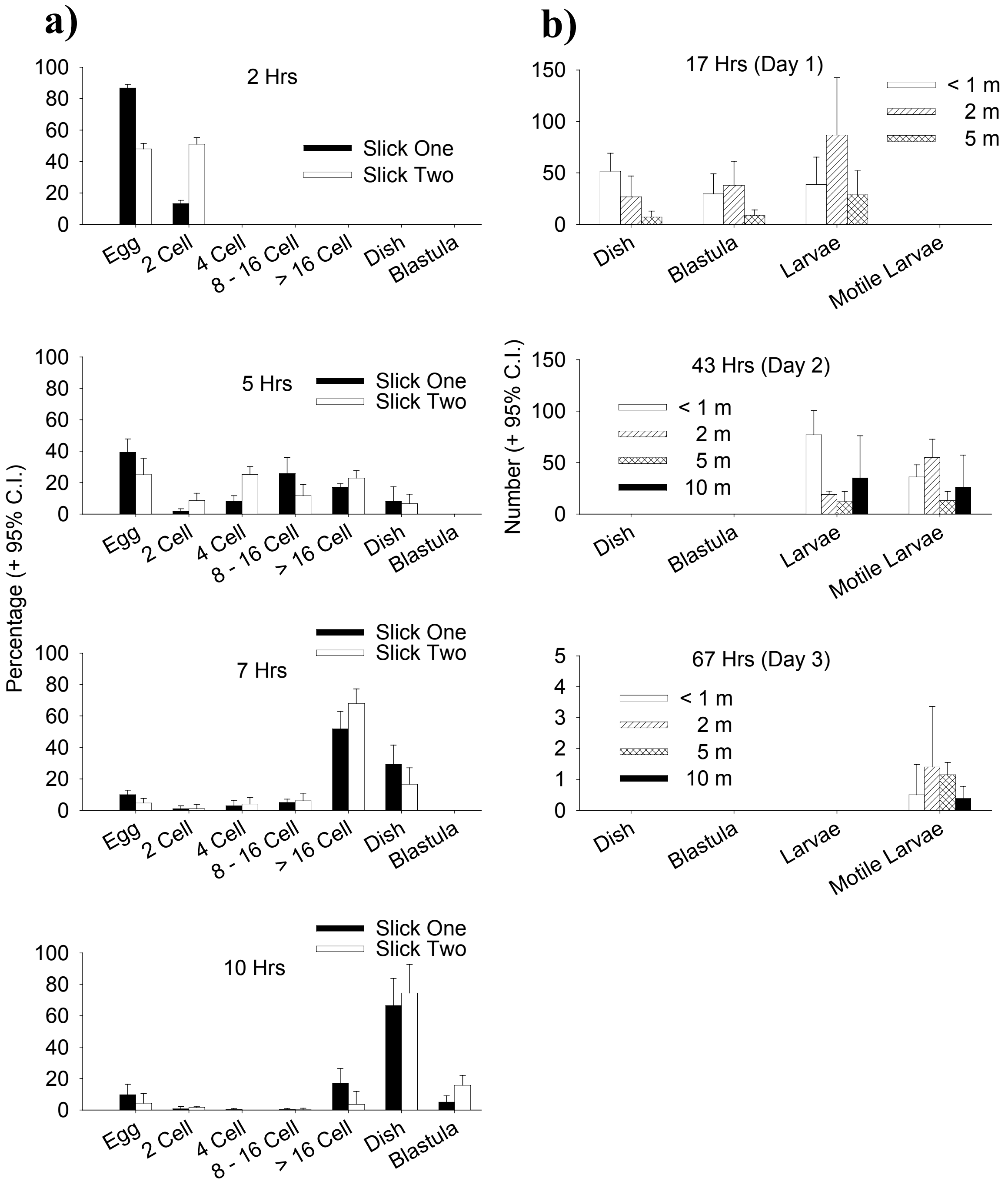

Figure 3. a) Rates of embryogenesis and larval development within slicks sampled from two to ten hours after spawning. b) Number of larvae collected in plankton tows. The first day after spawning most larvae were concentrated in the surface layers and tows were not conducted at 10 m depth. Note the change in the scale of the Y axis at three days after spawning. At four days after spawning a total of five larvae were collected in replicate tows.

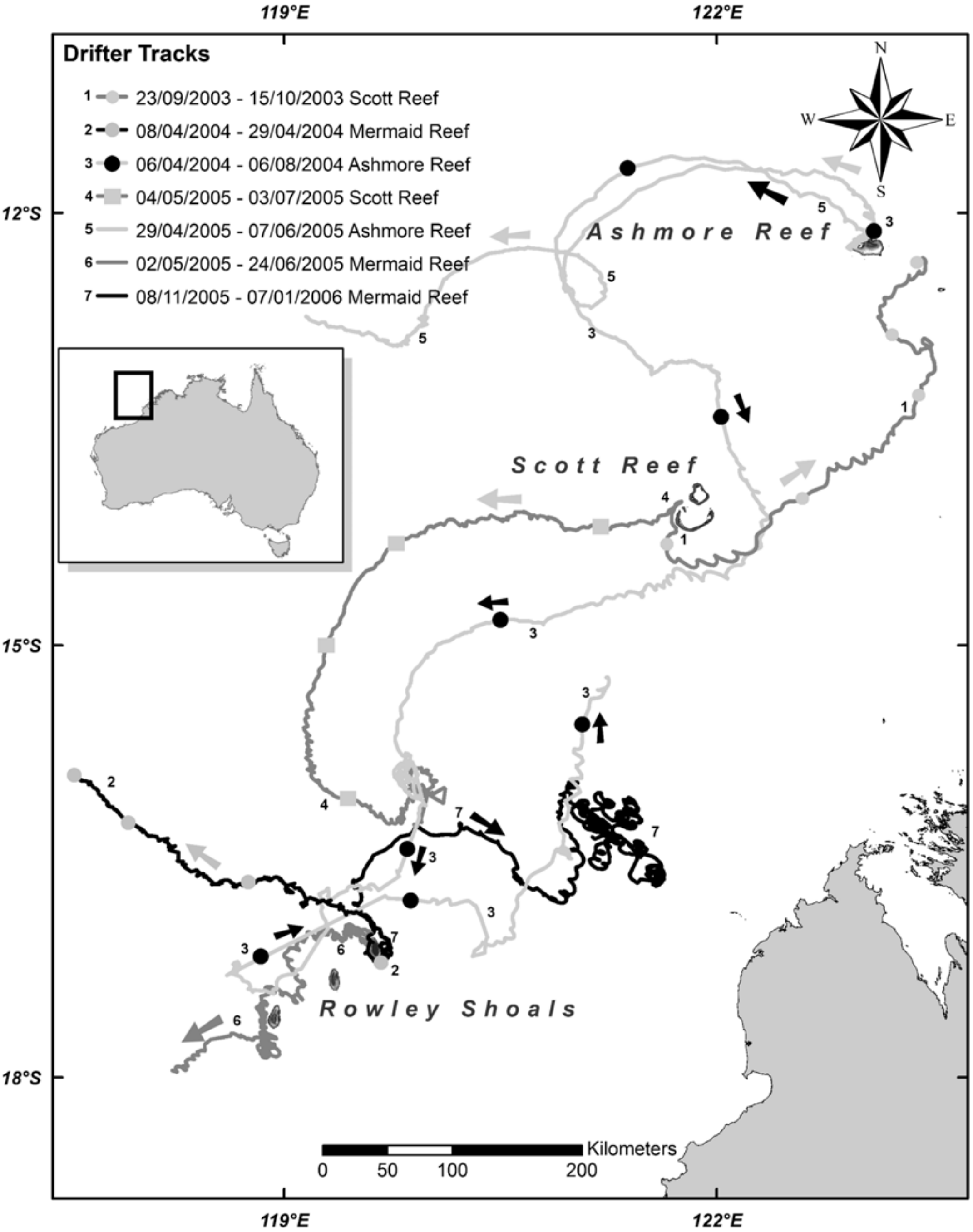

Figure 4. Tracks of sub-surface drifters released from adjacent to the Scott Reef, Ashmore Reef or Rowley Shoals reef systems.

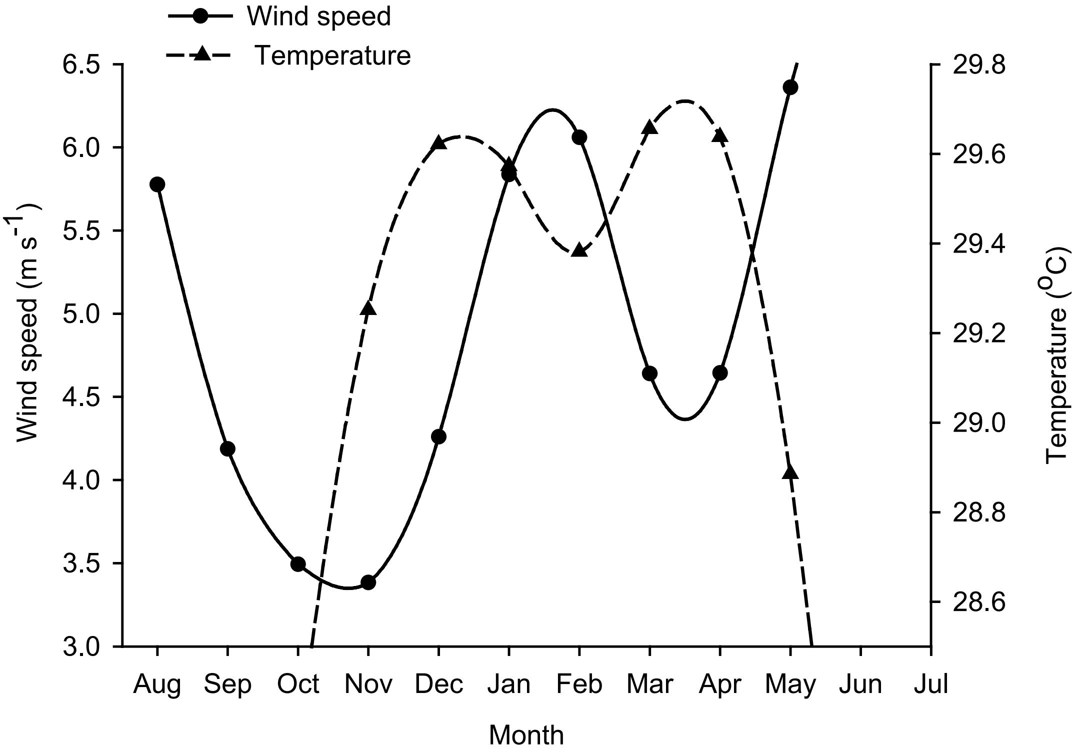

Figure 5. **Mean monthly sea-water temperatures and wind speeds at Scott Reef. Sea-water temperatures are mean monthly values obtained from the Hadley Centre Sea Surface Temperature data set (HadiSST1) from 1990 to 2000, and wind speeds are mean monthly averages obtained from the NOAA Earth Systems Research Laboratory, Physical Sciences Division, from 1968 to 1996. The times of multi-specific spawning are October/November and March/April.**

APPENDIX 2

Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching

This paper has been accepted in Coral Reefs (in press). Ii is essentially Chapter 6 of my thesis.

Key words: coral, bleaching, climate change, resilience, Scott Reef, disturbance

Abstract

As a result of climate change, sea-water temperatures around the world are expected to increase, potentially causing more frequent and severe episodes of coral bleaching. In this study, the impact of elevated water temperatures at an isolated system of reefs was assessed by quantifying the changes in benthic communities over almost ten years. Mass-coral bleaching in 1998 dramatically altered the community structure of the reefs, including a > 80% relative decrease in the cover of hard and soft corals and a two-fold increase in the cover of algae, but which did not include macroalgae. The magnitude of the impact varied among the different sites according to their initial cover and community structure, largely due to the differing susceptibilities of the dominant groups of hard corals. Subsequent increases in the cover of these groups varied according to their life history traits, such as modes of reproduction and rates of growth. Additionally, the increases in the cover were strongly correlated with the magnitude of the impact at the different sites, suggesting that recovery was driven by processes acting over local scales. Six years after the bleaching, the hard corals had returned to approximately 40% of their pre-bleaching cover, but there was little change in the cover of soft corals and the structure of most hard coral communities remained very different to that prior to the bleaching. These data provide insights into the degree to which coral communities are resilient to catastrophic disturbances, when they are isolated from other reef systems but not exposed to some of the chronic stressors affecting many reefs around the world.

Introduction

Predicted changes in the world's climate have lead scientists to question the resilience of coral communities should the frequency and severity of mass-bleaching events continue to increase (Hoegh-Guldberg 1999; Hughes et al. 2003; McWilliams et al. 2005). Mass-bleaching generally refers to the loss of zooxanthellae and/or pigments from hard corals on a reef following stress, usually due to elevated water temperatures. Most benthic organisms that contain zooxanthellae bleach when stressed, and because they have varying susceptibilities to elevated sea-water temperatures, dramatic changes in community structure can follow.

Patterns of susceptibility of different hard corals to bleaching have been identified in a variety of studies, but can vary within and among regions around the world (e.g. Loya et al. 2001; Baird and Marshall 2002; Kayanne et al. 2002; McClanahan et al. 2004). From these studies, branching species of *Millipora* (hydrocoral), *Acropora* and Pocilloporidae are often most likely to bleach and have the highest subsequent rates of mortality; encrusting or massive species such as the Poritidae and Faviidae are slower and less likely to bleach, and a variable assortment of other species may not bleach. The differing susceptibilities of different taxa means their relative abundance can change after a mass-bleaching event, and in the worst cases, the most susceptible and abundant species of corals are replaced by other benthic organisms (Shulman and Robertson 1996; Ostrander et al. 2000; Aronson et al. 2002). Changes in the community structure of coral reefs following mass-bleaching events has lead to speculation about whether they will undergo a long-term shift to a more degraded state should sea-water temperatures continue to rise, whereby corals are replaced by organisms such as algae or sponges as the dominant benthic component.

To determine whether coral communities are resilient to decreases in cover and diversity resulting from elevated sea-water temperatures requires long-term and large-scale studies of community structure both before and after mass-bleaching. Some species of corals are slower to bleach and die, some may be injured rather than die, and the consequences of sub-lethal effects such as reduced growth and reproduction are slow to manifest within the community (e.g., Harriott 1985; Meesters and Bak 1993; Baird and Marshall 2002). Also, the patterns of bleaching can vary among parts of a reef, and more commonly among reefs (e.g., Berklemans and Oliver 1999; Marshall and Baird 2000). Yet, many studies to date have been conducted shortly after a bleaching event at one or a few sites on a single reef, and provide no information about changes in community structure several years before and after the event. Additionally, when coral communities are followed through time, their recovery from bleaching is influenced by the supply of larvae from unaffected reefs (Brown and Suharsono 1990; Glynn 1993), or by additional stressors (Berkelmans and Willis 1999; Ostrander et al. 2000; Aronson et al. 2002). Stressors such as degraded water quality or over-fishing compound the effects of mass-bleaching and slow the recovery of coral communities. Indeed, some reefs have undergone phase-shifts following major disturbances due to the synergistic effects of anthropogenic stressors (Nyström et al. 2000).

This paper presents the results of a long-term study of benthic communities at reefs that do not receive a large and variable supply of recruits from other systems in the region and which are not exposed to terrestrial inputs and degraded water quality. Changes in the cover of coral families and other benthic organisms were quantified over a decade, four years before and almost six years after a catastrophic bleaching event that affected the entire reef-system. The results provide an insight into the degree of resilience of coral communities to mass-bleaching when they are not exposed to some of the localized and chronic anthropogenic stressors (e.g. sedimentation, eutrophication) that are increasingly affecting other reefs around the world.

MATERIAL AND METHODS

The Scott Reef system consists of South Scott, North Scott and Seringapatam reefs, but will be referred to here simply as Scott Reef. Scott Reef is located 270 km off the mainland of northwestern Australia (S14^{o}04’, E121^{o}46’), and is an isolated system of reefs on the edge of the continental shelf with over 500 km^2 of potential coral reef habitat. The closest reefs within the region are the Ashmore group 240 km to the north, and the Rowley Shoals 400 km to the south (Fig. 1). Dispersal times between the reef systems are estimated at greater than five weeks, based on the tracks of current driven surface drifters (Cresswell et al. 1978). The isolation of Scott Reef, coupled with the lack of terrestrial inputs or resident human population, means it is free of many anthropogenic stressors to which other reefs are exposed.

In 1994, a long-term benthic monitoring program was established to assess spatial and temporal changes within reef slope communities across Scott Reef. Eighteen monitoring sites were established along the reef slopes (9 m depth) at six locations (Heyward et al. 1997, Fig. 1). All were located in relatively sheltered areas of low water turbidity and not exposed to oceanic swells. However, some locations (ie. SL3, SL4) are likely to be bathed in more oceanic waters then others (SL1, SL2, SS1, SS2), as a result of their proximity to deepwater passages. At each location, the three sites were separated by approximately 300 m, and at each site were five permanent 50 m transects, marked at 10 m intervals and separated by approximately 10 m. Transects were surveyed annually between 1994 and 2000, and again in 2001 and 2004. During each survey, a tape was laid along each transect and the substrata filmed using a video camera held at a distance of 30 cm. The video footage was analyzed using a point sampling technique (Ninio and Meekan 2002), whereby the footage for each transect was paused at 40 regular intervals and the organism or substrata beneath each of five fixed points assigned to a benthic category. The hard and soft corals were identified to family and divided among growth forms.

In addition to quantifying the changes in benthic cover before and after the bleaching, temperature variation at 16 m depth at Location SL4 was recorded at 0.5 hour intervals for the duration of the study, using a Seabird (SBE37) tide gauge.

Data analysis

Linear mixed-effects models (Pinheiro and Bates 2000) were used to compare temporal changes in the percent cover of major benthic groups at Scott Reef between 1994 and 2004. Separate models were developed for five benthic categories: (1) Hard Coral; (2) Soft Coral; (3) Acroporidae; (4) Poritidae; and (5) Pocilloporidae. Mixed-effects models were used to account for dependencies associated with the repeated observations of benthic cover over time.

Fitted models for benthic categories included fixed-effects for differences in cover between years, and variation among sites was fitted at the random-effect after averaging the raw data across transects within sites. Customized contrasts were used to test whether the percent cover of the different benthic groups changed significantly: (a) prior to the 1998 bleaching event (1994 vs 1997); (b) as a result of the bleaching event (1997 vs 1998); (c) post-bleaching and four years following the event (1998 vs 2002); (d) post-bleaching and six years after the event (1998 vs 2004); and (e) in the final years of this study (2002 vs 2004).

To stabilize variances in accordance with model assumptions, the benthic group variables Acorporidae, Poritidae, and Pocilloporidae were square root transformed for analyses. The hard coral and soft coral data did not require transformation. The importance of temporal autocorrelation in the residuals was determined by fitting models with, and without, first-order autoregressive correlation structure, and then selecting the optimal model using Akaike's Information Criterion (AIC; Burnham and Anderson 1998). All selected models in our analyses were fitted with an autogressive correlation structure. The models were fitted using the MIXED command, and the contrasts using the TEST command in SPSS (for Windows Version 13).

A principal components analysis (PCA) was used to compare the multivariate changes in the structure of benthic communities from 1994 to 2003. The percentage cover data were square root transformed, and analyzed using the S-Plus program. Comparisons among years were made using the different benthic groups, averaged across sites within locations. The data points for the years before and after the bleaching were grouped using convex hulls for visualisation in a PCA biplot. Vectors representing the benthic groups, and arrows representing the magnitude and direction of mean change in communities, were also superimposed on the PCA biplot.

Results

Percentage cover of hard and soft corals

In the years prior to the bleaching, there were small annual increases in the cover of hard and soft corals across Scott Reef (Fig. 2). In 1994, the mean cover (± SE) of hard corals was 43% (± 3), which increased significantly ($P < 0.001$; Table 1) by 5.5% (± 1.4) over three years. By comparison, the mean cover (± SE) of soft corals in 1994 was 8% (± 2), after which there was a small but significant ($P < 0.05$; Table 1) increase of 1.8% (± 0.7) over three years. In March and April 1998, seawater temperatures ranged between 30 and 32^{o}C at 16 m depth, whereas during the previous three years temperatures at 16 m had rarely exceeded 31°C. As a result, the majority of corals bleached and died across a range of habitats and depths, and six months later there were relative decreases in the mean cover of hard and soft corals of > 80% (Fig. 2a). In 2004, almost six years after the bleaching, the hard corals were recovering, but there was little change in the cover of soft corals (Fig. 2a). There was no increase in the cover of hard corals three years after the bleaching, but there was a significant ($P < 0.001$) increase (± SE) of 6.4% (± 0.9) between 2002 and 2004 (Table 1). By the final census, hard coral cover had returned to approximately 40% of the pre-bleaching level, but the soft corals showed no sign of recovery (Table 1).

The bleaching killed many corals across Scott Reef, but the level of impact varied spatially within the system and in a similar way for both the hard and soft corals. The relative decreases in both hard and soft corals were similar among sites within locations, reflecting the spatial scale over which the variation in the impact of bleaching was occurring. For example, most of the ten sites with the highest relative decreases in cover (> 75%) for both the hard (9 sites) and soft corals (8 sites) were replicates within three locations (SL4, SS1, SS2); conversely, all of the five sites with the lowest relative decreases (< 50%) were replicates within two locations (SL3, SL4).

In addition to the factors causing bleaching and mortality over the scale of locations, variation in the levels of impact among the sites was influenced by the initial cover of corals. The cover of hard corals was strongly correlated with both the absolute (7 to 61%; Adj $R^2 = 0.95$, $P < 0.01$) and relative (24 to 92%; Adj $R^2 = 0.80$, $P < 0.01$) decreases following the bleaching (Fig 3a).

For the soft corals, initial cover was also positively correlated with the absolute decreases (0.5 to 21.6%; Adj $R^2 = 0.94$, $P < 0.01$) after the bleaching, but not the relative decreases (37 to 100%; Adj $R^2 = 0.00$, $P = 0.89$) in cover (Fig 3b).

Variation in the levels of impact among sites influenced their subsequent rates of recovery over the following years. For the hard corals, there was a strong negative correlation (Adj $R^2 = 0.91$, $P < 0.001$) between impact and recovery; the ten sites with the highest relative decreases in cover (> 75%) returned to between 10 and 40% of their pre-bleaching cover, compared with the five sites with the lowest decreases (< 50%) that returned to between 70 and 95% of their pre-bleaching cover after almost six years (Fig 3c). The correlation (Adj $R^2 = 0.33$, $P = 0.01$) was not as strong for the soft corals (Fig. 3d), and at some sites with high mortality cover had exceeded the pre-bleaching level, although this was at least partly due to the low and variable absolute cover of soft corals at those sites. Nevertheless, the relative impact of the bleaching on both the hard and soft corals at each site was an important factor determining the subsequent recovery over almost six years.

PERCENTAGE COVER OF THE DOMINANT FAMILIES OF HARD CORALS

All of the hard corals at Scott Reef were affected by the bleaching, but their changes in cover before (1994 to 1997) and after (1998 to 2004) the disturbance varied among the dominant families (Fig. 4). Prior to the bleaching, the Acroporidae were by far the dominant family of coral and their cover (± SE) increased significantly (*P* < 0.001; Table 1) from 20% (± 3) to 27% (± 5). Over this period, the mean cover (± SE) of Poritidae (10% ± 1) and Pocilloporidae (4% ± 1) was far lower and did not change (Table 1). During the elevated sea-water temperatures, corals in the families Acroporidae and Pocilloporidae were among the first to bleach, and six months later had relative decreases (± SE) in cover of 81% (± 6), and 86% (± 7), respectively. In contrast, the Family Poritidae was slower to bleach, with a smaller relative decrease (± SE) in cover of 56% (± 5) after six months. Almost six years later, the cover of Acroporidae, Pocilloporidae and Poritidae had increased significantly, but the patterns of recovery varied among the years and the families. The Acroporidae and Pocilloporidae had no increase in cover in the first three years after the bleaching. However, between three and six years after the bleaching there were significant (*P* < 0.001; Table 1) and rapid increases (± SE) in the cover of Acroporidae and Pocilloporidae, of 1.7% (± 0.8) and 1.0% (± 0.3), respectively (Fig. 4). The Poritidae displayed a very different pattern of recovery, with a rapid and significant (*P* < 0.001; Table 1) increase (± SE) in cover of 2.1% (± 0.6) within three years of bleaching, but no change thereafter (Fig. 4).

COMMUNITY STRUCTURE

There was little change in the community structure of benthic organisms at Scott Reef in the years prior to the bleaching, apart from a small annual shift towards a greater dominance of hard corals, particularly the Acroporidae (Fig. 5). Following the bleaching, the cover of all benthic groups decreased by at least a half (hard corals, soft corals, sponges), with the exception of the turfing and coralline algae that increased in cover (± SE) from 37% (± 2) in the years prior to the bleaching to 75% (± 4) the year after. However, this did not include the fleshy macroalgae, whose cover was < 1% at all locations both before and after the bleaching. Although the cover of all families of hard corals was reduced by > 50% following their bleaching, variation in susceptibility among the families altered their community structure. Smaller relative decreases in cover resulted in the Poritidae becoming the spatial dominant, changing from 20% to 40% of the coral community, whereas the large decreases in the cover Acroporidae reduced their relative abundance from > 50% to < 25% of the coral community across all locations. Changes in the relative abundances of the Acroporidae and Poritidae drove the structural changes in the hard coral communities at different sites, from communities previously dominated by branching *Acropora* (47%) and other branching corals (9%), to communities with a lower coral cover in which massive corals had the highest (45%) relative abundance (Fig. 6). Indeed, it was the sites with the highest cover of branching corals that were worst affected by the bleaching and underwent the largest changes in community structure.

Almost six years after the bleaching there had been few changes in the benthic community at Scott Reef. At the final census, turfing and coralline algae remained by far the dominant benthic group at all locations, with a mean (± SE) cover of 65% (± 4), and the mean (± SE) cover of soft corals (3% ± 1) and sponges (<1%) remained low. The decreases in the cover of algae since the bleaching were matched by increases in coral cover, initially

(< 3 years) the Poritidae and then (3 to 6 years) the Pocilloporidae and Acroporidae, indicating the commencement of a return to a relative abundance of coral families similar to that prior to the bleaching (Fig. 5). However, the structure of the hard coral communities at most sites was still very different to that prior to the bleaching, particularly those previously dominated by branching corals (Fig. 6). The absolute increases in coral cover since the bleaching were similar for the branching *Acropora* (2%), other branching corals (1%), and tabulate (1%), foliaceous (1%) and massive (3%) corals. Consequently, the branching *Acropora* had returned to only 21% of its previous cover, whereas the massive corals and tabulate corals had returned to 59% and 100% of their previous cover, respectively; the other groups had returned to between 30 and 40% of their previous cover (Fig. 6).

Discussion

The temperature induced mass-bleaching at the Scott Reef system was a major disturbance that dramatically decreased coral cover at all reefs. Coral reefs have historically been resilient to major disturbances (Grigg and Dollar 1990; Pandolfi et al. 2003), which can promote diversity and structural complexity (Connell 1978; Karlson 1999). Today, however, the frequency, severity and types of disturbances to coral communities are increasing, and their rates of recovery are slowing (Nyström et al. 2000; Hughes et al. 2003). In the worst instances, communities show little sign of recovery following severe disturbances and benthic organisms such as algae (e.g. Ostrander et al. 2000), sponges (e.g. Aronson et al. 2002) or soft corals

(Stobart et al. 2005) occupy the available space, potentially excluding corals. Long-term shifts in community structure usually occur on reefs that are exposed to anthropogenic stressors, such as the reduced abundances of herbivores and/or decreased water quality (Shulman and Robertson 1996; Bellwood et al. 2004). In contrast, the Scott Reef system is free of anthropogenic stressors that reduce water quality, and the benthic organisms that can exclude or outcompete corals (e.g. macroalgae, sponges, soft corals) did not occupy the available substrata following the bleaching.

The bleaching reduced the cover of hard and soft corals across the Scott Reef system by > 80%, but the level of impact varied among locations and was similar among adjacent sites, indicating that variation in the conditions responsible was occurring over scales of a few kilometers. Indeed, the exposure of locations to cooler oceanic water and higher flow may well have been responsible for their communities having lower levels of mortality (Nakamura and van Woesik 2001; McClanahan et al. 2004), as opposed to other variables such as cloud cover that act over larger spatial scales (Mumby et al. 2001). However, at the scale of individual sites, the levels of impact were strongly influenced by the initial coral cover and community structure. For the hard corals, both the absolute and relative decreases in cover following the bleaching were correlated with that prior to the disturbance, reflecting not only the impact on all of the major groups of corals, but also the dominance of the groups that were most susceptible. Both the magnitude of the increases in water temperatures and the abundances of the most susceptible species (McClanahan 2000) have been found to drive the levels of impact, and changes in the structure of communities, following bleaching events on reefs throughout the Indian Ocean (McClanahan 2007). Similarly, the communities with the highest coral cover at Scott Reef also underwent the largest changes in community structure, illustrating how the structure of a community and its history of exposure to disturbances can influence perceived levels of impact (Hughes 1989, McClanahan et al. 2007).

The increases in coral cover over almost six years after the bleaching also varied among sites, according to the level of impact. Sites that had the smallest relative decreases in cover had the fastest recovery, particularly for the hard corals. These data suggest that the increases in cover within six years of the bleaching were mostly driven by the growth of survivors, rather than the recruitment and growth of new individuals (e.g. Brown and Suharsono 1990; Kayanne et al. 2002). Localized recruitment was probably reduced by the lack of remaining broodstock at Scott Reef following the bleaching. Additionally, the supply of larvae from other reef systems was insufficient to greatly increase rates of recovery in the years following the bleaching. The speed and direction of surface currents in the region indicates dispersal times of larval of at least five weeks between reef systems (Cresswell *et al.* 1978), which is greater than the competency periods for most coral larvae (Ayre and Hughes 2000; Nishikawa et al 2003; Miller and Mundy 2004). Consequently, the coral communities that best survive large-scale, severe disturbances recover faster and provide valuable broodstock to facilitate the recovery of heavily damaged areas. To maximize the resilience of isolated reef systems to increasing water temperatures, the highest level of protection should therefore be given to areas that are least susceptible to bleaching.

All hard corals were affected by the bleaching, but the differing susceptibilities and resilience of the different families were evident in their short- and longer-term changes in cover. The Poritidae were initially least susceptible to the elevated water temperatures, and because many colonies suffered partial- rather than whole-colony mortality, their relative decreases in cover were less than for the Acroporidae and Pocilloporidae (cf. Brown and Suharsono 1990; Loya et al. 2001). The re-growth of survivors resulted in the Poritidae initially having the most rapid increases in cover, but more than three years after the bleaching there was little further change in their cover. Given the characteristically slow growth and low reproductive output of the Poritidae, recovery to their pre-bleaching cover beyond these initial increases is likely to be slow, and may take far longer than for other groups of corals that underwent greater decreases in cover. Conversely, negligible initial increases in the cover of the Acroporidae and Pocilloporidae shortly after the bleaching were followed by significant and rapid increases from three years after the disturbance.. Families such as the Acroporidae and Pocilloporidae tend to have the highest mortality after bleaching, but their recovery can accelerate through time due to comparatively high recruitment and rapid growth (Harrison and Wallace 1990; Glynn 1993), particularly several years after a major disturbance (Halford et al. 2004). Thus, the

Acroporidae are expected to again become the dominant coral across the Scott Reef system, barring any further disturbances, reflecting the extent to which the patterns of recovery of different groups of hard coral can vary through time.

As with the most susceptible families of hard corals, there were dramatic decreases in the cover of soft corals after the bleaching, but with no significant increases in cover almost six years later. By far the most abundant (> 80% cover) species of soft coral were in the Family Alcyoniidae, which have had high levels of impact following bleaching events on other Indian Ocean reefs (McClanahan et al. 2001, Flores et al 2004). The Alcyoniidea tend to grow slowly and maintain populations through asexual propagation rather than sexual recruitment (McFadden 1991; Fabricius 1995), yet there was limited potential for recovery by asexual propagation following the bleaching because most colonies were killed. The high rates of mortality of the Alcyoniidae, and their slow growth and low rates of sexual recruitment, suggest populations are particularly vulnerable to predicted increases in sea-water temperatures, which may become evident in their reduced contribution to communities on coral reefs.

This study documented almost ten years of change in the benthic communities at an isolated system of reefs, which included a major disturbance in the form of elevated sea-water temperatures. The temperature anomalies caused the mass-mortality of hard and soft corals across three reefs to a depth of at least 20 m. Within six years, the hard corals had returned to approximately 40% of their pre-bleaching cover, but there was little change in the cover of soft corals and the structure of most communities was still very different to that prior to the bleaching. Most notably, sites that had a comparatively high cover of branching corals, particularly *Acropora*, had a much lower coral cover that was dominated by massive corals, but with an increased relative abundance of tabulate corals. A lack of recovery of the previously dominant branching corals, and a major shift in the abundance of functional groups of hard corals, reef structure, and fish communities, has been reported for other Indian Ocean reefs several years after mass-bleaching (e.g. Sheppard et al. 2002, Schuhmacher et al. 2005, Graham et al 2006). However, in the absence of major disturbances we would expect more rapid increases in the cover of branching corals (Halford et al. 2004), and for the communities at Scott Reef to continue to return to a cover and structure more similar to that prior the bleaching. The longer-term resilience of Scott Reef depends on the frequency and severity of bleaching events in the future (e.g., Sheppard 2003), as isolated reef systems may be among the most vulnerable to the impacts of climate change (Graham et al. 2001, Ayre and Hughes 2004). To give coral communities the best chance to maintain their resilience in the face of a changing climate, additional anthropogenic stressors that reduce the population growth rates of corals and promote the growth of competitors must be reduced, by incorporating appropriate initiatives into management strategies (Wooldridge et al. 2005)..

Reference List

Aronson RB, Precht WF, Toscano MA, Koltes KH (2002) The 1998 bleaching event and its aftermath on a coral reef in Belize. Mar Biol 141:435-447

Ayre DJ, Hughes TP (2000) Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. Evolution 54:1590-1605

Ayre DJ, Hughes TP (2004) Climate change, genotypic diversity and gene flow in reef-building corals. Ecol Lett 7:273–278

Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 237:133-141

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. Nature 429:827-833

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

Berkelmans R, Willis BL (1999) Seasonal and local spatial patterns in the upper thermal limits of corals on the inshore Central Great Barrier Reef. Coral Reefs 18:219-228

Brown BE, Suharsono (1990) Damage and recovery of coral reefs affected by El Nino related seawater warming in the Thousand Islands, Indonesia. Coral Reefs. 8:163-170

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer Verlag, New York

Connell, JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302-1210

Cresswell G, Frische A, Peterson J, Quadfasel D (1978) Circulation in the Timor Sea. J Geophys Res 98:14379-14389

Fabricius KE (1995) Slow population turnover in the soft coral genera *Sinularia* and *Sarcophyton* on mid- and outer-shelf reefs on the Great Barrier Reef. Mar Ecol Prog Ser 126:145-152

Floros CD, Samways MJ, Armstrong B (2004) Taxonomic patterns of bleaching within and South African coral assemblage. Biodivers Conserv 13:1175-1194

Glynn PW (1993) Coral reef bleaching: ecological perspectives. Coral Reefs 12:1-17

Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP (2006) Dynamic fragility of oceanic coral reef ecosystems. Proc Natl Acad Sci USA 103:8425-8429

Grigg RW, Dollar SJ (1990) Natural and anthropogenic disturbances on coral reefs. In: Dubinsky Z (ed) Ecosystems of the world 25: Coral Reefs. Elsevier, Amsterdam pp439-452

Halford A, Cheal AJ, Ryan D, Williams D McB (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. Ecology 85:1892-1905

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Z Dubinsky (ed) Ecosystems of the World: Coral Reefs. Elsevier Publishers, Amsterdam pp 133-207

Harriott VJ (1985) Mortality rates of scleractinian corals before and during a mass bleaching event. Mar Ecol Prog Ser 21:81-88

Heyward AJ, Halford A, Smith LD, Willams DM (1997) Coral Reefs of Northwest Australia: baseline monitoring of an oceanic reef ecosystem. Proc 8th Int Coral Reef Symp 1:289-294

Hoegh-Guldberg O (199) Climate change, coral bleaching and the future of coral reefs. Mar Freshw Res 50:839-866

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

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate Change, Human Impacts, and the Resilience of Coral Reefs. Science 301:929-933

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

Kayanne H, Hari S, Ide Y, Akimoto F (2002) Recovery of coral populations after the 1998 bleaching on Shiraho Reef, in the southern Ryukyus, NW Pacific. Mar Ecol Prog Ser 239:93-103

Loya Y, Sakai K, Yamazato Y, Nakano H, Sambali, van Woesik R (2001) Coral bleaching: the winners and the losers. Ecol Lett 4:122-131

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19:155-163

McClanahan (2000) Bleaching damage and recovery potential of Maldivian coral reefs. Mar Poll Bull 40:587-597

McClanahan TR, Muthiga NA, 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

McClanahan TR, Baird AH, Marshall PA, Toscano MA (2004) Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. Mar Pollut Bull 48:327-335

McClanahan TR, Maina R, Moothien-Pillay R, Baker AC (2005) Effects of geography, taxa, water flow, and temperature on coral bleaching intensity in Mauritius. Mar Ecol Prog Ser 298:131-142

McClanahan TR Ateweberhan M, Graham NAJ, Wilson SK, Sebastian Ruiz C, Guillaume MMM, Bruggemann JH (2007) Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. Mar Ecol Prog Ser 337:1-13

McFadden CS (1991). A comparative demographic analysis of clonal reproduction in a temperate soft coral. Ecology 72:1849-1866

McWilliams JP, Cote IM, Gill JA, Sutherland WJ, Watkinson AR (2005) Accelerating impacts of temperature-induced coral bleaching in the Caribbean. Ecology 86:2055-2060

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

Miller K, Mundy C (2003) Rapid settlement in broadcast spawning corals: implications for larval dispersal. Coral Reefs 22:99-106

Mumby PJ, Chisholm JRM. Edwards AJ. Andrefouet S. Jaubert J (2001) Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. Mar Ecol Prog Ser 222:209-216

Nakamura t, van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar Ecol Prog Ser 212:301-304

Ninio R, Meekan MG (2002) Spatial pattern in benthic communities and the dynamics of a mosaic ecosystem on the Great Barrier Reef, Australia. Coral Reefs 21:95-103

Nishikawa A, Katoh M, Sakai K (2003) Larval settlement and gene flow of broadcast spawning (*Acropora tenuis*) and planula-brooding (*Stylophora pistillata*) corals. Mar Ecol Prog Ser 256:87-97

Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol Evol 15:413-417

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

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke R, McArdle D, McClanahan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955-958

Pinheiro JC, Bates DM (2000) Mixed-Effects Models in S and S-Plus. Spinger Verlag Publishers, New York

Schuhmacher H, Loch K, Loch W, See WR (2005) The aftermath of coral bleaching on a Maldivian reef - a quantitative study. Facies 51:80-92

Sheppard CRC (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. Nature 425:294-297

Sheppard, CRC, Spalding M, Bradshaw C, Wilson S (2002) Erosion vs. recovery of coral reefs after 1998 El Nino: Chagos Reefs, Indian Ocean. Ambio 31:40-48

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

Stobart B, Teleki K, Buckley R, Downing N, Callow M (2005) Coral recovery at Aldabra Atoll, Sechelles: five years after the 1998 bleaching event. Phil Trans R Soc A 363:251-155

Wooldridge S, Done T, Berkelmans R, Jones R, Marshall P (2005) Precursors for resilience in coral communities in a warming climate: a belief network approach. Mar Ecol Prog Ser 295:157-169

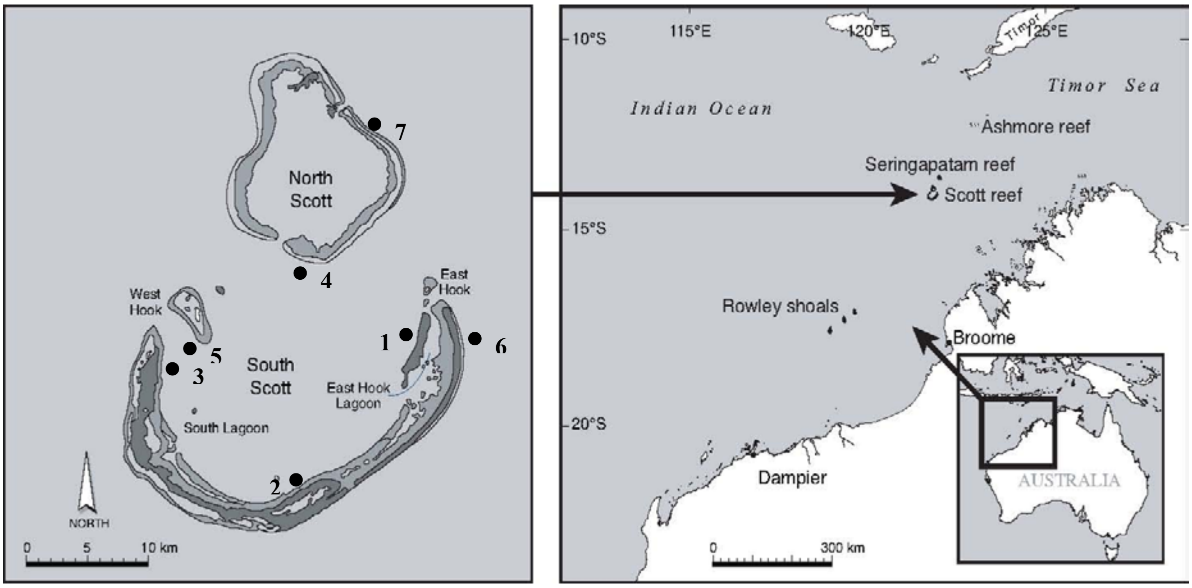

Figure 1. Position of the Scott Reef system and the monitoring locations. At each location there are three monitoring sites.

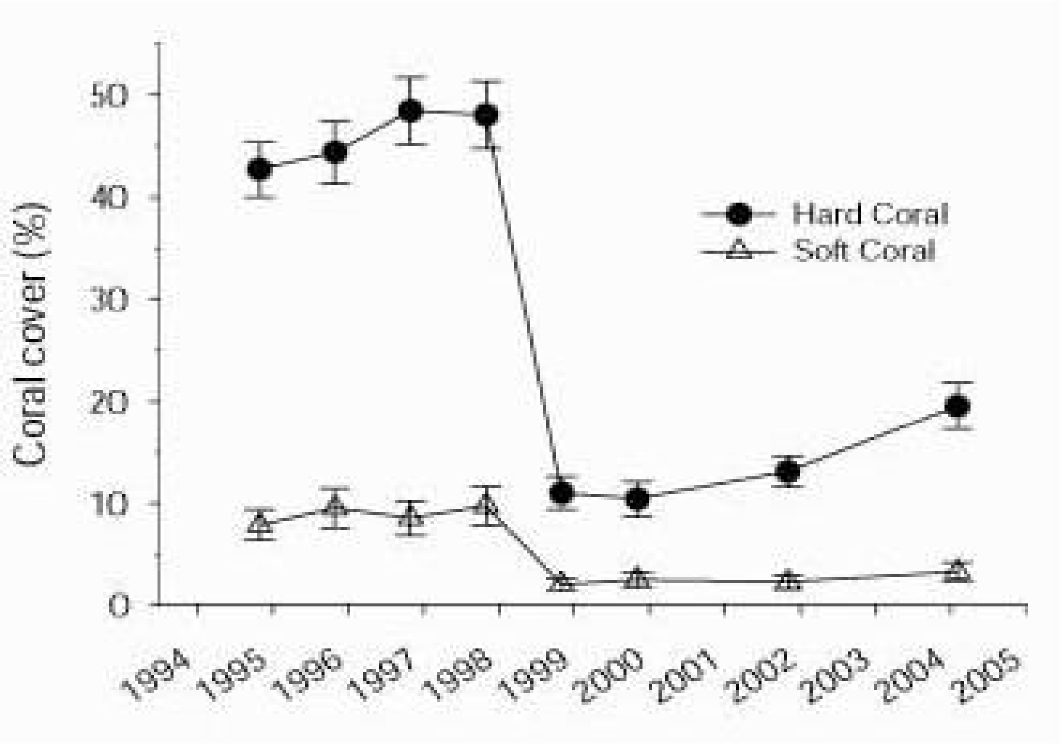

Figure 2. Changes in the mean cover (± SE) of hard and soft corals at permanent transects across the Scott Reef system. The bleaching occurred in March/April 1998.

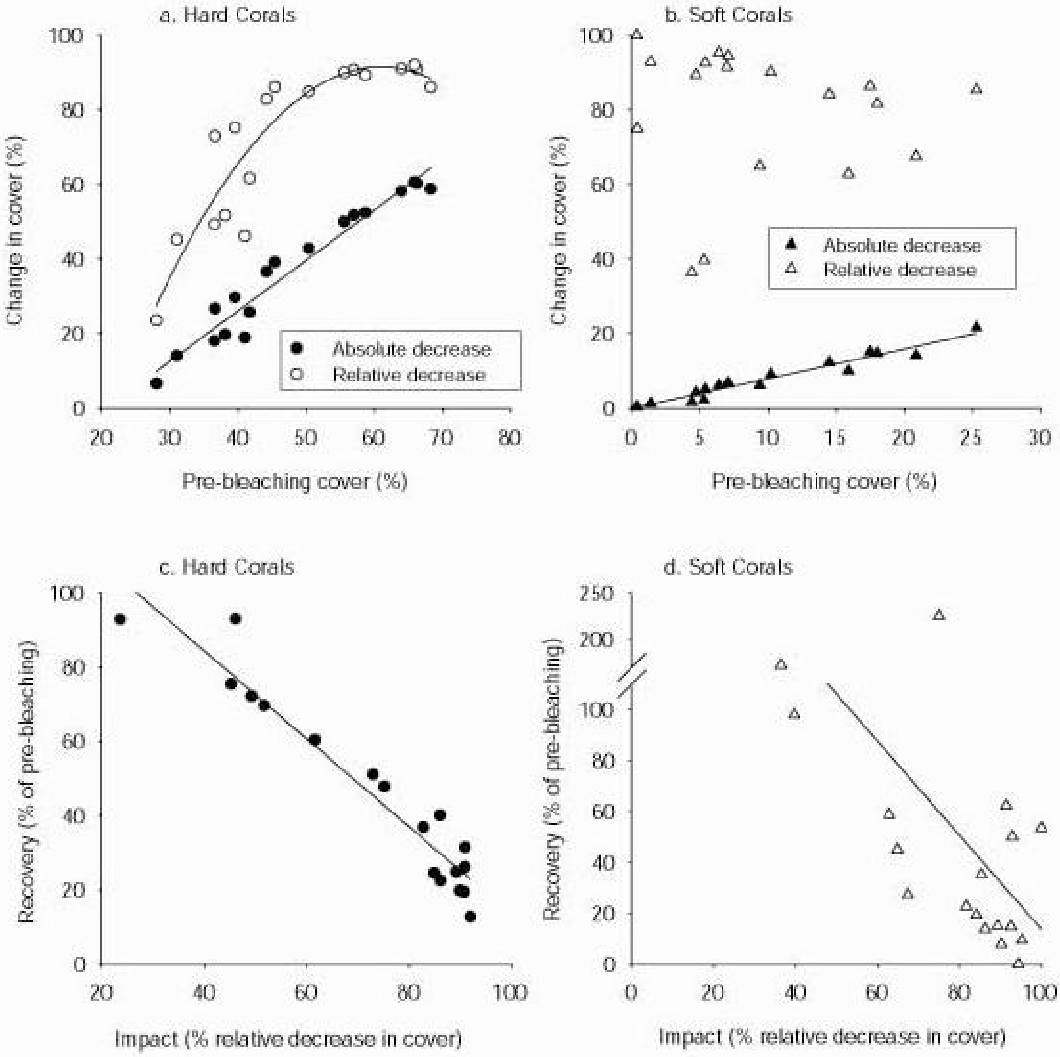

Figure 3. **Variation in levels of impact and recovery for corals at replicate sites (N = 18) across Scott Reef. Relationship between the initial cover of (a) hard and (b) soft corals and their absolute and relative decreases in cover approximately six months after the bleaching. Relationship between the level of impact and recovery of (c) hard and (d) soft corals; impact is the relative decrease in cover between the census before and after the bleaching and recovery is the percentage of pre-bleaching cover almost six years after the bleaching.**

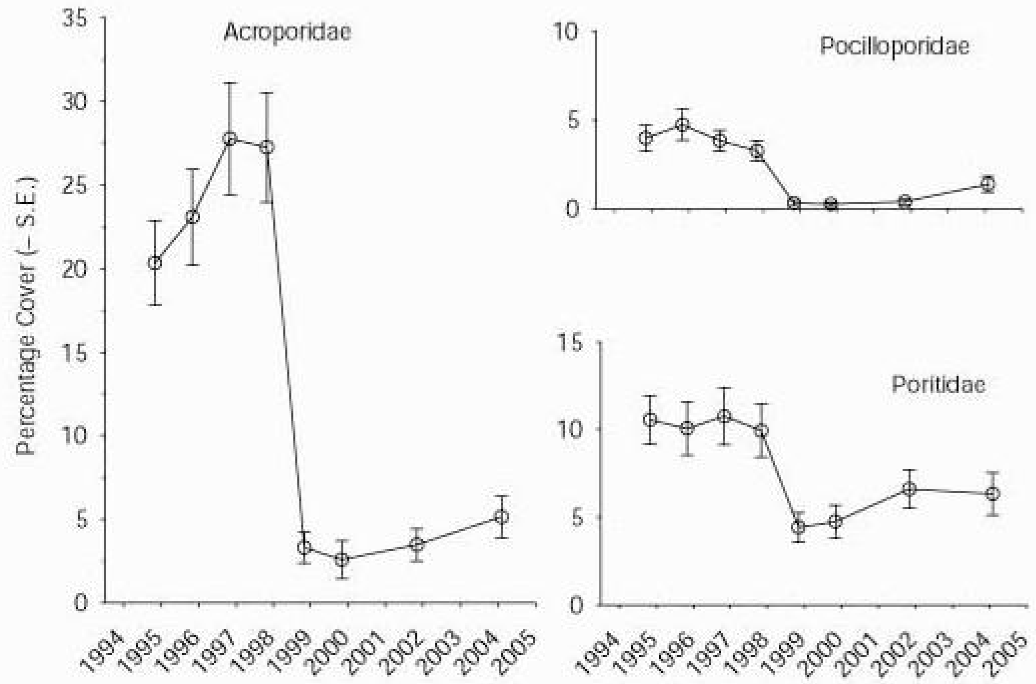

Figure 4. Changes in the mean cover (± SE) of the dominant families of hard coral across the Scott Reef system. The bleaching occurred in March/April 1998.

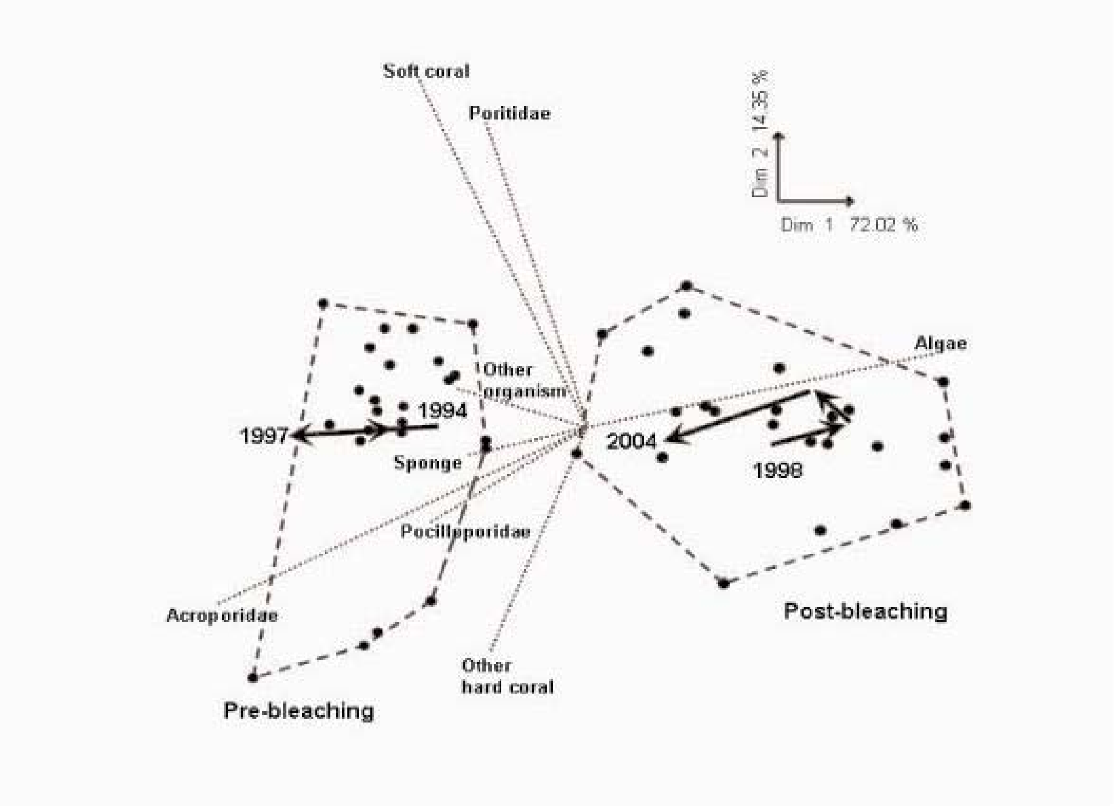

Figure 5. Temporal changes in the benthic communities at the Scott Reef system. The groups of benthic organisms are: Acroporidae, Poritidae, Pocilloporidae, soft coral, sponge, other hard coral, other organism, and algae (mostly turfing and coralline). Groups are represented by a vector on the biplot, the length of which reflects their influence on changes in community composition. Each location is a single point and all the locations during the years before (dashed line) and after (dotted line) the bleaching are grouped within a polygon. The direction of the arrows represents the mean changes in community composition, towards or away from the different benthic groups, and the length of the arrows represents the magnitude of the change before and after the bleaching.

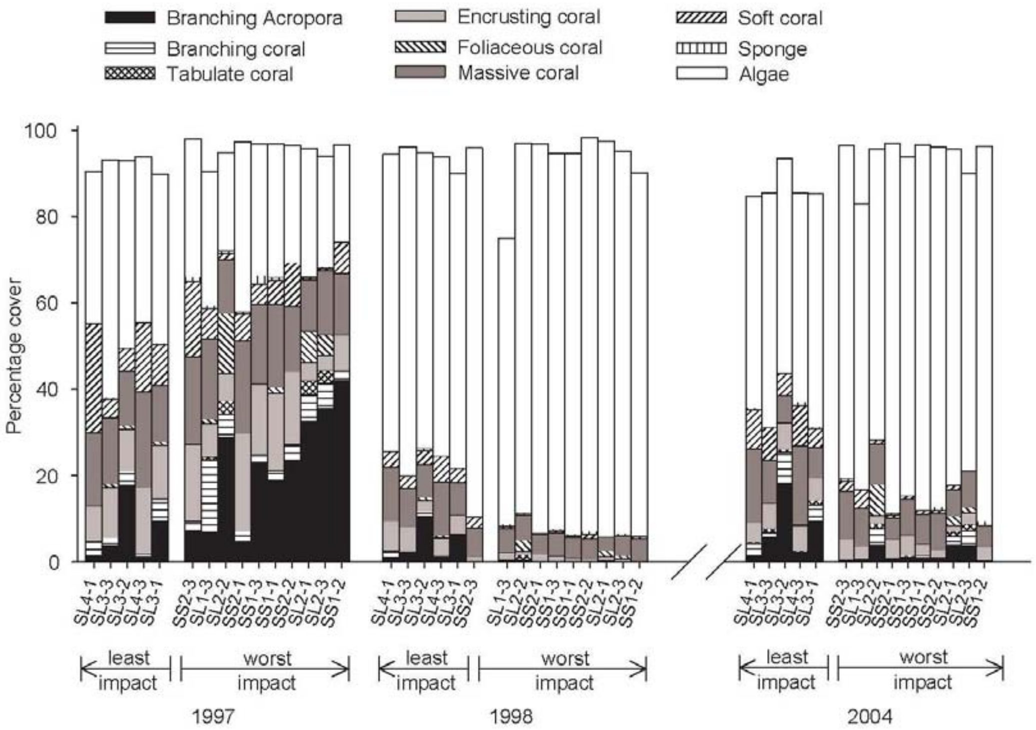

Figure 6. **Variation in community structure among sites across Scott Reef. Benthic groups defined by broad taxonomic and morphological characteristics are: branching *Acropora*, branching coral, tabulate coral, encrusting coral, foliaceous coral, massive coral, soft coral, sponge and algae (mostly turfing and coralline). Stacked bar graphs represent the percentage cover of the different benthic groups at the five sites least affected by the bleaching and the ten sites worst affected, the year before the bleaching (1997), and approximately six months (1998) and six years (2004) after the bleaching; for each year sites are positioned along the x-axis in increasing order of impact.**