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Long-term Monitoring of Shallow Water Coral and Fish
Communities at Scott Reef



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Long-term monitoring of shallow water coral and fish communities at Scott Reef



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Preamble

Background and Scope of Works

The Australian Institute of Marine Science (AIMS) entered into a contract (No. 4600001754) with Woodside Energy Ltd (Woodside), as operator of the Browse LNG Development, on 28 February 2008, to undertake a three year research program at Scott Reef. For the purpose of this report, this research program is known as the Scott Reef Research Project (SRRP).

The research activity within the SRRP is divided among three projects:

- Project 1: Long-term monitoring of shallow-water coral and fish communities at Scott Reef
- Project 2: Physiological performance of deep water corals at South Scott Reef
- Project 3: Understanding water column and pelagic ecosystem processes affecting the lagoon of South Reef, Scott Reef

This is the final report for Project 1: Long-term monitoring of shallow-water coral and fish communities at Scott Reef, which updates the data collected in the final field trip in October 2010 and subsequent analyses of these data.

These data and analyses are reported in the context of historic studies at Scott Reef. The scope of this work outlined in the CTR for this 2011 Report is as follows.

“Finalise the processing, qualitative analysis and entry of data collected from field trip 5124 in October 2010 for use in compiling the 2011 Final Report for Project 1, including the following:

- *Finalise all data collected in October 2010 and integrate with historic data.*
- *Data entry, analysis and write up of fish data collected in October 2010 from 30 sites at Scott Reef, Seringapatam Reef and Rowley Shoals; incorporating all fish data collected historically.*
- *Summarise and interpret relative changes to benthic data analysis, sediment data and temperature data collected from 12 sites in October 2010.*
- *Summarise with historic data download, backup together with a summary of data from temperature loggers and sediment traps in October 2010.*
- *Data entry and analysis of coral size-frequency data collected from 7 sites at Scott Reef in October 2010.*

A detailed analysis of all data prior to the October 2010 field trip, and its integration with relevant data from Projects 2 and 3, was provided in the Final Annual Report for Project 1 in September 2010.

This 2011 report for Project 1 aims to combine the most recent 2010 data with historic data to address the following key questions about the benthic communities at Scott Reef:

- What is the history of disturbance at Scott Reef in 2010 and how has this impacted the benthic communities?
- Have the coral and fish communities at Scott Reef recovered from the mass-bleaching in 1998?
- Does the extent of community recovery vary among locations across Scott Reef?
- What are the key processes underlying the recovery of the coral communities at Scott Reef following the bleaching?

- How do coral and fish communities in 2010 compare to those prior to the mass-bleaching (1994-1997), and what are the possible reasons for these differences?
- How resilient are the benthic communities at Scott Reef to regimes of disturbance similar to, or more severe than, those observed since monitoring commenced?

Structure of this report

This report contains eight subsequent chapters, structured according to the above aims and the analytical updates for each of the Project I sub-projects. Chapter 2 summarises the exposure of coral communities at Scott Reef to disturbances in 2010. Chapter 3 provides an overview of monitoring programs and the key Project I findings for addressing the above aims. The remaining chapters update recent analyses in the context of the above aims for the long-term monitoring of coral (Chapter 4) and fish (Chapter 5) communities, the size-structure (Chapter 6) and patterns of reproduction (Chapter 7) and recruitment (Chapter 8) of coral communities, and the regimes of temperature and sedimentation at monitoring locations across Scott Reef (Chapter 9).

1. Executive Summary

In the early 1990's, the Australian Institute of Marine Science (AIMS) surveyed the three offshore reef systems of Western Australia, quantifying the diversity of coral and fish species and general habitat conditions. Based on these data, AIMS established long-term monitoring (LTM) programs at the Rowley Shoals and Scott Reef systems in 1994. The AIMS LTM protocol was used to quantify percentage cover of targeted groups of benthic organisms and abundances of fish, enabling their division into groups according to taxonomy, reproductive modes, functional roles and growth forms.

At the largest of the three reef systems (Scott Reef), the timing of reproduction and the rates of recruitment for the most representative corals were also quantified. The monitoring program was adapted over the following years to include a range of data describing community dynamics and environmental conditions. These additional data included variation in life history stages and traits for representative species of corals, patterns of genetic connectivity for species of corals and fish, and key parameters associated with water quality and oceanography. This large-scale monitoring program documented the impact and subsequent dynamics of coral communities following the catastrophic mass-bleaching in 1998 that affected the entire reef system.

Following an 80% reduction in coral cover due to mass-bleaching in 1998, and four subsequent disturbances over the following decade, the cover (43%) of hard corals and their number of genera in 2010 were again similar to that prior to mass-bleaching, but the soft corals (4%) had returned to only approximately half their pre-bleaching cover. Given the lack of larval connectivity to other reef systems in the region, we attribute the resilience of communities at Scott Reef to high rates of growth and survival, particularly in the early post-recruitment stages ($> 80\% \text{ yr}^{-1}$), due to the persistence of suitable substrata after the bleaching and favourable water quality. However, determining whether individual communities across Scott Reef had recovered from the mass-bleaching in 2010 required an assessment of both the cover and the relative abundance of different groups; at some locations coral cover was well below that in pre-bleaching years but the relative abundance of different groups was similar, while at other locations coral cover was similar to that pre-bleaching but the abundance of different groups differed. Clear differences in the recovery trajectories among locations were driven by:

- (1) routine habitat conditions (e.g. substrata, sedimentation, current speeds),
- (2) extreme conditions during acute disturbances (e.g. sea-water temperature, wave heights) and
- (3) the life histories (e.g. reproductive mode, growth rates, susceptibility to disturbance) of the dominant corals.

Routine habitat conditions at Scott Reef ranged from the outer-slope habitat exposed to the open ocean, to inner-slope locations adjacent to the deep channel or in the sheltered south lagoon. Much of the variation among locations was explained by their substrata, water temperatures, regimes of sedimentation, turbidity, maximum current speeds and wave heights. In addition to these routine habitat conditions, communities were exposed to five major acute disturbances over sixteen years of monitoring: one severe and widespread mass-bleaching (1998), one severe but more localised cyclone, and three moderate and localised disturbances (cyclone, disease, bleaching).

Throughout the monitoring period, benthic communities were characterised by the groups of hard corals least susceptible to disturbances, including encrusting corals, massive *Porites*, *Pocillopora* and *Faviidae*. In contrast, community structures in 2010 were distinguished from those in pre-bleaching years by a lower abundance of *Isopora*, and the absence of *Millepora* and branching *Porites* at locations where they had been moderately abundant. More specific differences in community structure were seen for a few groups that were periodically abundant at only a few locations. The cover of soft corals in 2010 was much lower than in pre-bleaching years at all locations, with the exception of those at West Hook (SL3) and the Deep Channel (SL4) that were least impacted by the bleaching and had the highest initial cover of soft corals. In contrast, the relative cover and structure of hard coral communities at most locations in 2010 was similar to that in pre-bleaching years, with the exception of those worst impacted by the mass-bleaching and subsequent disturbance (SL2, SS1, SS2). However, habitat conditions and disturbance regimes at Scott Reef during the period of monitoring exemplify conditions approaching a tipping point, beyond which communities are likely to exist in a prolonged state of reduced cover, diversity and structural complexity.

The fish community at Scott Reef has undergone significant change in composition throughout the 17 year period of study, and is now quite different to the assemblage that occurred on the reef prior to a mass coral bleaching there in 1998. The effect of the bleaching event was most striking on species that used coral either for food, such as butterflyfishes, or for protection, such as many planktivorous damselfishes. Fish assemblages on the reef underwent three distinct phases during the study from

- (1) a pre-bleached community (1994 to 1997) dominated by habitat and dietary specialists (predominantly coral and plankton feeders) through
- (2) a post-bleach community (1998 to 2006) characterized by species that have a preference for the habitat types resulting from coral bleaching, either directly through the erosion of dead coral into rubble habitats or from the increase in area available for turf algae to
- (3) the most recent fish community (2008 to 2010) characterized by fish that have more generalist diet and habitat requirements overlaid by mid-sized carnivorous species that have increased in number presumably due to the reduction of their main predators (sharks) through fishing.

The passage of Cyclone Fay directly over Scott Reef in early 2004, is likely to have caused additional changes to the composition of the benthic community and stalled the recovery of the fish community. Unlike benthic communities, for which disturbance due to bleaching and cyclones are the principal and obvious drivers of change in patterns of abundance and structure, we detected significant trends in fish assemblages during the 17 years of our study that had no clear or simple explanation. For example, we found that the numbers of larger, mobile reef fishes steadily increased during the study, particularly in the case of carnivorous species belonging to the families Lethrinidae, Lutjanidae and Serranidae. This increase in abundance was accompanied by an increase in fish species richness, and both trends were apparently unaffected by the major bleaching event or the passage of cyclones across the reef. One possibility is that these patterns were the result of increasing fishing pressure on Scott Reef by Indonesian fishermen that have targeted large predatory sharks over the last decade. Studies on other reef systems have shown that apex predator reduction can result in fundamental changes to the biomass and abundance of lower trophic levels in coral reef ecosystems, which might account for some of the changes recorded by our study. In particular, this might explain the increasing number of mid-sized carnivorous species (meso-predators) that have been released from predation by sharks over the duration of the study. The trophic consequences the release of

meso-predators can have on ecosystem structure can be profound, thus necessitating further research on predator-prey relationships at Scott Reef.

In addition to quantifying percentage cover of coral communities, the size-frequency distributions of selected genera of hard corals were recorded at 6 long-term monitoring locations across Scott Reef, between 1996 and 2010. The most obvious change in community size-structures were the dramatic decreases in abundance following the mass-bleaching in 1998. Through the recovery period, subsequent changes in size-structure were correlated with changes in sexual recruitment. Following the return to pre-bleaching rates of recruitment in 2008, were large increases in the number of small *Acropora* colonies at all locations in October 2010. Two smaller scale disturbances were recorded at Scott Reef between 2008 and 2010. The recent outbreak of disease at location SL2 dramatically reduced the abundance of large (tabulate) *Acropora*, but there remained an abundance of small colonies. In May 2010 a bleaching event reduced the abundance of large *Pocillopora* colonies at the outer reef slope locations (SS1, SS2) along with smaller reductions at the 4 lagoon locations (SL1-4). The size-structure of massive *Porites* was recorded in 2010 for the first time since 2003. The slow growing massive *Porites* were least affected by the 1998 bleaching, but their size-structure has changed little throughout the monitoring period and in 2010 was similar to that prior to the mass-bleaching.

Mass coral spawning at Scott Reef and Rowley Shoals occurs biannually, with a primary spawning event in autumn (March / April) and a smaller event occurring in spring (October / November). Of the broadcast spawning corals sampled, 33 species spawned only during autumn, 5 spawned only in spring, and 30 spawned in both seasons. All of the species of broadcast spawning coral participated in at least one of the two mass spawning events, with the exception of the massive *Porites* that may spawn at several times through the year. For most species of biannual spawners, a larger percentage (60 to 99%) of colonies spawned in autumn than spring, but a relatively high percentage (54-96%) of colonies spawned in spring for at least three *Acropora* species. Individual colonies appeared to spawn consistently in either autumn or spring, with little evidence of two annual gametogenic cycles. Among the biannual spawners, polyp fecundity and size of mature eggs varied among species, days prior to spawning, seasons and years, but with no consistent patterns evident. Species of brooding corals are likely to release sperm and planulae larvae over several months through the year, around the two mass spawning events.

A strong stock-recruitment relationship exists for broadcast spawning and brooding corals at Scott Reef. Consequently, the recovery of coral communities at Scott Reef following disturbances is facilitated by the survivors, and not by the supply of recruits from other reefs in the region. Coral cover and larval supply of scleractinian corals following the autumn mass spawning event was quantified for ten years between 1996 and 2010. The mass-bleaching in 1998 reduced recruitment rates over the following four years to less than 3% of that in pre-bleaching years, and they did not return to pre-bleaching levels until 2008. The stock-recruitment relationship for communities broke down at the location scale (< 5km) for the spawning corals, but not for the brooding corals. Recruitment of the brooding *Isopora* was strongly dependant on the presence of adult stock at the location scale (<5 km), with communities failing to recover by 2010 if all colonies were removed from monitoring transects following the 1998 bleaching; conversely, communities with the highest abundance of *Isopora* following the bleaching were fastest to recover. For the spawning corals, patterns of recruitment varied consistently among locations throughout the study, with the highest recruitment at locations SL1 and SS2 (73% of total) and the lowest recruitment at SL4 and SS1 (8%

of total). Local hydrodynamics were responsible for decoupling the stock-recruitment relationship for spawning corals at the local scale, and creating sources and sinks of recruitment across the reef system. The variation in recruitment influenced the size-structure of corals and the rates of community recovery from disturbances. These data highlight the susceptibility of communities at Scott Reef to widespread and severe disturbances, over scales of more than approximately ten kilometres for the spawning corals and a few kilometres for the brooding corals, particularly for those communities that are primarily sources of larval supply.

2. Recent disturbances at Scott Reef: Outbreak of bleaching and disease in 2010

2.1 Disease

The most protected southern lagoon site at Scott Reef (SL2) is characterised by high levels of turbidity, chlorophyll and small sediment size. These conditions combined with high cover of susceptible corals, predispose this location to outbreaks of coral disease. An outbreak of coral disease was first detected at this location in 2009 and in May 2010 increased water temperatures exacerbated this outbreak. Cover of hard coral decreased by approximately 10% between 2008 and 2010 with the selective loss of cover of Acroporan corals. The largest impacts of coral disease were observed among tabulate *Acropora*, which decreased in cover by nine percent (Figure 2.1). Declines in cover of tabulate *Acropora* were also observed at SL1, possibly due to bleaching and disease events in the region, however both cover of Acroporan corals and total hard coral cover stabilised during this time frame.

In the size-frequency data for corals, large *Acropora* colonies were seen to be affected by disease at location SL2 between 2008 and 2010. The total number of adult *Acropora* colonies (>15cm) decreased at SL2 by 81% from 1454 to 267 colonies on the LTMP transects. The number of small colonies at SL2 increased during this period either through new recruitment or partial mortality (Figure 2.2).

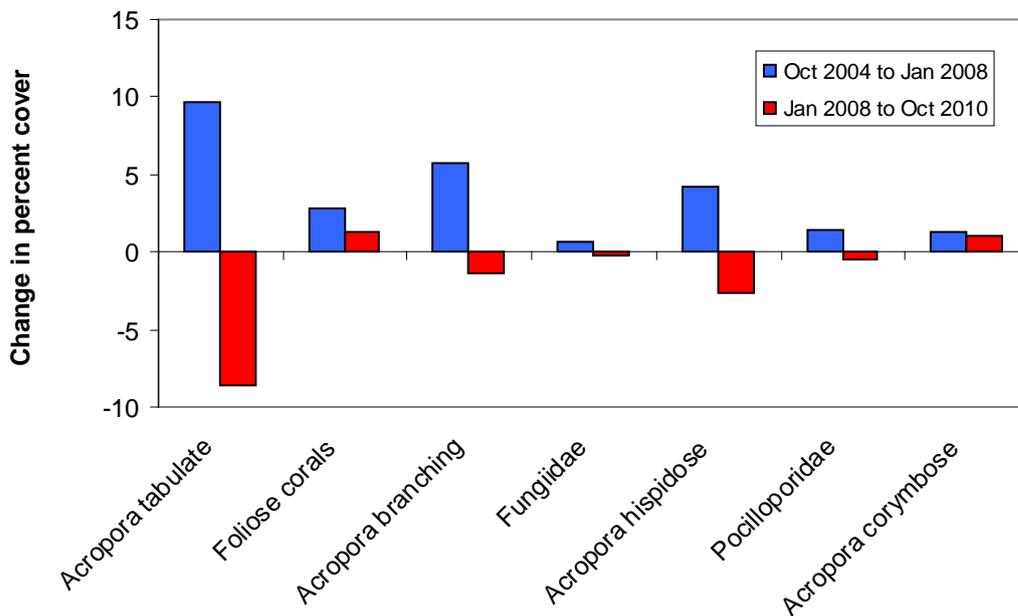


Figure 2.1. A comparison of change in cover of abundant hard corals (>3 percent cover) at SL2 between consecutive survey periods.

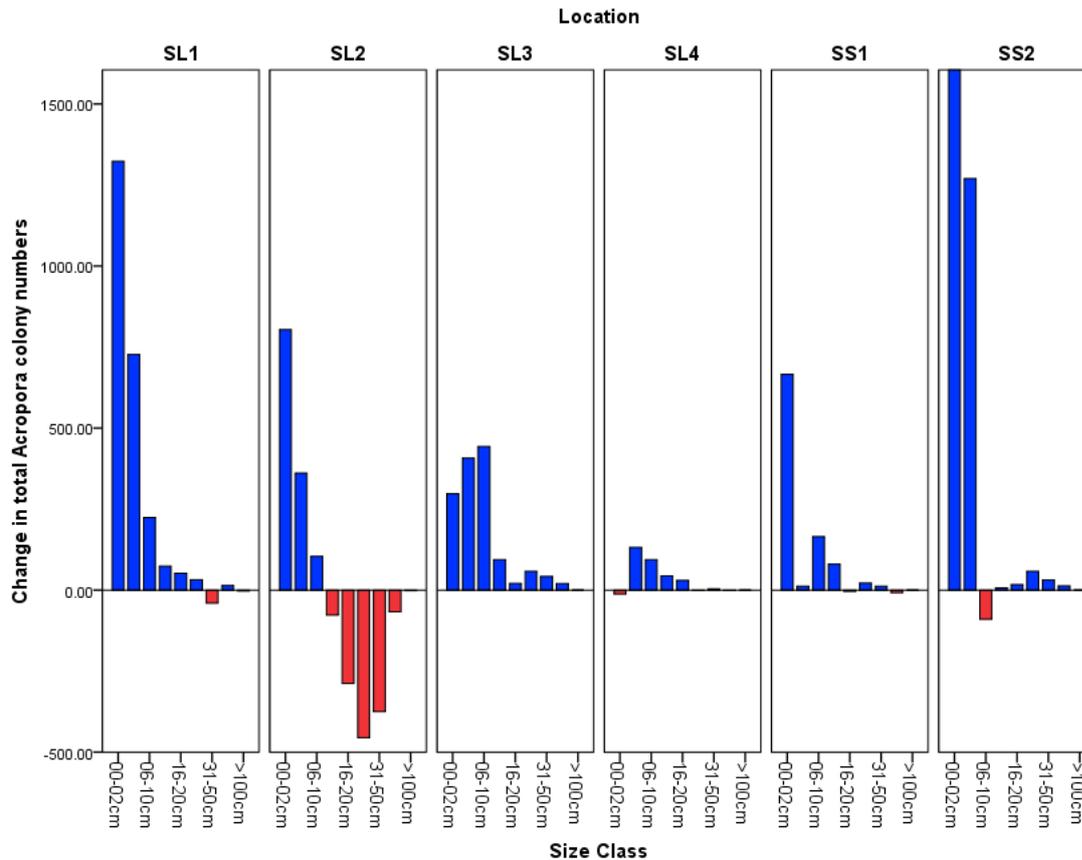


Figure 2.2. Change in the total number of *Acropora* colonies of each size class between 2008 and 2010 at each location. Note evidence of a significant loss of large *Acropora* colonies at Location SL2.

2.2 Bleaching

In May 2010 increased sea water temperatures caused bleaching across Scott Reef. During this time, temperatures at outer slope locations were higher and/or exhibited less daily variation than at lagoon locations. Water temperature at the most southern location on the inner side of south Scott lagoon (SL2), where water circulation is low, tended not to vary by more than 1°C in a 24h period, whereas temperatures at locations with high tidal influence and short distances to deeper oceanic water (SL3 and SL4) exhibited wider ranges of > 1°C in a 24 h period (Figure 2.5 and Figure 9.3). This latter pattern provides an example of the cooling influence of water originating from the deep channel separating North and South Scott Reef (Brinkman et al. 2010 SRRP Report).

Approximately five percent of all corals surveyed between March and May 2010 showed signs of bleaching. Hard corals in the families Fungiidae and Pocilloporidae were most susceptible and more than 13% of these corals were affected. Acroporan corals showed high rates of mortality during increased water temperatures in 1998, however these corals had relatively low incidence of bleaching during the 2010 exposure (Figure 2.3).

High amounts of bleaching were observed on deeper reef slope sites where over 35% of all corals surveyed at 9 m depth showed signs of bleaching (Figure 2.3). Despite a high incidence of bleaching on deep reef slope locations, cover of hard coral increased by approximately 10% at SSI and SS2. Increases in cover of hard coral was driven by corals least impacted by bleaching such as corymbose

and digitate *Acropora* that increased by approximately 5%. Cover of Pocilloporid corals remained stable at SS1 and SS2 where it is likely that these and other more susceptible corals were able to recover from the bleaching event between survey periods. Overall cover of hard coral declined by approximately 2% at Seringapatam where cover of Pocilloporid corals decreased by approximately 5%.

In shallow water locations in the lagoon < 5 % of hard corals showed signs of bleaching at depths of six meters (Figure 2.3). Cover of hard coral increased at the majority of 9 m deep lagoonal monitoring locations and these increases ranged from 3% at SL1 to 16% at SL3. Decreases in cover of hard coral were only observed at SL2 and these decreases have been attributed to disease outbreaks in the region (see above).

In the size-frequency data, bleaching was most evident in the Pocilloporid corals, at the two outer reef locations SS1 and SS2. The number of *Pocillopora* colonies decreased significantly between 2008 and 2010 at locations SS1 and SS2 (Figure 2.4). In total, 76% of *Pocillopora* colonies were lost at SS1 and 59% at SS2, most likely due to bleaching.

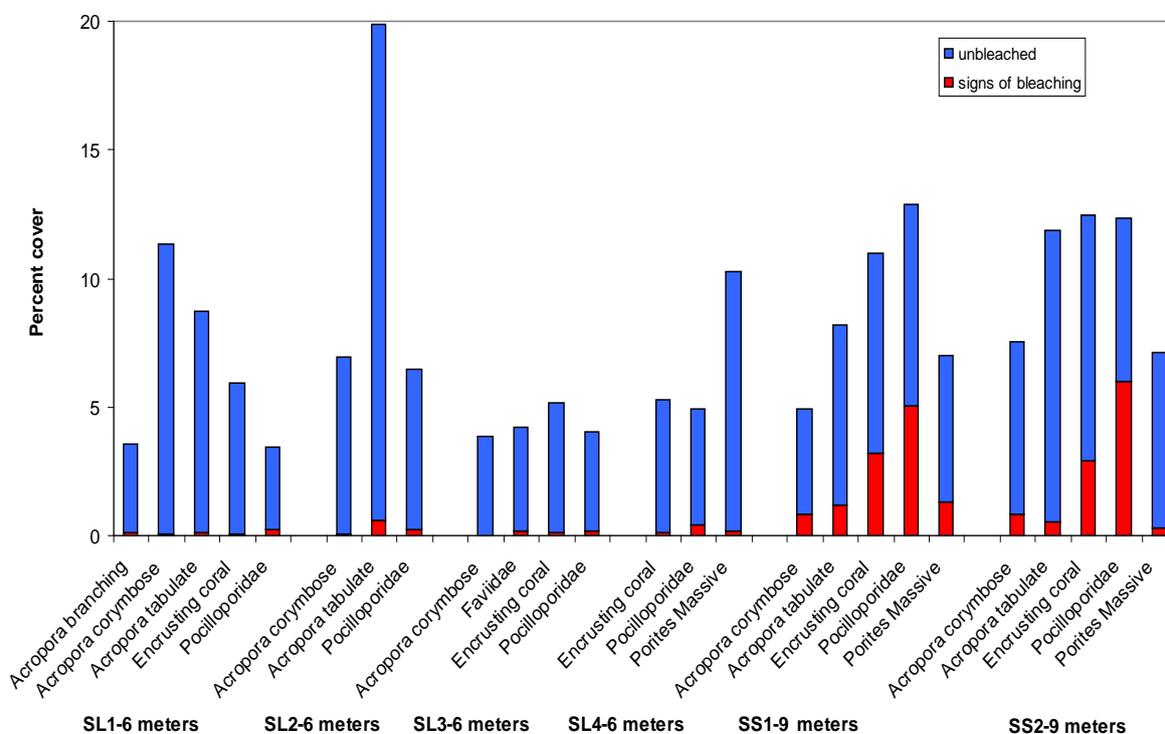


Figure 2.3 Percentage cover of bleached and unbleached life-forms of abundant hard coral (>3 percent cover) at Scott Reef.

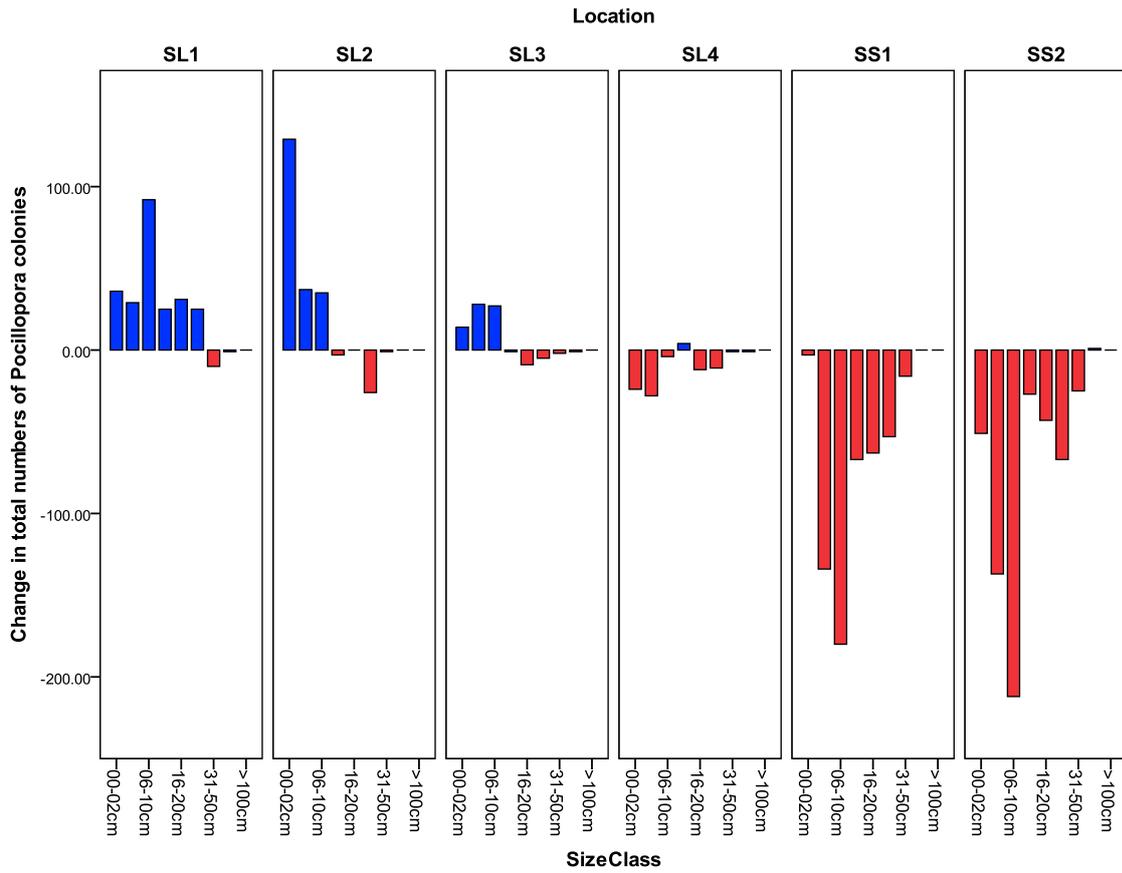


Figure 2.4 Change in total number of *Pocillopora* colonies between 2008 and 2010 on the long term monitoring Size Frequency transects. Negative change is indicated by red bars.

3. A summary of Project 1 results in the context of the monitoring and resilience of coral reefs

3.1 Summary

Worldwide, the increasing severity of disturbance regimes to coral reefs is causing prolonged shifts to degraded states. Some monitoring studies provide only equivocal evidence of degradation due to issues of scale and method, and most provide few insights into the demographic processes underlying the degradation or resilience of communities. Consequently, there have been renewed calls for monitoring programs of coral reefs to explain mechanisms of change in community structure and to provide conclusive links to the external drivers. Here, we summarise the key results of a large-scale monitoring program at an isolated atoll system off north-western Australia, which documented the impact and subsequent dynamics of coral communities following a catastrophic mass-bleaching event. Mass-bleaching in 1998 reduced the cover of hard corals across all shallow-water (< 20 m) habitats by between 60 and 90%, and caused a corresponding reduction in sexual recruitment. Recruitment remained well below pre-bleaching rates for more than 8 years, and a strong stock-recruitment relationship ($R^2 = 0.9$) existed at the scale of the atoll system. Despite this stock-recruitment relationship and exposure to several additional disturbances of moderate intensity, coral communities had returned to a similar pre-bleaching cover and structure within 12 years. We attribute this level of resilience to high rates of survival, particularly in the early post-recruitment stages ($> 80\% \text{ yr}^{-1}$), due to the persistence of suitable substrata after the bleaching and favourable water quality. These data provide valuable insights into the dynamics of coral communities when exposed to an increasingly common regime of disturbances over decadal time-steps, and highlight the importance of minimising chronic stressors (e.g. overfishing, degraded water quality) if communities are to be resilient to the much larger scale disturbances (e.g. mass-bleaching) to which they are now exposed.

3.2 Introduction

The degradation of coral reef ecosystems commenced hundreds of years ago through chronic overfishing of large vertebrates (Jackson 1997; Pandolfi et al. 2003b) and has since been compounded by additional disturbances. Early research into disturbances to coral reefs focused on the impacts of individual disturbances on life history traits of corals over short periods of time (days to weeks), often in the form of descriptive and manipulative experiments (e.g. Stephenson 1930; Connell 1973; Lang 1973; Williams 1975; Glynn 1976; Dodge and Vaisnys 1977; Bak 1978; Bak 1979; Jackson et al. 1985). As formal monitoring programs emerged, they shifted to a more community focus and the changes in the abundance of multiple species, also usually over small spatial (m) and/or temporal (months) scales (Loya 1976; Randall and Eldredge 1977; Connell 1978; Bak and Luckhurst 1980; Colgan 1981; Pearson 1981; Smith et al. 1981; Woodley et al. 1981). These early studies characterised the impacts of disturbances as either ongoing stressors (press, chronic, slow) of usually moderate severity, or short and periodic disturbances (pulse, acute, fast) of usually high severity (Connell and Slatyer 1977; Pickett and White 1985; Hughes et al. 2010). Additionally, impacts displayed varying degrees of selectivity, or heterogeneity, with more selective disturbances having impacts that were spatially patchy, affecting a subset of species, and/or injuring rather than killing individual corals. This work provided insights into how some disturbances affected community structure and how quickly coral reef communities could recover from periodic disturbances with selective impacts. However, it provided limited ability to predict or understand the degradation of coral reefs that was to be documented in subsequent monitoring programs.

Coral reefs have evolved to cope with a range of periodic disturbances, but in the last two decades there has been an unprecedented increase in the types, frequency, scale and severity of disturbances. Reviews of disturbance to coral reefs initially highlighted cycles of impact and recovery within decadal time steps, often from single events causing selective or local impacts (e.g. storms, degraded water quality, predation), and concluded there was little evidence of global degradation (Grigg and Dollar 1990; Connell 1997; Stoddart 1969). In stark contrast, many recent reviews have redefined disturbance regimes to include multiple events of reduced selectivity acting over regional scales (e.g. overfishing, mass-bleaching, diseases, acidification), and provide evidence of global degradation (e.g. Done 1999; Pandolfi et al. 2003a; Bellwood et al. 2004; Hughes et al. 2010; Graham et al. 2011). The background disturbances with which coral reefs have evolved are now compounded by a suite of human impacts, causing a shift in scientific focus to concepts of resilience, thresholds, stable-states and phase-shifts (e.g. Done 1992b; Knowlton 1992; Done 1999; Hughes et al. 2007; Mumby et al. 2007). Despite this shift in focus, many monitoring programs to date have still provided few insights into the mechanisms responsible for the degradation or resilience of communities experiencing common regimes of disturbance.

Many recent monitoring programs have merely documented the degradation of coral reefs. Even these findings are sometimes inconclusive because of inappropriate scales, with subsequent monitoring programs having similar limitations in addition to those arising from sliding baselines and spatial variation among random sites (Dayton et al. 1998; Knowlton and Jackson 2008). Consequently, there have been calls for monitoring programs to be conducted over larger temporal and spatial scales and to explain the mechanisms underlying observed changes in community structure (Pearson 1981; Hughes et al. 1992; Hughes et al. 2010; Graham et al. 2011). Monitoring programs aimed at understanding the dynamics of coral reef communities must be conducted over many years (decades) to match cycles of impact and recovery from regimes of disturbance, to include episodic but significant events, account for annual variation in demographic processes, and to reflect the life-span of organisms and their rates of population turnover. Similarly, large spatial scales are required because the impacts of many disturbances are spatially variable, as are the demographic processes underlying the resilience of communities.

In addition to monitoring changes in abundance of species over appropriate scales, the mechanisms underlying structural changes in communities are addressed by quantifying the abundances of key life history stages and traits for representative species. The life cycle is the fundamental unit of description of the organisms being monitored (Caswell 1989). Variation in the abundance of different life history stages is the corollary of their underlying traits (Bak and Meesters 1999; Ebert 1999), providing insights into future maintenance and resilience. New recruits and juvenile corals maintain communities and facilitate their resilience, yet these stages are often the most susceptible to disturbances and contribute least to percentage cover. Percentage cover data may provide little warning of an approaching phase-shift due to an acute disturbance and the mass-mortality of adults, which were resistant to less severe disturbances that had previously caused recruitment failure or low post-recruitment survival (Hughes et al. 2010). Ultimately, monitoring studies would also directly quantify key demographic processes. Among these processes, sexual reproduction and recruitment underlies the maintenance and resilience of most communities, and recruitment failure often underlies their degradation (Done et al. 2010; Hughes et al. 2010; Thompson and Dolman 2010). Corals have complex patterns of reproduction and recruitment that vary among regions, years and species (Harrison et al. 1990; Baird et al. 2009; Harrison 2011). However, knowing the times of reproduction, connectivity within and among reefs, and rates of recruitment, provides valuable insights into the consequences of different disturbance regimes and community structure in the future. Post-recruitment growth and survival closes the life cycle and enables estimates of transition rates through stage classes for representative species within the community. Combining demographic data with changes in life history stages and community structure is an insightful approach to understanding community degradation or resilience under different disturbance regimes (Done 1987; Fong and Glynn 1998; Ebert 1999; Caswell 2000; Edmunds and Elahi 2007).

Critical to the interpretation of these monitoring data is the choice of target species, their associated descriptors and the quantification of key external drivers of change. Better insights into why disturbances have caused structural changes in communities are obtained from abundance data when there is a considered grouping of species, such as the functional groups of fish (Wilson et al. 2008; Cheal et al. 2010) or combinations of taxa, reproductive mode and growth form in corals (Woodley et al. 1981; Hughes 1988; Done 1992a). Similarly, detailed demographic data are more useful when collected for species that are broadly representative of community dynamics, rather than species with unique life histories. Consideration must also be given to the likely drivers of change in community structure. Key biological drivers of change on coral reefs include the abundances of herbivores (e.g. fish, urchins) and predators (e.g. *Drupella*, *Acanthaster planci*), while physical drivers include chronic parameters associated with water quality (e.g. turbidity, nutrients) and acute changes associated with severe disturbances (e.g. temperature, wave energy, sedimentation). Given that coral reefs are impacted by a regime of disturbances, there is an increasing need to systematically quantify several drivers of change that are singularly, or synergistically, predicted to cause significant impacts to communities and to reconsider which are included through an adaptive framework to monitoring.

Monitoring studies of coral reefs that employ appropriate scales and methods are most useful when they include disturbance regimes of global relevance. In today's climate, this includes both severe and selective disturbances, with or without a background of chronic stress (Done et al. 2007; Baker et al. 2008; Hughes et al. 2010; Graham et al. 2011). Ideally, structural and demographic data are available for communities in a near-climax state with no recent history of major disturbance, followed by a severe disturbance and a sufficient period for recovery to a similar pre-disturbance state. Additionally, during a potential recovery period, the monitoring program would be of sufficient scale to include replicate communities exposed to less severe and more selective disturbances that routinely impact coral reefs. In the early 1990's, the Western Australian Museum (WAM) and the Australian Institute of Marine Science (AIMS) surveyed the three offshore reef systems of Western Australia, quantifying the diversity of coral and fish species and general habitat conditions (Done et al. 1994). Based on these data, AIMS established long-term monitoring (LTM) programs at the Rowley Shoals and Scott Reef systems in 1994 (Heyward et al. 1997). The AIMS LTM protocol was used to quantify percentage cover and abundances of targeted groups of benthic organisms and fish, enabling their division into groups according to taxonomy, reproductive modes, functional roles and growth forms. At the largest of the three reef systems (Scott Reef), the times of reproduction and the rates of recruitment for the most representative corals (in terms of benthic cover) were also quantified. The monitoring program was adapted over the following years to include a range of data describing community dynamics and environmental conditions. These additional data included variation in life history stages and traits for representative species of corals, patterns of genetic connectivity for species of corals and fish, and key parameters associated with water quality and oceanography. Here, we provide an overview of this large-scale monitoring program, which documents the impact and subsequent dynamics of coral communities following a catastrophic mass-bleaching in 1998 that affected the entire reef system. In particular, we highlight the conditions and parameter states underlying the resilience of communities a decade after the bleaching, despite their lack of connectivity to other reef systems in the region and their exposure to three additional disturbances of moderate severity.

3.3 Results

3.3.1 Mass-bleaching and mortality across habitats

Across the shallow-water habitats, mean cover of hard corals at Scott Reef prior to the mass-bleaching was 42%, and ranged between 35 and 50% (Figure 3.1). The mass-bleaching in April 1998 severely impacted all of these habitats and communities, causing relative decreases in coral cover of 60% in the upper reef slope, and between 80 and 90% in the reef crest and reef slope (Figure 3.1).

Observations at the time of bleaching indicated a much lower incidence of bleaching below 20 m depth, where there are also extensive coral communities. A decade later, mean coral cover across the shallow-water habitats was the same (42%) as that prior to the bleaching, and similar or greater than that prior to the bleaching within each of the habitats (35 to 50%) (Figure 3.1). Additionally, the number of hard coral genera and their percentage cover at the reef slope communities were also similar to that prior to the bleaching (Figure 3.2).

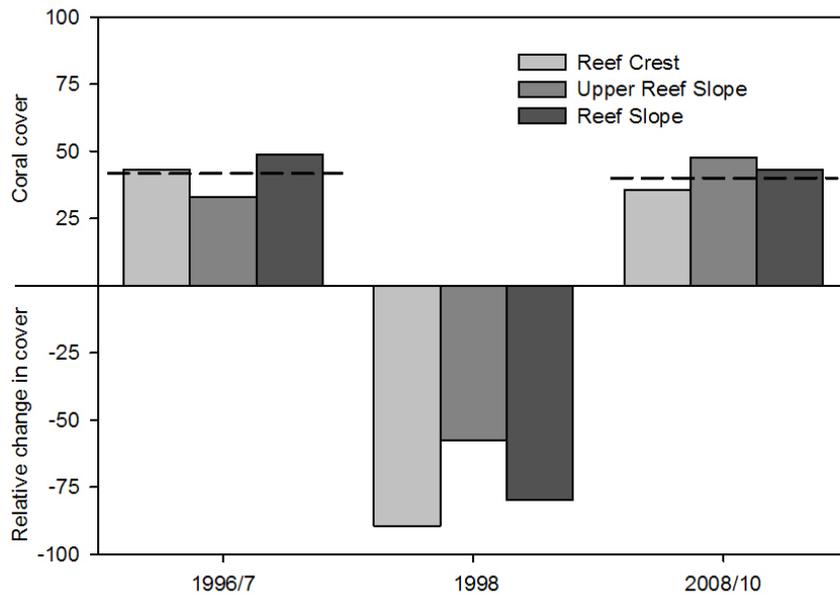
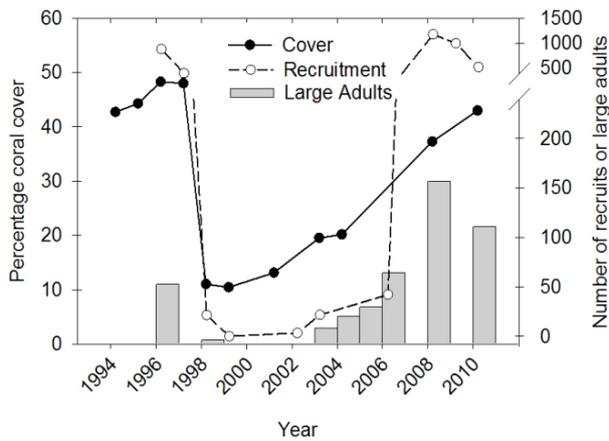
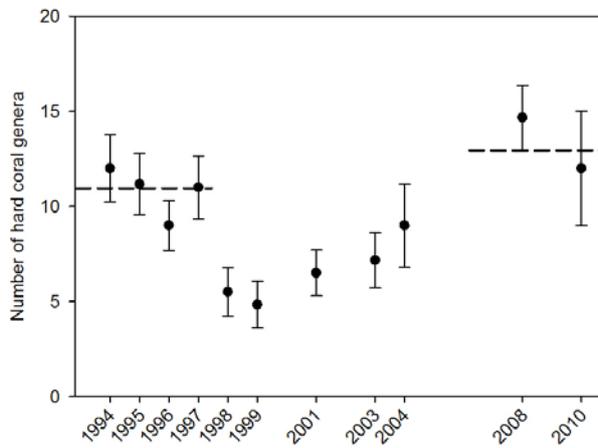


Figure 3.1. Percentage coral cover in shallow-water (< 20 m) habitats across Scott Reef prior to the bleaching (1996/7), the relative decreases in percentage cover following bleaching (1998), and the return to a similar pre-bleaching cover ten years later (2008/10). Dotted lines represent mean cover across habitats in 1996/7 and 2008/10.

a)



b)



c)

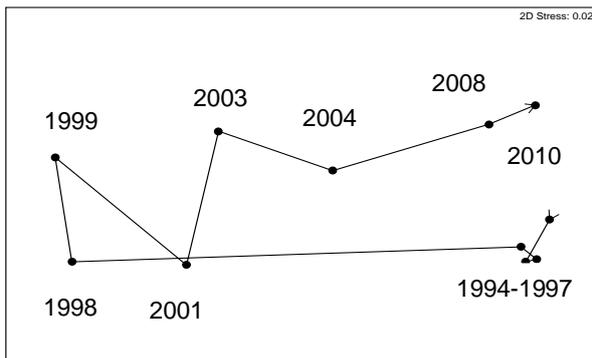


Figure 3.2. The impact of mass-bleaching (1998) on hard coral communities in the reef slope habitat and their return to a similar pre-bleaching state by 2010. a) Percentage cover of hard corals and rates of recruitment and abundance of large adult (> 30 cm Ø) corals in the dominant family, the Acroporidae. b) Number of genera of hard corals. c) MDS of Bray-Curtis similarities of square-root transformed percentage cover data for different genera of hard corals.

3.3.2 Stock-recruitment and resilience

Throughout the period of monitoring, there was a strong stock-recruitment relationship for the hard corals in the reef slope habitat (Figure 3.2). The rates of recruitment of the dominant coral family, the Acroporidae, were highly correlated ($R^2 = 0.9$) with variation in percentage cover (Figure 3.2). The consistently low rates of recruitment several years after the mass bleaching (Figure 3.2 note scale) indicated that communities were reproductively isolated from those in the deeper-water (> 20 m) habitats and from other reef systems in the region that were not impacted by the mass bleaching.

Following the mass bleaching, the increase in coral cover at the reef slope communities was initially slow, but increased more rapidly after 2001 to return to 90% of their pre-bleaching cover by 2010 (Figure 3.2). The initial increases in coral cover were < 0.5 % yr⁻¹, compared with approximately 3% yr⁻¹ during the more rapid period of recovery (post-2001), despite communities being exposed to four additional disturbances. Communities were impacted by cyclone disturbances in 2004 and 2007, and then by an outbreak of disease and moderate bleaching in 2010. However, these disturbances were far less severe and more selective than the mass bleaching in 1998, with impacts restricted to a subset of species, growth forms and locations.

The rapid increases in coral recruitment following the mass bleaching lagged behind those for coral cover (Figure 3.2), but coincided with the increases in the abundance of large adult (> 30 cm Ø) colonies. By 2008, the number of large adult colonies in the family Acroporidae (excluding *Montipora*) had more than doubled that prior to the mass bleaching, yet the communities had not yet returned to their pre-bleaching cover (Figure 3.2). However, large stands of branching *Isopora* and *Acropora* had contributed to the high cover at some locations prior to the mass bleaching, but were not recorded in size-frequency distributions. In all but the most recent (2010) post-bleaching surveys, these stands of branching corals were rare and many of the large adult colonies were tabulate *Acropora*. The mortality of these table *Acropora* following a disease outbreak at two locations was almost exclusively responsible for the decrease in abundance of large adult colonies in 2010 (Figure 3.2a).

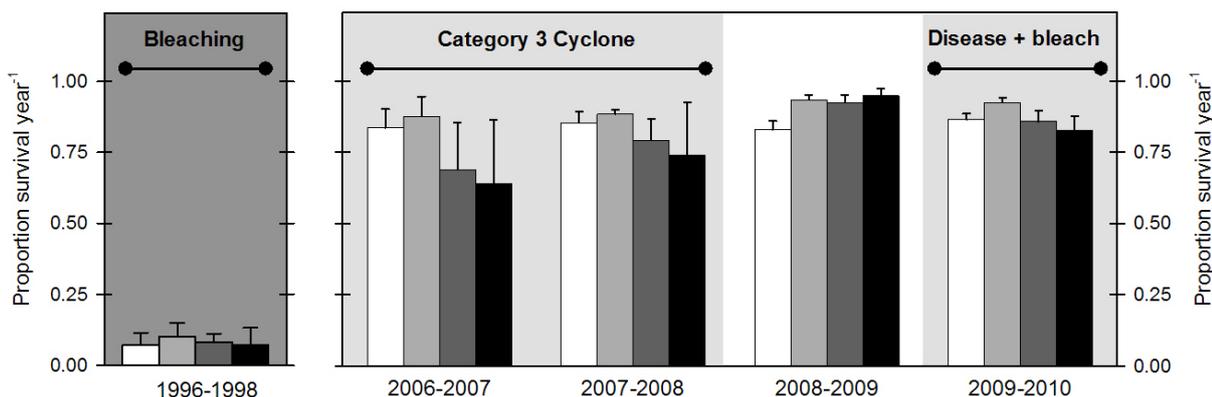


Figure 3.3 Annual rates of colony survival following mass-bleaching (dark grey background), Category 3 Cyclone George (grey background), no major disturbance (white background), and a moderate bleaching and outbreak of disease (grey background). The proportion of colonies surviving the mass-bleaching in 1998 was inferred from changes in size-frequency distributions of *Acropora* before (2006) and after (1998) the mass-bleaching. For the remaining years (2006-2010), the rates of survival were quantified from tagged colonies of *Acropora spicifera*. Category 3 Cyclone George occurred two months before the end of the 2006-2007 survey period, reducing the survival of colonies over two survey periods (2006-2008).

3.3.3 Survival and resilience

The rapid increases in coral cover, large adults and recruits more than six years after the bleaching reflected the high rates of survival of early colonisers. Rates of survival were quantified from tagged *Acropora spicifera* colonies ($n = 3416$) from 2006, but not following the mass-bleaching in 1998 or category 5 Cyclone Fay in 2004. Rates of survival inferred from changes in size-frequency distributions of *Acropora* before (1996) and after (1998) the bleaching were less than $10\% \text{ yr}^{-1}$ for all size classes (Figure 3.3), highlighting the severity and lack of selectivity of the disturbance. Rates of survival could not be inferred for Category 5 Cyclone Fay, but were directly quantified for Category 3 Cyclone George in 2007. Variation in the rates of survival among colony size-classes and sites highlighted the selectivity of impacts from Cyclone George (Figure 3.3). Colonies of the largest sizes and at the most exposed sites were more likely to be killed immediately by the cyclone (2006-2007), while other colonies that were injured died in the following year (2007-2008). For the worst affected sites and size-classes ($>15 \text{ cm } \varnothing$), annual rates of survival following Cyclone George ranged between 10 and 35%. In contrast, most of the colonies that were injured by the cyclone but decreased by less than half their initial area survived the following year. Additionally, the survival of the smaller ($<15 \text{ cm } \varnothing$) colony size classes at even the worst affected sites was $>69\% \text{ yr}^{-1}$, and the survival of all size classes at the remaining sites was $>80\% \text{ yr}^{-1}$. During the calm conditions that followed (2008-2009), the mean rates of survival of colonies were consistently high across all size classes ($>83\% \text{ yr}^{-1}$). Survival remained high ($>83\% \text{ yr}^{-1}$) during the moderate bleaching and outbreak of disease that occurred during the following year (2009-2010), because these disturbances selectively impacted other species and growth forms, having a minor impact on *A. spicifera* colonies (Figure 3).

3.3.4 Habitat and resilience

Throughout the monitoring period habitat conditions facilitated the recruitment, growth and survival of corals. Water quality across Scott Reef is typical of an oceanic atoll, and favours coral growth and survival. Light penetration is high and usually above 10% in depths less than 25 m. The rates of sedimentation are low at times other than after tropical storms and cyclones, as are turbidity (NTU) and chlorophyll concentrations (Table 3.1). The space created after the bleaching and the mortality of corals in 1998 was covered by fine turfing and coralline algae, and remained available for re-colonisation by corals (Figure 3.4). Changes in the cover of turfing and coralline algae were matched by changes in the abundances of herbivorous fish, and the cover of macroalgae, sponges, and all other benthic organisms remained low (Figure 3.4). Additionally, the extensive cover of turfing and coralline algae at most sites was consolidated, within no increases in the cover of rubble or other unconsolidated substrata following the bleaching.

Table 3.1 Indicative water quality parameters at Scott Reef. Parameters were measured at between 4 and 6 locations across Scott Reef, adjacent to long-term monitoring sites. Parameter estimates are similar at all locations, with the exception of one location in the sheltered lagoon which has comparatively low current speeds, rates of sedimentation of fine particle sizes and light penetration, and comparatively high turbidity and chlorophyll concentrations. Averages are presented for all locations combined, plus the range of values for all locations excluding that at the sheltered lagoon.

Physical parameter	Average (all locations)	Range (not Sheltered Lagoon)	Sheltered lagoon
Turbidity (NTU)	0.3	0.1 to 0.2	0.8
Chlorophyll (mg m^{-3})	0.6	0.3 to 0.4	1.5
PAR ($\text{micromol photons m}^{-2} \text{ s}^{-1}$)	725	650 to 1000	440
Sedimentation ($\text{mg day}^{-1} \text{ cm}^{-2}$)	1.8	1.0 to 3.2	1.3

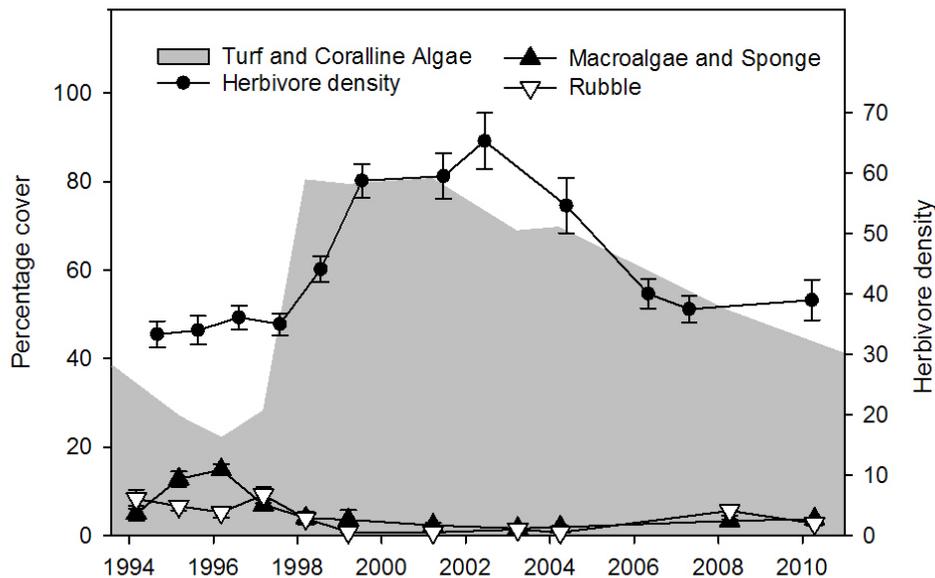


Figure 3.4 Key drivers of habitat conditions before and after mass-bleaching in 1998. Suitable substrata remained available for recolonisation by corals following the bleaching. The increase in cover of coralline and turf algae was followed by an increase in abundance of herbivorous fishes, while the cover of unconsolidated rubble, macroalgae and sponges remained low.

3.4 Discussion

3.4.1 Monitoring the resilience of coral communities

Coral reefs are under threat of global degradation due to a recent shift in their regimes of disturbance (Pandolfi et al. 2003a; Hoegh-Guldberg and Bruno 2010). Yet, dissent remains over the degree to which coral reefs can maintain their resilience to human exploitation and persist in their current state. Monitoring programs remain the primary tool by which the condition of coral reefs are assessed, but inadequacies in scale and method mean that evidence of degradation and links to external drivers on some reefs are equivocal. Additionally, monitoring programs that provide few insights into the mechanisms of change make pre-empting degradation more difficult, which is by far the most effective management option given the difficulties in reversing phase-shifts (Bellwood et al. 2004; Mumby 2009). Monitoring studies must therefore produce more substantive insights into the past and future dynamics of communities.

Addressing issues of global degradation of coral reefs requires monitoring programs to be conducted over large spatial (regions; 10s – 100s km) and temporal (decades) scales (Pearson 1981; Hughes et al. 1992; Hughes et al. 2010; Graham et al. 2011). Many large-scale monitoring programs of community structure have provided invaluable insights into condition of coral reefs and some underlying dynamics (Hughes 1994; Done et al. 1997; Bak et al. 2005; Done et al. 2007; Sweatman et al. 2011), particularly because they negate the distortion of data due to sliding baselines (Dayton et al. 2000; Pandolfi et al. 2005), or the assumptions of meta-analyses (Hughes et al. 2010; Graham et al. 2011; Sweatman et al. 2011). A considered approach to the inclusion of species (functional groups), external drivers (Fabricius 1997; Williams and Speare 2002) and methods of analysis (Fabricius and De'Ath 2004; De'ath and Fabricius 2010; Thompson and Dolman 2010) provide further insights into mechanisms underlying changes in community structure. This approach also enables the collection

of more detailed demographic data to be effectively stratified, given that logistics preclude all abundance data being supplemented with demographic data.

Mechanisms of change in community structure are more directly quantified through the collection of demographic data, including the abundances of life history stages for key groups of species (Bak and Meesters 1998; Gilmour 2004; McClanahan et al. 2008) and their demographic traits (Done 1987; Tanner et al. 1994; Hughes 1996; Fong and Glynn 1998; Fong and Glynn 2000; Connell et al. 2004; Edmunds 2007; Edmunds and Elahi 2007; Edmunds 2010). Inferences about demographic traits can be drawn from changes in stage-structures of corals, but this must be done cautiously because coral are clonal organisms with a high degree of plasticity and variability in life history traits (Hughes et al. 1992; Ebert et al. 1993). In particular, variation in the abundances of new recruits and juvenile size classes can provide valuable insights into the future structure and resilience of communities, given they reflect the sum of recruitment and early post-recruitment processes over several years. Indeed, inferences based on these stage-frequency data can be more reliable than directly quantifying larval supply (recruitment) with limited replication, given the considerable spatial and temporal variability inherent in this process (Wallace 1985; Harrison et al. 1990; Baird and Hughes 1996; Caley et al. 1996; Hughes et al. 1999; Guest 2004; Penin et al. 2010). Supplementing abundance and stage-frequency data with direct measurements of recruitment, growth and survival for key groups of species can then explain the mechanisms of change in community structure under different disturbance regimes and the likely implications in the future. Together, these data provide estimates of population growth, the contribution of different stages and their susceptibility, under a range of disturbance regimes (Ebert 1999; Caswell 2000). Inferences based on this suite of information can be investigated further through experimental manipulations to provide unequivocal links to external drivers, which may be required to justify mitigation.

The choice of additional methods to supplement data on community structure depends on logistic constraints and the aims of the monitoring programs, both of which are likely to change through time. However, the most useful insights into the current and future condition of coral reefs has consistently come from large-scale studies that collect complementary data that provides insights into mechanisms of change (Hughes 1996; Connell et al. 1997; Done et al. 2010), and/or those that address key hypotheses about these mechanisms by combining natural and manipulative approaches to experimental design (McClanahan 2000; McClanahan et al. 2001; Bellwood et al. 2006).

3.4.2 The resilience of Scott Reef communities

The Scott Reef system has extensive habitats for coral growth in both shallow- (< 20 m) and deeper-water (20 – 70m) (Cooper et al. 2010). Elevated water temperatures in 1998 caused widespread bleaching and mass-mortality of benthic organisms throughout the shallow-water habitat, reducing coral cover by between 60 and 90%, whereas visual surveys indicated little impact in the deeper-water habitat (Smith et al. 2008). Early recovery in the shallow habitat was slow, and as with other severe bleaching events, was driven by the re-growth of massive corals and other taxa at the least impacted locations. The mass-mortality of corals and the levels of stress and injury (partial-mortality) in the survivors (Michalek-Wagner and Willis 2001; Baird and Marshall 2002; Ward et al. 2002) dramatically reduced reproductive output across Scott Reef, with mean annual rates of recruitment five years after the bleaching <2% of those prior to the disturbance.

A strong stock-recruitment relationship existed for the reef-slope communities at Scott Reef for the duration of the study. There was no evidence of significant larval supply from deeper-water communities or from the nearest reefs systems, neither of which were affected by the bleaching. The lack of recruitment from deeper-water communities is a likely consequence of little overlap in community structures between the habitats. For deeper-water communities to contribute to the resilience of those in the shallows requires that they not only escape the disturbances and are separated by less than routine distances of dispersal, but also overlap in abundant species (Baker et

al. 2008; Bongaerts et al. 2010). An exception at Scott Reef is perhaps the ubiquitous brooding coral *Seriatopora hystrix*, for which there is evidence of genetic connectivity between the shallow- and deeper-habitats (van Oppen et al. 2011). The lack of larval supply from other reef systems in the region is also not surprising, given the isolation of Scott Reef. Routine distances of dispersal for spawning corals at Scott Reef were inferred at around ten kilometres, with little connectivity over ecological time scales to the closest reef system to the south (> 350 km), the Rowley Shoals (Gilmour et al. 2009; Underwood et al. 2009). Inferences from ocean models, the dispersal of drogues and larval competency periods also suggested little connectivity to the closest reef system to the north (> 200 km), Ashmore Reef. The strong stock recruitment relationship at Scott Reef supports this evidence of physical isolation.

The low rates of recruitment following the bleaching at Scott Reef mean that recovery relied heavily on the growth and survival of recruits. The rates of survival of new recruits (< 5 cm) and juveniles (5-15 cm) of *Acropora spicifera* were consistently > 85% yr⁻¹ during all survey years (2006-2010), and > 90% yr⁻¹ for the massive coral *Goniastrea sp.* (2008-2010) (data not included here). Cyclones, moderate bleaching and disease all had little impact on colonies of juvenile size (< 15 cm). Thus, in a recovery state, high post-recruitment survival of corals facilitated the resilience of communities following mass-bleaching at Scott Reef, whereas survival of these early life history stages is generally far lower on reefs experiencing chronic stressors (Bak and Engel 1979; Birrell et al. 2005). Low recruitment and post-recruitment survival is often a consequence of exclusion and competition within macro-algae, or other benthic organisms that can proliferate following mass-mortality of corals. At Scott Reef, suitable space remained for settlement and survival and there was no evidence of reduced recruitment or post-recruitment survival due to the proliferation of other organisms, a high density of corals (Baird and Hughes 2000; Fabricius and Metzner 2004), or secondary predation by fish (Penin et al. 2010). The reductions in survival of corals at Scott Reef during this recovery phase were driven primarily by acute disturbances with selective impacts.

The recovery of coral communities at Scott Reef twelve years after the mass-bleaching was slowed by occasional acute disturbances, but coral cover and recruitment continued to increase between consecutive surveys because the impacts from these disturbances were moderate and selective. The first of these was Category 5 Cyclone Fay in 2004, which caused only small decreases in coral cover at some locations, primarily because there was limited recovery from the bleaching and a low abundance of large corals with fragile growth forms. However, Cyclone Fay did slow recovery by killing or injuring many of the large colonies that were present. By comparison, the impacts from Category 3 Cyclone George in 2007 were less severe and more selective, and mostly restricted to large and fragile colonies at the worst affected locations. The impacts from the bleaching in 2010 were also restricted to a few locations and taxa, primarily the *Pocillopora* and *Fungia*. The Acroporidae were comparatively unaffected by this bleaching event, in contrast to that in 1998, and a similar variation in susceptibility was reported at other Indo-Pacific reefs (Krishnan et al. 2010; Normile 2010). The outbreak of white-syndrome disease in 2010 preceded the bleaching, and primarily impacted the table *Acropora* at one location. A drop in the number of large Acroporidae across Scott Reef was due to the subsequent mortality of table *Acropora*. Conditions at the worst affected location were typical of those that can trigger and sustain an outbreak of white-syndrome, including comparatively low water circulation and high turbidity, the re-suspension of sediments due to storm swell, periods of elevated water temperatures and a high density of susceptible species (Sutherland et al. 2004; Bruno et al. 2007; Harvell et al. 2007; Heron et al. 2010).

Rates of larval supply and the selective impacts of subsequent disturbances influenced variation in the recovery of coral communities at locations across Scott Reef following the mass-bleaching in 1998. However, good water quality and favourable environmental conditions ensured that suitable substrata remained available for corals to recolonise all communities and that they had high rates of growth and survival. Thus, after 12 years, the cover of hard corals, the abundance of genera and the structure of communities were again similar to that prior to the mass-bleaching that had so dramatically reduced coral cover and altered community structure.

3.4.3 The resilience of coral reefs and emerging regimes of disturbance

The regimes of disturbance to coral reefs have shifted in recent decades to include multiple chronic and acute disturbances, of increasing scale and severity, and reduced selectivity. Within these regimes, the specific disturbances are perhaps less important to the resilience of communities than the impact characteristics, particularly the degree to which impacts are chronic or acute, severe or selective, local or widespread (Baker et al. 2008; Graham et al. 2011). A background of chronic stress is often implicated in the degradation of coral reefs, particularly as the loss of herbivores and/or reductions in water quality. Under these conditions, further impacts can push communities past a tipping point and into a phase-shift (Wilkinson and Souter 2008; Diaz-Pulido et al. 2009). This prolonged shift to a degraded state often involves the proliferation of alternate taxa, usually macroalgae, that occupy available space following the mass-mortality of corals (Hughes 1994; Aronson and Precht 2001; Williams and Polunin 2001). To become dominant, macro-algae must previously have been common and conditions must favour its proliferation, which is often related to the initial chronic stressors of poor water quality and the reduced abundance of herbivores. Reductions in even key species of herbivores can therefore play critical roles in community dynamics following severe disturbances (Bellwood et al. 2006; Ledlie et al. 2007; Cheal et al. 2010). The cover of macroalgae then reduces recruitment and post-recruitment survival of corals and a negative feedback ensues (Bellwood et al. 2004)(Hoey and Bellwood 2011). Scott Reef currently lacks these chronic stressors, having oligotrophic water (Bird 2005) and a low cover of macroalgae (or alternate taxa) throughout the study period. Following the mass-mortality of corals, the available space was colonised by coralline and turfing algae, and there were comparative increases in abundance of herbivorous fishes, either as the migration of large herbivores from other habitats and/or population growth in smaller herbivores with rapid turnover. Consequently, suitable substrata remained available for colonisation by corals. In all instances, the persistence of suitable substrata and favourable habitat conditions are necessary for the recovery of communities following major disturbances, even if tempered by low rates of larval supply (Adjeroud et al. 2007), recruitment onto unconsolidated substrata (Lasagna et al. 2008; Morri et al. 2010), or subsequent disturbances (Graham et al. 2011).

In the absence of chronic stressors and the exclusion of suitable substrata, coral communities can be resilient to multiple acute disturbances. The worst acute disturbance is often temperature induced mass-bleaching (Baker et al. 2008; Graham et al. 2011), after which communities are typically exposed to less severe acute disturbances. At Scott Reef, these subsequent disturbances included two cyclones, an outbreak of disease and a second bleaching. Cyclones severely impacted communities at only some locations, with a degree of patchiness over small spatial scales within locations; mortality and injury were mostly restricted to large colonies or those with fragile growth forms. Similarly, the outbreak of disease and moderate bleaching were also highly selective, affecting a few locations and taxa. Consequently, mean coral cover and rates of recruitment at Scott Reef following the mass-bleaching continued to increase between each census interval. Among other drivers, the severity and selectivity of subsequent disturbances can play an important role in community recovery following mass-bleaching (Graham et al. 2011). The more selective these disturbances the more likely they are to impact a smaller proportion of taxa, life history stages and growth forms, to injure rather than kill colonies, and to have patchy impacts over smaller spatial scales. Reproductive output and larval supply are therefore less likely to be compromised by selective disturbances and resilience is less reliant on the supply of new recruits from distant locations. However, small increases in the frequency and severity of multiple disturbances can have large consequences for rates of community recovery. At Scott Reef, a more severe regime of disturbances following the mass-bleaching is likely to have shifted the period of community recovery and persistence in a degraded state by one or more decades, particularly given the lack of larval supply from outside.

Connectivity and larval supply have important implications for the recovery of communities through common regimes of disturbance. Given the isolation of Scott Reef, rates of recruitment following the bleaching remained low for several years and recovery to a pre-bleaching state after approximately 12 years relied on good post-recruitment survival. Under similar regimes of disturbance and environmental conditions, other isolated reefs are also likely to be resilient to severe bleaching events, albeit over a recovery period of years to decades. However, isolated reefs are certainly more susceptible to prolonged shifts to a degraded state following severe disturbance(s), particularly when degradation is assessed as a shift away from the pre-bleaching structure, rather than a phase-shift to an alternate state in which corals are not dominant. A return to a pre-bleaching structure requires the survival of all species in sufficient density to facilitate fertilisation (Knowlton and Jackson 2008) and recruitment, if few larvae are supplied from less impacted communities. If a mass-bleaching (or other disturbance) is so severe and widespread that it kills most colonies of the most susceptible species beyond routine distances of connectivity to unaffected communities, then recovery over ecological time is unlikely. A shift away from a pre-disturbance structure is also possible on isolated reefs following multiple disturbances of moderate severity and selectivity that impact the same groups of corals. Indeed, similar groups of corals are often most susceptible to common disturbances, such as bleaching, predation, disease and cyclone disturbance. At Scott Reef, similar families and genera were impacted by multiple disturbances, but with some variation among species; branching *Acropora*, *Isopora* and *Pocillopora* were most susceptible to the mass-bleaching (1998), groups with fragile growth forms (branching, table) were most susceptible to cyclone disturbances, the table *Acropora* were primarily affected by disease (2010) and the *Pocillopora* and *Fungia* were primarily affected by moderate bleaching (2010). A degree of selectivity in impacts among locations and taxa therefore enabled communities to return to their pre-bleaching structure, despite the Scott Reef system being self-seeded over ecological time. Coral communities on other isolated reefs have been less resilient to severe mass-bleaching or multiple acute disturbances, with a persistent shift in community structure for the duration of monitoring (Adjeroud et al. 2007).

3.5 Conclusions

A new regime of disturbances to coral reefs is increasingly causing shifts to a degraded state. In the worst instances, chronic stressors underlie a phase-shift to an ecosystem no longer characterised by moderate to high cover and diversity of hard corals. In the absence of chronic stressors and when suitable substrata remains for recolonisation, coral reefs may be resilient to even multiple acute disturbances of moderate severity and selectivity. However, more severe regimes of acute disturbance can also cause prolonged shifts to a degraded state, particularly when they impact the same groups of corals on isolated reefs. These shifts may be characterised by a reduction in coral cover and diversity, or a reduction in the most susceptible groups of corals that had previously been among the most abundant. The loss of species that are most susceptible can also have profound implications for ecosystem goods and services when they contribute most to the structural complexity of coral reefs, and in turn, the persistence of other iconic coral reef organisms (Pratchett et al. 2008). To maintain coral reefs in a desired state clearly requires that chronic stressors are minimised, reducing the likelihood of a phase-shift following additional disturbances. However, the synergistic effects of more frequent and severe acute disturbances beyond current levels are also likely to cause a prolonged shift to a degraded state, leaving insufficient periods of favourable conditions and community recovery. Local management initiatives can be effective in minimising chronic stressors, but reducing the frequency and severity of many common acute disturbances requires action over regional and global scales. Addressing these new regimes of disturbance requires united efforts spanning the smallest to largest spatial scales, among community, industry, managers, politicians and scientists. Priorities for scientists are to provide a considered and relatively united consensus about the current and future state of coral reef communities, mechanisms underlying their degradation, and definitive links to external drivers, which begins with a shift in scale and method in monitoring programs.

3.6 References

- Adjeroud M, Pratchett MS, Kospartov MC, Lejeune C, Penin L (2007) Small-scale variability in the size structure of scleractinian corals around Moorea, French Polynesia: patterns across depths and locations. *Hydrobiologia* 589: 117-126
- Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460: 25-38
- Baird AH, Guest JR, Willis BL (2009) Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology and Systematics* 40: 551-557
- Baird AH, Hughes TP (1996) Spatial variation in coral recruitment around Lizard Island. In: Lessios HA (ed) *Proceedings of the Eighth International Coral Reef Symposium*, pp 1207-1210
- Baird AH, Hughes TP (2000) Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understory assemblages. *Journal of Experimental Marine Biology and Ecology* 251: 117-132
- 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
- Bak RPM (1978) Lethal and sublethal effects of dredging on reef corals. *Marine Pollution Bulletin* 9: 14-16
- Bak RPM (1979) Growth and regeneration in the scleractinian reef coral *Acropora palmata*. *Proceedings of the Association of Island Marine Laboratories of the Caribbean.*, Mayaguez, pp 13
- Bak RPM, Engel MS (1979) Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life-history strategies in the parent coral community. *Marine Biology* 54: 341-352
- Bak RPM, Luckhurst BE (1980) Constancy and Change in Coral Reef Habitats Along Depth Gradients at Curacao. *Oecologia* 47: 145-155
- Bak RPM, Meesters EH (1998) Coral population structure: the hidden information of colony size-frequency distributions. *Marine Ecology Progress Series* 162: 301-306
- Bak RPM, Meesters EH (1999) Population structure as a response of coral communities to global change. *American Zoologist* 39: 56-65
- Bak RPM, Nieuwland G, Meesters EH (2005) Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. *Coral Reefs (Online First)* 24: 475-479
- Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science* 80: 435-471
- Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* 429: 827-833
- Bellwood DR, Hughes TP, Hoey AS (2006) Sleeping functional group drives coral-reef recovery. *Current Biology* 16: 2434-2439
- Bird J (2005) Modeling sub-reef thermodynamics to predict coral bleaching: A case study at Scott Reef WA. *Marine Science*, Townsville
- Birrell CL, McCook LJ, Willis BL (2005) Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin* 51: 408-414
- Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O (2010) Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs *Coral Reefs* 29: 309-327
- Bruno JF, Selig ER, Casey KS, Page CA, Willis BL, Harvell CD, Sweatman H, Melendy AM (2007) Thermal stress and coral cover as drivers of coral disease outbreaks. *Public Library of Science: Biology* 5

- 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 and Systematics* 27: 477-500
- Caswell H (1989) *Matrix population models: construction, analysis and interpretation*. Sinauer, Sunderland, Massachusetts
- Caswell H (2000) Prospective and retrospective perturbation analyses: Their roles in conservation biology. *Ecology* 81
- Cheal AJ, MacNeil MA, Cripps E, Emslie MJ, Jonker M, Schaffelke B, Sweatman H (2010) Coral-macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs* 29: 1005-1015
- Colgan MW (1981) Succession and recovery of a coral reef after predation by *Acanthaster planci* (L.) *Proceedings of the Fourth International Coral Reef Symposium*, pp 333-338
- Connell JH (1973) Population ecology of reef-building corals. In: Jones OA, Endean R (eds) *Biology and Geology of Coral Reefs*, pp 205-245
- Connell JH (1978) Diversity in tropical rainforests and coral reefs – High diversity of trees and corals is maintained only in a non-equilibrium state. *Science* 199: 1302-1310
- Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16 (Suppl): 101-113
- Connell JH, Hughes TP, Wallace CC (1997) Long-term dynamics of reef crest corals on Heron Island: 1960's to 1990's. *State of the Great Barrier Reef World Heritage Area Workshop*: 114-124
- Connell JH, Hughes TP, Wallace CC, Tanner JE, Harms KE, Kerr AM (2004) A Long-Term Study of Competition and Diversity of Corals. *Ecological Monographs* 74: 179-210
- Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organisation. *The American Naturalist* 111: 1119-1144
- Cooper TF, Ulstrup KE, et al (2010) Niche specialization of reef-building corals in the mesophotic zone: metabolic trade-offs between divergent *Symbiodinium* types. *Proceedings of the Royal Society B: Biological Sciences*
- Dayton PK, Sala E, Tegner MJ, Thrush S (2000) Marine reserves: Parks, baselines, and fishery enhancement. *Bulletin Of Marine Science* 66: 617-634
- Dayton PK, Tegner MJ, Edwards PB, Riser KL (1998) Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications* 8: 309-322
- De'ath G, Fabricius K (2010) Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. *Ecological Applications* 20: 840-850
- Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R, Roff G, Kline DI, Weeks S, Evans RD, Williamson DH, Hoegh-Guldberg O (2009) Doom and Boom on a Resilient Reef: Climate Change, Algal Overgrowth and Coral Recovery. *Plos one* 4: e5239
- Dodge RE, Vaisnys JR (1977) Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. *Journal of Marine Research* 35: 715-730
- Done TJ (1987) Simulation of the effects of *Acanthaster planci* on the population structure of massive corals in the genus *Porites*: Evidence of population resilience? *Coral Reefs* 6: 75-90
- Done TJ (1992a) Constancy and change in some Great Barrier Reef coral communities: 1980–1990. *American Zoologist* 32: 655-662
- Done TJ (1992b) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247: 121-132
- Done TJ (1999) Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. *American Zoologist* 39: 66
- Done TJ, DeVantier L, Turak E, McCook LJ, Fabricius K (1997) Decadal changes in community structure in Great Barrier Reef coral reefs. In: Wachenfeld D, Oliver JK, Davies K (eds) *State of the Great Barrier Reef World Heritage Area Workshop. Proceeding of a Technical Workshop*, Townsville
- Done TJ, DeVantier LM, Turak E, Fisk DA, Wakeford M, van Woesik R (2010) Coral growth on three reefs: development of recovery benchmarks using a space for time approach. *Coral Reefs Online* First 26 May 2010

- Done TJ, Turak E, Wakeford M, DeVantier L, McDonald A, Fisk D (2007) Decadal changes in turbid-water coral communities at Pandora Reef: loss of resilience or too soon to tell? *Coral Reefs* 26: 789-805
- Done TJ, Williams DM, Speare P, Turak E, Davidson J, De Vantier LM, Newman Sj, Hutchins (1994) Surveys of coral and fish communities at Scott Reef and Rowley Shoals
- Ebert TA (1999) Plant and Animal Populations. Methods in Demography. Academic Press, New York
- Ebert TA, Schroeter SC, Dixon JD (1993) Inferring demographic processes from size-frequency distributions: Effect of pulsed recruitment on simple models. *Fisheries Bulletin* 91: 237-243
- Edmunds PJ (2007) Evidence for a decadal-scale decline in the growth rates of juvenile scleractinian corals. *Marine Ecology-Progress Series* 341: 1-13
- Edmunds PJ (2010) Population biology of *Porites astreoides* and *Diploria strigosa* on a shallow Caribbean reef. *Marine Ecology Progress Series* 418: 87-104
- Edmunds PJ, Elahi R (2007) The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastraea annularis*. *Ecological Monographs* 77: 3-18
- Fabricius KE (1997) Soft coral abundance on the central Great Barrier Reef: Effects of *Acanthaster planci*, space availability, and aspects of the physical environment. *Coral Reefs* 16: 159-167
- Fabricius KE, De'Ath G (2004) Identifying ecological change and its causes: A case study on coral reefs. *Ecological Applications* 14: 1448-1465
- Fabricius KE, Metzner J (2004) Scleractinian walls of mouths; Predation on coral larvae by corals. *Coral Reefs* 23 245-248
- Fong P, Glynn PW (1998) A dynamic size-structured population model: Does disturbance control size structure of a population of the massive coral *Gardineroseris planulata* in the eastern Pacific? *Marine Biology* 130: 663-674
- Fong P, Glynn PW (2000) A regional model to predict coral population dynamics in response to El Nino-Southern Oscillation. *Ecological Applications* 10: 842-854
- Gilmour J, Gates EN, McKinney DW (2009) Biannual coral spawning off north-western Australia. *Coral Reefs*
- Gilmour JP (2004) Size-structures of populations of the mushroom coral *Fungia fungites*: the role of disturbance. *Coral Reefs* 23: 493-504
- Glynn PW (1976) Some physical and biological determinants of coral community structure in Eastern Pacific. *Ecological Monographs* 46: 431-456
- Graham N, Nash K, Kool J (2011) Coral reef recovery dynamics in a changing world. *Coral Reefs*: 1-12
- 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, pp 439-452
- Guest JR (2004) Reproductive patterns of Scleractinian corals on Singapore's reefs. PhD. Department of Biological Sciences, National University of Singapore
- Harrison P, Wallace C, Dubinsky Z (1990) Reproduction, dispersal, and recruitment of scleractinian corals *Ecosystems of the World: Coral Reefs*. Elsevier Publishers New York
- Harvell D, Jordan-Dahlgren E, Merkel S, Rosenberg E, Raymundo L, Smith G, Weil E, Willis B, Global Environm Facility C (2007) Coral disease, environmental drivers, and the balance between coral and microbial associates. *Oceanography* 20: 172-195
- Heron SF, Willis BL, Skirving WJ, Eakin CM, Page CA, Miller IR (2010) Summer hot snaps and winter conditions: Modelling white syndrome outbreaks on Great Barrier Reef corals. *PLoS ONE* 5: 1-11
- Heyward AJ, Halford A, Smith L, Williams D (1997) Coral reefs of North West Australia: Baseline monitoring of an oceanic reef ecosystem. 8th International Coral Reef Symposium, Panama, pp 289-294
- Hoegh-Guldberg O, Bruno JF (2010) The Impact of Climate Change on the World's Marine Ecosystems. *Science* 328: 1523-1528
- Hoey AS, Bellwood DR (2011) Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecology Letters* 14: 267-273
- Hughes TP (1988) Long-term dynamics of coral populations: Contrasting reproductive modes *Proceedings of the Sixth International Coral Reef Symposium*, pp 721-725

- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551
- Hughes TP (1996) Demographic approaches to community dynamics: A coral reef example. *Ecology* 77: 2256-2260
- Hughes TP, Ayre D, Connell JH (1992) The evolutionary ecology of corals. *Trends in Ecology and Evolution* 7: 292-295
- Hughes TP, Baird AH, Dinsdale EA, Molschaniwskij NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397: 59-63
- Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution* 25: 633-642
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Molschaniwskij N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* 17: 360-365
- Jackson JBC (1997) Reefs since Columbus. *Coral Reefs* 16: S23-S32
- Jackson JBC, Buss LW, Cook RE (1985) Population biology and evolution of clonal organisms. Yale University Press New Haven, Connecticut, USA
- Knowlton N (1992) Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist*: 674-682
- Knowlton N, Jackson JBC (2008) Shifting baselines, local impacts, and global change on coral reefs. *PLoS Biology* 6: 215-220
- Krishnan P, Roy SD, George G, Srivastava RC, Anand A, Murugesan S, Kaliyamoorthy M, Vikas N, Soundararajan R (2010) Elevated sea surface temperature during May 2010 induces mass bleaching of corals in the Andaman. *Current Science* 100: 111-117
- Lang J (1973) Interspecific Aggression by Scleractinian Corals. 2. Why the race is not only to the swift. *Bulletin of Marine Science* 23: 260-277
- Lasagna R, Albertelli G, Giovannetti E, Grondona M, Milani A, Morri C, Bianchi CN (2008) Status of Maldivian reefs eight years after the 1998 coral mass mortality. *Chemistry and Ecology* 24: 67-72
- Ledlie MH, Graham NAJ, Bythell JC, Wilson SK, Jennings S, Polunin NVC, Hardcastle J (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs* 26: 641-653
- Loya Y (1976) Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. *Ecology* 57: 278-289
- McClanahan TR (2000) Recovery of a coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. *Biological Conservation* 94: 191-198
- McClanahan TR, Ateweberhan M, Omukoto J (2008) Long-term changes in coral colony size distributions on Kenyan reefs under different management regimes and across the 1998 bleaching event. *Marine Biology* 153: 755-768
- 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
- Michalek-Wagner K, Willis BL (2001) Impacts of bleaching on the soft coral *Lobophytum compactum*. I. Fecundity, fertilization and offspring viability. *Coral Reefs* 19: 231-239
- Morri C, Aliani S, Bianchi CN (2010) Reef status in the Rasfari region (North Male Atoll, Maldives) five years before the mass mortality event of 1998. *Estuarine Coastal and Shelf Science* 86: 258-264
- Mumby PJ (2009) Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* 28: 761-773
- Mumby PJ, Hastings A, Edwards HJ (2007) Thresholds and the resilience of Caribbean coral reefs. *Nature* 450: 98-101
- Normile D (2010) Hard summer for corals kindles fears for survival of reefs. *Science* 329: 1001
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke R, McArdle D, McClanahan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003a) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301: 955-958

- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003b) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301: 955-958
- Pandolfi JM, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden JC, Possingham HP, Sala E (2005) *Ecology* - Are US coral reefs on the slippery slope to slime? *Science* 307: 1725-1726
- Pearson RG (1981) Recovery and Recolonization of Coral Reefs. *Marine Ecology Progress Series* 4: 105
- Penin L, Michonneau F, Baird AH, Connolly SR, Pratchett MS, Kayal M, Adjeroud M (2010) Early post-settlement mortality and the structure of coral assemblages. *Marine Ecology-Progress Series* 408: 55-U76
- Pickett STA, White PS (1985) *The ecology of natural disturbance and patch dynamics*. Academic Press, New York
- Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR (2008) Effects of climate-induced coral bleaching on coral-reef fishes - Ecological and economic consequences. *Oceanography And Marine Biology: An Annual Review* 46: 251-296
- Randall RH, Eldredge LG (1977) Effects of Typhoon Pamela on the Coral Reefs of Guam Proceedings of the Third International Coral Reef Symposium, pp 525
- Smith LD, Gilmour JP, Heyward AJ (2008) Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. *Coral Reefs* 27: 197-205
- Smith SV, Kimmerer WJ, Laws EA, Brock RE, Walsh TW (1981) Kaneohe bay sewage Hawaii USA diversion experiment perspectives on ecosystem responses to nutritional perturbation. *Pacific Science* 35: 279-395
- Stephenson TA (1930) Growth and asexual reproduction in corals
- Sutherland KP, Porter JW, Torres C (2004) Disease and immunity in Caribbean and Indo-Pacific zooxanthellate corals. *Marine Ecology Progress Series* 266: 273-302
- Sweatman H, Delean S, Syms C (2011) Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends. *Coral Reefs* 30: 521-531
- Tanner JE, Hughes TP, Connell JH (1994) Species coexistence, keystone species, and succession: A sensitivity analysis. *Ecology* 75: 2204-2219
- Thompson A, Dolman A (2010) Coral bleaching: one disturbance too many for near-shore reefs of the Great Barrier Reef. *Coral Reefs* 29: 637-648
- Underwood JN, Smith LD, van Oppen MJH, Gilmour JP (2009) Ecologically relevant dispersal of a brooding and a broadcast spawning coral at isolated reefs: implications for managing community resilience. *Ecological Applications* 19: 18-29
- van Oppen MJH, Bongaerts P, Underwood JN, Peplow LM, Cooper TF (2011) The role of deep reefs in shallow reef recovery: an assessment of vertical connectivity in a brooding coral from west and east Australia. *Molecular Ecology* 20: 1647-1660
- Wallace CC (1985) Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. *Marine Biology* 88: 217-233
- Ward S, Harrison P, Hoegh-Guldberg O (2002) Coral bleaching reduces reproduction of scleractinian corals and increases susceptibility to future stress. 9th International Coral Reef Symposium, Bali, pp 1123-1128
- Wilkinson CR, Souter D (2008) Status of Caribbean coral reefs after bleaching and hurricanes in 2005. *Global Coral Reef Monitoring Network*
- Williams DM, Speare PJ (2002) Long-term (17 y.) impacts of crown-of-thorns outbreak and loss of live coral cover on reef fish communities (Central Great Barrier Reef) 9th International Coral Reef Symposium, Bali, Indonesia
- Williams GC (1975) *Sex and evolution*. Princeton Univ Pr, Princeton
- Williams ID, Polunin NVC (2001) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* 19: 358-366

- Wilson SK, Burgess SC, Cheal AJ, Emslie M, Fisher R, Miller I, Polunin NVC, Sweatman HPA (2008) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology* 77: 220-228
- Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe VJ, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides EM (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* 214: 749-755

4. Long-term monitoring of coral communities

4.1 Summary

Recovery of coral communities from the mass-bleaching in 1998 varied according to the severity of the bleaching impact, their exposure to less severe and more localised disturbances, and routine habitat conditions. However, communities responded in predictable way to these conditions, following patterns of community succession through periods of recovery. Among the communities, the recovery of soft corals and *Isopora* varied most among locations; the cover of soft coral remains at less than half pre-bleaching levels at most communities and there has been negligible recovery of *Isopora* at some communities. In contrast, groups such as the massive *Porites*, encrusting corals and Faviidae characterised most communities through most periods, especially following the bleaching. Other groups such as the *Isopora* or branching and tabulate *Acropora*, which rapidly increased to high cover in some communities, made significant contributions to community structure during only one or two periods. Thus, despite being periodically conspicuous, these fast growing but susceptible corals contributed little to the underlying structure of communities through a decade of repeated disturbances. Nonetheless, in the absence of local disturbances these groups drove the successional patterns of change from a high relative abundance of massive and encrusting corals, to corymbose *Acropora* and Pocilloporidae, to table *Acropora*, and in some communities, branching *Isopora* and *Acropora*. Behind these more conspicuous successional patterns were more consistent but small increases in the cover of groups such as the Faviidae and soft corals.

4.2 Introduction

Coral reefs are dynamic ecosystems that have adapted to variation in habitat conditions and exposure to disturbances over a variety of spatial and temporal scales. The influence of routine habitat conditions on the distribution and structure of coral communities has been widely documented. In addition to these background conditions, coral communities are structured by periodic acute disturbances of varying severity. Acute disturbances (e.g. cyclones, bleaching crown-of-thorns outbreaks etc) occur with a period of roughly a decade, with corresponding cycles of recovery for communities. Of these disturbances, tropical cyclones are among the most important drivers of change (Connell 1978; Hughes 1989; Bythell et al. 2000). Cyclones tend to have highly localised and selective impacts that influence species diversity and structural complexity of reefs (Connell 1978; Karlson and Hurd 1993; Jones and Syms 1998). More recently, other disturbances are also structuring coral communities, with elevated water temperatures and coral bleaching having greater impacts. With increased global warming, coral reefs have been exposed to disturbances that are more frequent, severe and widespread (Hoegh-Guldberg et al. 2007). In particular, reefs are now exposed to coral bleaching and outbreaks of disease that can impact communities over broad spatial scales. Predictions of an increased frequency and severity of disturbances (Hoegh-Guldberg 2004) have led to concerns about the resilience of coral reef communities to this increased disturbance regime.

Assessing the resilience of coral communities to changing regimes of disturbance requires long-term data over large spatial scales. Communities that return to previous levels of coral cover within years to decades after impact may be considered as being 'resilient' (Smith et al. 2008; Done et al. 2010). However, return to a prior percentage of cover alone is a low criterion for recovery. Of greater relevance to the restoration of reef-building capacity and biodiversity of coral-associated reef species is the rate and degree to which the structure of coral communities is restored (Done 1992; Ninio and Meekan 2002). In this study, we monitor spatial and temporal changes in the structure of coral communities over 17 years, through regimes of disturbance of varying scale and severity, and assess the extent to which communities return to their pre-disturbance states through time.

4.3 Methods

4.3.1 Scott Reef and study locations

Scott Reef is a large atoll-like reef system on the edge of the continental shelf, 270 km from the mainland off north-western Australia (Figure 4.1). The system consists of South, North and Seringapatam Reefs. Surveys of biological communities and their habitat conditions were conducted at locations throughout the reef-slope (9 m) habitat. Three outer-slope locations were exposed to oceanic conditions on the eastern side of South (SL1), North (SS2) and Seringapatam Reefs (SS3). Additionally, four inner-slope locations were adjacent to the West Hook (SL1), South Lagoon (SL2), East Hook (SL3) and the Deep Channel (SL4) between North and South Reefs.

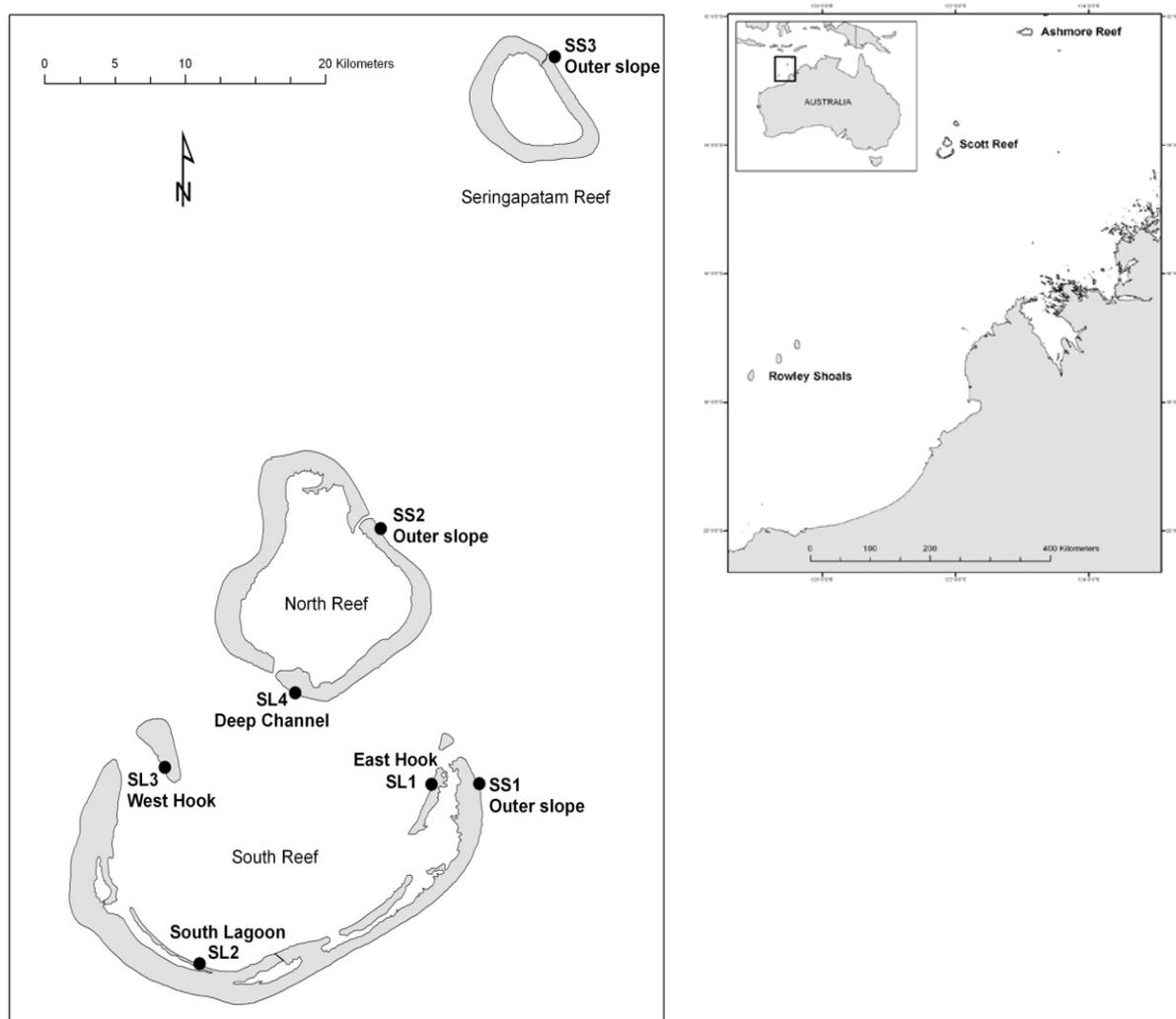


Figure 4.1 Position of Scott Reef off north-western Australia and its study locations. Locations are on the outer- (SS1, SS2, SS3) and inner-slope, with further distinction among inner-slope locations according to their proximity to East Hook (SL1), the Southern Lagoon (SL2), the West Hook (SL3) and the Deep Channel (SL4).

4.3.2 Environmental data: routine conditions

Differences in environmental conditions among locations were quantified by summarising variation in physical parameters that were predicted to have the greatest influence on biological communities. Temperature and sedimentation rates were measured at all reef-slope locations. At the inner-slope locations (SL1, SL2, SL3, SL4), current speed, wave height, chlorophyll and turbidity were measured (Table 4.1); insufficient data were available for Seringapatam (SS3). For each parameter, data were summarised in ways to best explain the most relevant variation among locations (Table 4.1). The contribution of parameter statistics to variation among locations was explored using Principal Components Analysis (PCA) of normalised data in the software PRIMER. Parameter statistics that explained a low proportion of the variation among locations, and those that were highly correlated ($r > 0.9$) with another parameter that better explained variation, were excluded and the analyses repeated.

The influence of habitat conditions on the structure of benthic communities was explored through BEST analysis in PRIMER. The contribution of physical parameters to the variation in the structure of coral communities was quantified for the parameters measured at all locations, and at the inner-slope locations.

4.3.3. Environmental data: acute disturbances

The history of exposure of coral communities at Scott Reef to the most frequent acute disturbances was investigated for cyclones and bleaching events. Variation in the spatial and temporal impact of acute disturbances on coral communities across Scott Reef during the monitoring period was Investigated for 1) mass-bleaching in 1998, 2) Category 5 Cyclone Fay in 2004, 3) Category 3 Cyclone George in 2007, and 4) a moderate outbreak of disease and bleaching in 2009-10. Periods (2 to 4 years) of impact and recovery occurred around these acute disturbances and dictated the grouping of years when investigating community structures.

Table 4.1 Parameters used to characterise routine habitat conditions at locations across Scott Reef. Six parameters were quantified at all but one (SS3) location and an additional 9 parameters at the inner-slope locations (SL1, SL2, SL3, SL4). All data are for the long-term monitoring locations (9 m), unless stated. Summary statistics were produced for each parameter, and a reduced number used in the final analysis after removing statistics that explained a low proportion of the variation among locations, and those that were highly correlated ($r > 0.9$) with another parameter that better explained variation.

	Parameter	Initial estimate	Revision of parameters	Final estimate
All locations	Temperature (July 06 to May 10)	Mean daily temperature ($^{\circ}\text{C}$)	Excluded. Correlated with range in temperature but with lower contribution to variation.	
		Mean range in daily temperature ($^{\circ}\text{C}$)	Summarised as seasonal categories. Excluded winter seasonal temperature ranges which were correlated with summer but with lower contribution to variation.	Summer range in daily temperature ($^{\circ}\text{C}$)
	Sedimentation (May 08 to April 09)	Mean daily weight of sedimentation ($\text{mg cm}^{-2} \text{day}^{-1}$)	Divided between summer and winter months.	Mean daily weight of sedimentation in summer and in winter ($\text{mg cm}^{-2} \text{day}^{-1}$)
		Mean sediment particle size (μm)	Excluded. Correlated with percentage sediment sizes but with lower contribution to variance.	
		Percentage composition of sediment particle sizes, for nine size classes ranging from clay to coarse sand (μm)	Divided between summer and winter months. Correlated size classes combined.	Mean percentage of silt and clay ($<63\mu\text{m}$), sand ($63\text{-}500\mu\text{m}$) and coarse sand ($>500\mu\text{m}$) in summer and winter months
Cover of sand (Oct 94 to Oct 10)	Cover of sand on substrata (%)	Averaged over all years.	Mean cover of sand (%)	
Inner-slope locations (SL1, SL2, SL3, SL4)	Current speed (Nov to May 08)	Mean current speed (ms^{-1})	Excluded. Correlated with maximum current speed but with lower contribution to variance.	
		Maximum current speed (ms^{-1})		Maximum current speed (ms^{-1})
		Range in current speed (ms^{-1})	Excluded. Correlated with maximum current speed but with lower contribution to variance.	
	Wave height (Nov to May 08)	Mean wave height (m)	Excluded. Correlated with maximum wave height but with lower contribution to variance.	
		Maximum wave height (m)	Excluded. Correlated with maximum current speed but with lower contribution to variance.	Maximum wave height (m)
	Fluorescence (Mar 08 to Feb 09)	Mean chlorophyll concentration (mg/m^3) at substrata adjacent to sites (25 m to 36 m depth)	Divided between summer and winter months.	Mean chlorophyll concentration (mg/m^3) in summer and winter months
	Salinity (Mar 08 to Feb 09)	Mean salinity (PSU) at substrata adjacent to sites (25 m to 36 m depth)	Excluded. Low contribution to variance.	
Range in mean salinity (PSU) at substrata adjacent to sites (25 m to 36 m depth)		Excluded. Low contribution to variance.		
Turbidity (Mar 08 to Feb 09)	Mean turbidity (NTU) at substrata adjacent to sites (25m to 36m depth)	Divided between summer and winter months.	Mean turbidity (NTU) in summer and winter months	

4.3.4 Benthic communities

At each of the seven study locations were three sites separated by approximately 300 m. (Figure 4.1) At each site there were 5 permanent 50 m transects, surveyed annually between 1994 and 1999, and then in 2003, 2004, 2005 and 2008. During each survey, a tape was laid along the permanent transect and a video or camera used to capture an image of the benthic community at a distance of approximately 30 cm from the substrata. Images were analysed using point sampling technique (Christie et al. 1996) and benthic groups identified to the lowest taxonomic resolution achievable by each observer.

4.3.5 Benthic groups

The most meaningful insights into the impacts of disturbances and the resilience of communities were obtained when the structure of coral communities was divided among benthic groups according to taxonomy (i.e. family, genus, species), reproductive mode (brooders, spawners) and growth form (encrusting, massive, corymbose, foliose, tabulate, branching). A total of 52 genera of hard coral were recorded at Scott Reef, but the 9 most abundant genera accounted for 97% percent of total hard coral cover. In instances where genera were low in cover or difficult to distinguish, they were grouped to the family level. Alternately, genera were grouped according to growth forms that strongly influenced their response to disturbances. Growth form was also used to further distinguish the three most abundant genera (*Isopora*, *Acropora*, and *Porites*). Finally, benthic groups were included in the analyses only if their cover was > 3% at any one location or time (Table 4.2).

All comparisons of community structure were investigated through multivariate analyses using the various procedures in the software PRIMER. Percentage cover of each benthic group, at each site, location and year were square-root transformed to reduce the influence of dominant groups (e.g. turf and coralline algae) but to retain the major differences in community structure due to relative abundance. Specific comparisons among communities in space or time were investigated by calculating Bray-Curtis measures of dissimilarity. To reduce the number of separate sites and years, cluster analysis was used to produce a dendrogram of spatial and temporal variation in community structure. The SIMPROF procedure was used to determine the scale at which spatial (sites) and temporal (years) replicates differed significantly from each other, with non-significant groups combined and averaged for further analyses. Differences in community structure were illustrated using two-dimensional plots of non-metric multidimensional scaling (nMDS). Benthic groups that characterised communities within periods, or distinguished communities between periods, were investigated using the SIMPER procedure. Whether groups characterised or distinguished communities was based on 1) their percentage contribution to dissimilarity among communities within a period, or between periods within a community, 2) whether they were consistently represented within a group ($S_i/SD [S_i]$), and 3) their changes in percentage cover.

Table 4.2 Benthic groups used to describe changes in structure of coral communities at locations across Scott Reef. Most groups were common at most communities during one or more periods, with the exception of groups that characterised the unique community at South Lagoon (SL2)

Benthic group	Further description
Non-coral	
Turf and coralline algae	
<i>Millepora</i>	
Soft coral	
Soft Coral	Mostly <i>Sinularia</i> (43%), <i>Lobophytum</i> (25%), <i>Sarcophyton</i> (15%).
Hard coral	
<i>Acropora</i> branching	
<i>Acropora</i> hispidose	Characteristic of the South Lagoon community only.
<i>Acropora</i> tabulate	<i>Acropora</i> table and plate
<i>Acropora</i> corymbose	Corymbose and digitate <i>Acropora</i>
Encrusting coral	Mostly (>80%) <i>Montipora</i>
Faviidae	Massive and encrusting Faviidae
Foliose coral	Mostly (>50%) <i>Echinopora</i> . Most characteristic of the South Lagoon community.
Fungiidae	Characteristic of the South Lagoon community only.
<i>Isopora</i>	<i>I. brueggemanni</i> (68%) and <i>I. palifera</i> (32%)
Pocilloporidae	
<i>Porites</i> branching	
<i>Porites</i> massive	

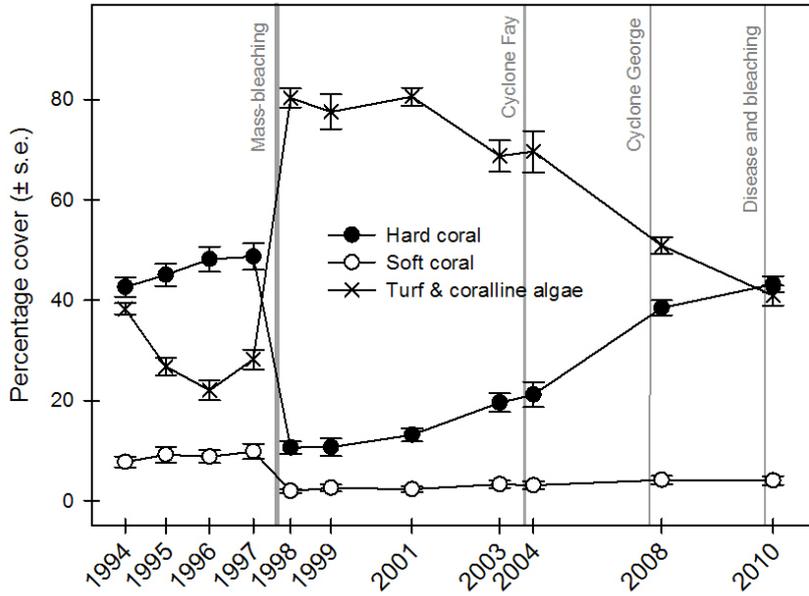
4.4 Results.

4.4.1 Coral cover at Scott Reef

The coral communities at Scott Reef were broadly characterised by an abundance of hard corals, soft corals and substrata covered by coralline and turfing algae. However, the cover of these benthic groups and the relative abundance of their constituent species changed dramatically through the monitoring period (1994 to 2010) due to patterns of impact and recovery from five disturbances. Of these disturbances, by far the most severe were elevated water temperatures in 1998 that caused mass bleaching and mortality of benthic organisms across all shallow-water (<20 m) communities. Mass-bleaching caused a relative decrease in coral cover of approximately 80%, from 46 to 10% for hard corals, and 9 to 2% for soft corals (Figure 4.2a). Most of the hard corals were affected by the mass-bleaching and their number of genera was reduced by 45% (Figure 4.2b). The available substrata was subsequently colonised by coralline and turfing algae, which increased in absolute cover from 28 to 80% (Figure 4.2a).

Following the mass-bleaching, coral communities were then exposed to two cyclones in 2004 and 2007 and a moderate outbreak of disease and bleaching (2010). Despite this regime of disturbances, the cover (43%) of hard corals and their number of genera in 2010 were again similar to that prior to mass-bleaching, but the soft corals (4%) had returned to only approximately half their pre-bleaching cover (Figure 4.2). Although the mean cover and number of genera of hard corals in 2010 was again similar to that prior to the bleaching, there were clear differences in recovery trajectories among communities at locations across Scott Reef. Underlying this variability in impact and recovery were the routine habitat conditions at locations, their exposure to acute disturbances and the relative abundance of susceptible species.

a)



b)

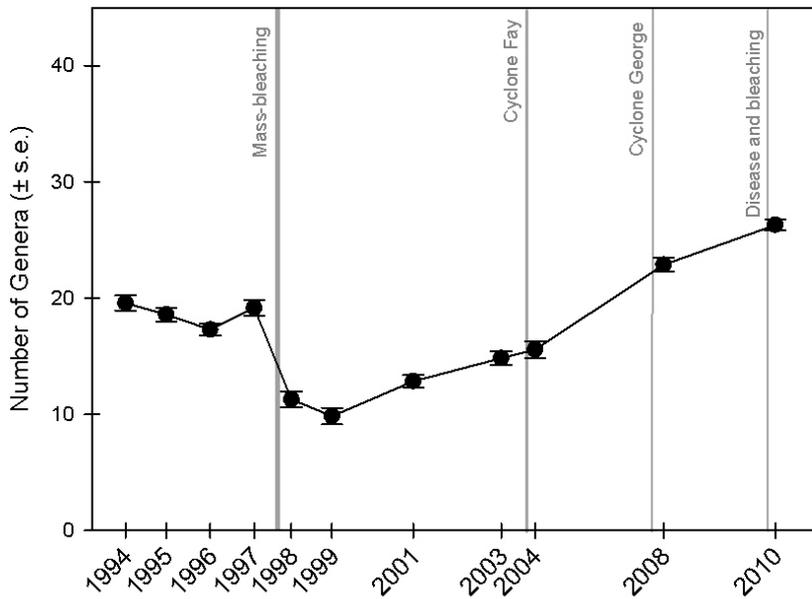


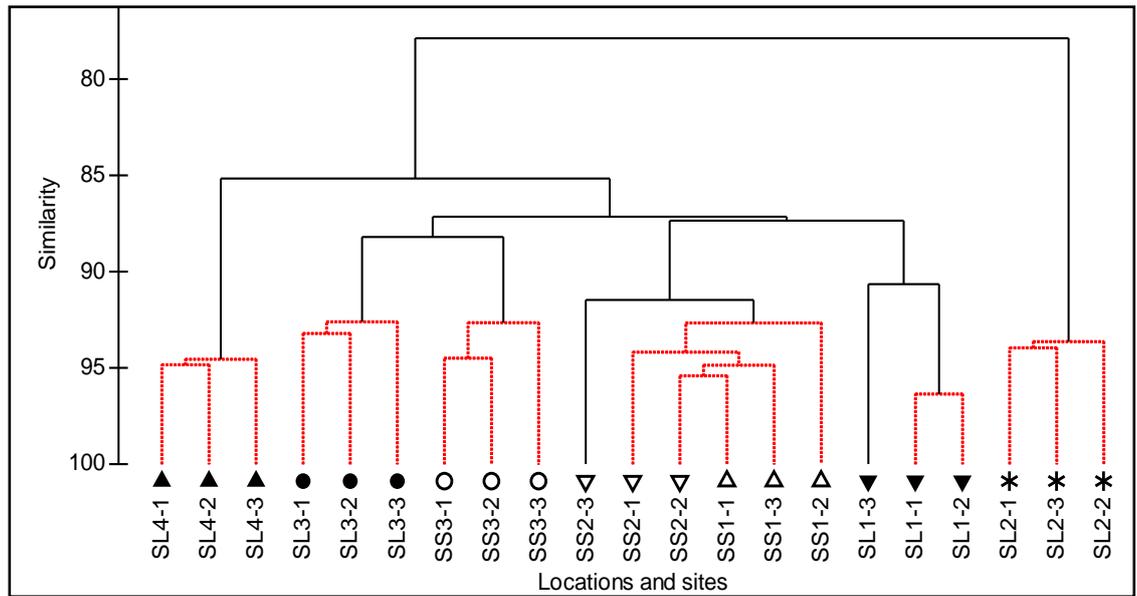
Figure 4.2 Broad indicators of impact and recovery of coral communities at Scott Reef. Changes in a) the mean percentage cover of hard corals, soft corals and turf and coralline algae, and b) the mean number genera of hard corals. Mass-bleaching (1998) was by far the most severe disturbance, but was followed by Category 5 Cyclone Fay (2004), Category 3 Cyclone George (2007), and a moderate bleaching and outbreak of disease (2010).

4.4.2 Spatial and temporal variation in community structure

Across Scott Reef over the entire monitoring period, changes in community structure clearly varied among locations separated by several kilometres, but not among sites separated by < 2km; the exception being most sites at the outer-slope communities at North (SS1) and South (SS2) Reef (Figure 4.3). Thus, changes in communities are discussed at the scale of locations, rather than individual sites within locations.

Among the survey years over all monitoring locations, changes in community structure clearly grouped according to their exposure to, and recovery from, various disturbances (Figure 4.4). For example, there was comparatively little variation in community structure among the years within the pre-bleaching (1994 to 1997) and bleached (1998-2001) periods. Consequently, changes in communities through time are usually discussed in terms of periods, rather than individual survey years. Periods generally span a similar number (2 - 4) of years and are distinguished by the disturbance within each, although recovery towards a pre-bleaching community structure was also a feature of most periods. The periods were: pre-bleaching (1994-1997), bleaching (1998-2001), Cyclone Fay (2002-2004), Cyclone George (2005-2008) and disease and bleaching (2009-2010).

a)



b)

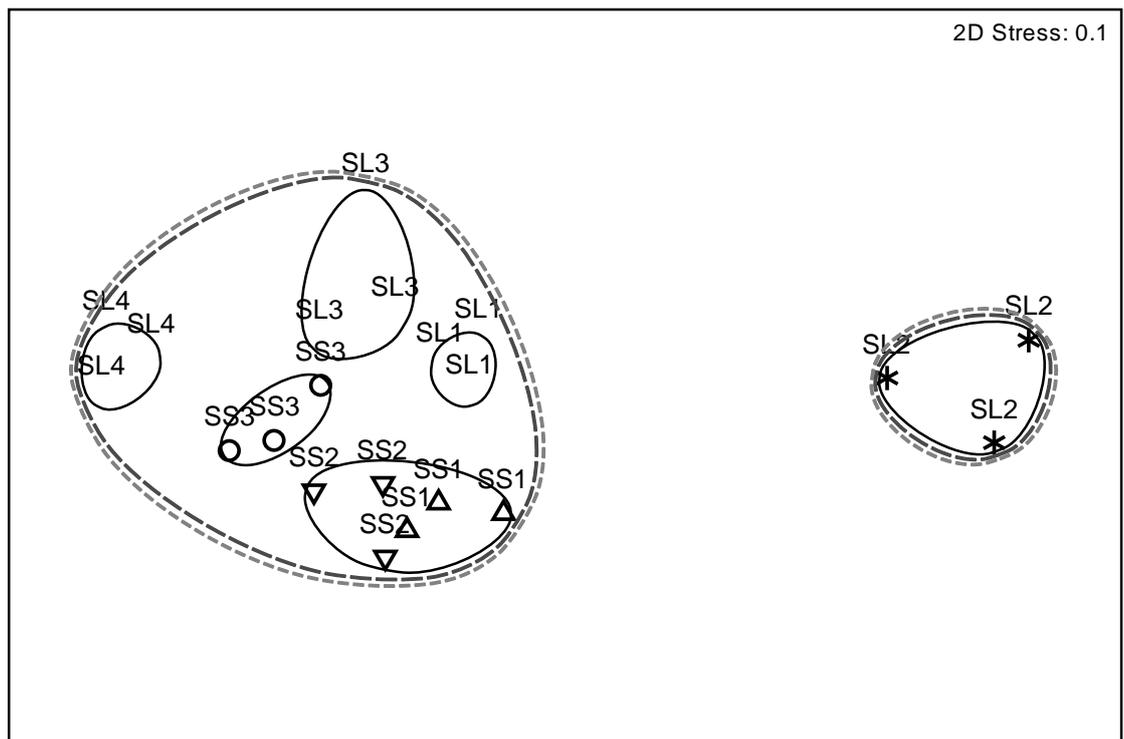


Figure 4.3. Spatial variation in community dynamics. a) dendrogram and b) MDS with superimposed clusters from dendrogram, highlighting significant variation in community structure among most locations separated by several kilometres, but not among most sites within locations (red lines) separated by < 2 km. Clusters on MDS represent similarity measures at 80% light grey dashed line, at 85% dark grey dashed line and at 90% solid black line. Study locations are illustrated in Figure 4.1.

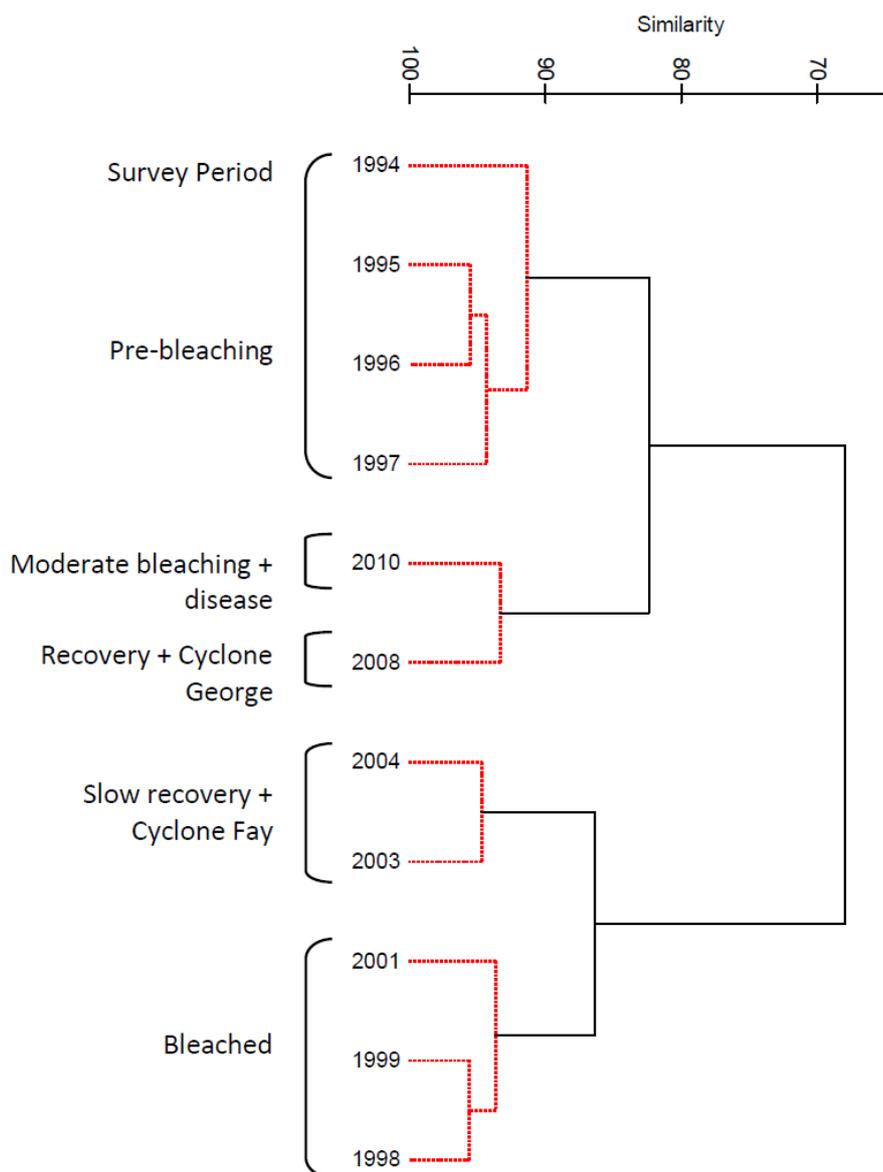


Figure 4.4 Temporal variation in community dynamics. Dendrogram highlighting significant variation in community structure at Scott Reef among, but not within (red lines), years grouped by periods. The years 2008 and 2010 were treated as separate periods to better consider the impact of their respective disturbances and the structure of communities at the final survey (2010).

4.4.3 Variation in habitat conditions among locations across Scott Reef

4.4.3.1 Routine habitat conditions

Variation in habitat conditions reflected the geographic position of locations on the reef (Figure 4.1), with primary differences between the exposed outer-slopes locations (SS1, SS2, SS3) and the inner-slope locations near the sheltered lagoon at South Reef (SL1, SL2, SL3, SL4). Similar pattern of variation in habitat conditions were evident for the conditions quantified at all locations and the

additional parameters quantified only at the inner-slope locations (Figure 4.5). Much of the variation among locations was explained by their contrasting regimes of sedimentation, cover of sediment on the substrata and range in water temperatures. Of the additional parameters, turbidity, chlorophyll concentrations, and maximum current speeds and wave heights in summer also differentiated the inner-slope locations (Table 4.3, Figure 4.5).

Habitat conditions were similar between the outer-slope locations on the eastern side of South Reef (SS1) and North Reef (SS2). These locations were exposed to the open ocean and characterised by a steep sloping substrata with a low cover of sand. Qualitative observations indicate they experienced moderate current speeds and wave heights, except when exposed to storm swell. Consequently, they had moderate rates of sediment deposition across a range of particle sizes that were likely to have increased periodically during storm swell. These outer-slope locations experienced moderate temperature regimes, but with occasional increases in temperature range at SS2, and probably SS3, following the flow of warm water out of the lagoon and over the reef flat in summer.

By comparison, there was greater variability in habitat conditions among the inner-slope locations that was driven by their proximity to the sheltered lagoon in South Reef and the deep channel between North and South Reef (Figure 4.1). Conditions at the East Hook (SL1) fell between those at the inner- and outer-slope locations (Figure 4.5). The East Hook location was relatively sheltered and was characterised by a moderately sloping substrata and cover of sand. Maximum current speeds and wave heights in summer were moderate for the inner-slope locations, as were the levels of turbidity and sediment deposition across a range of particle sizes. Chlorophyll concentrations were low and there was a moderate range of water temperatures.

Among the remaining locations, the West Hook (SL3) and Deep Channel (SL4) were most similar to East Hook (SL1). The West Hook (SL3) location was most exposed to storm swell from the north-west, and had a relatively flat substrata and a high cover of sand with patchy coral outcrops. By comparison, the Deep Channel (SL4) location was less exposed to storm swell, and had a high cover of sand on a steep slope. Both locations had high maximum current speeds and wave heights in summer, compared with the other inner-slope locations. Given this energy regime, there was relatively high sediment deposition of larger particle sizes (sand, coarse sand), and low levels of turbidity and chlorophyll concentrations. In addition, the West Hook and Deep Channel locations were distinguished by a large temperature range due to the flow of warm water out of north lagoon and cool water from around the deep channel (Figure 4.6).

Of all the locations across the Scott Reef system, the most distinct habitat conditions were at the South Lagoon (SL2). This was the most sheltered of all locations, characterised by a fragile and moderately sloping substrata with a low cover of sand. It had the lowest maximum current speeds and wave heights in summer, resulting in a relatively low deposition of fine particle sizes (silt, clay), comparatively high turbidity and chlorophyll concentrations, and a moderate temperature regime.

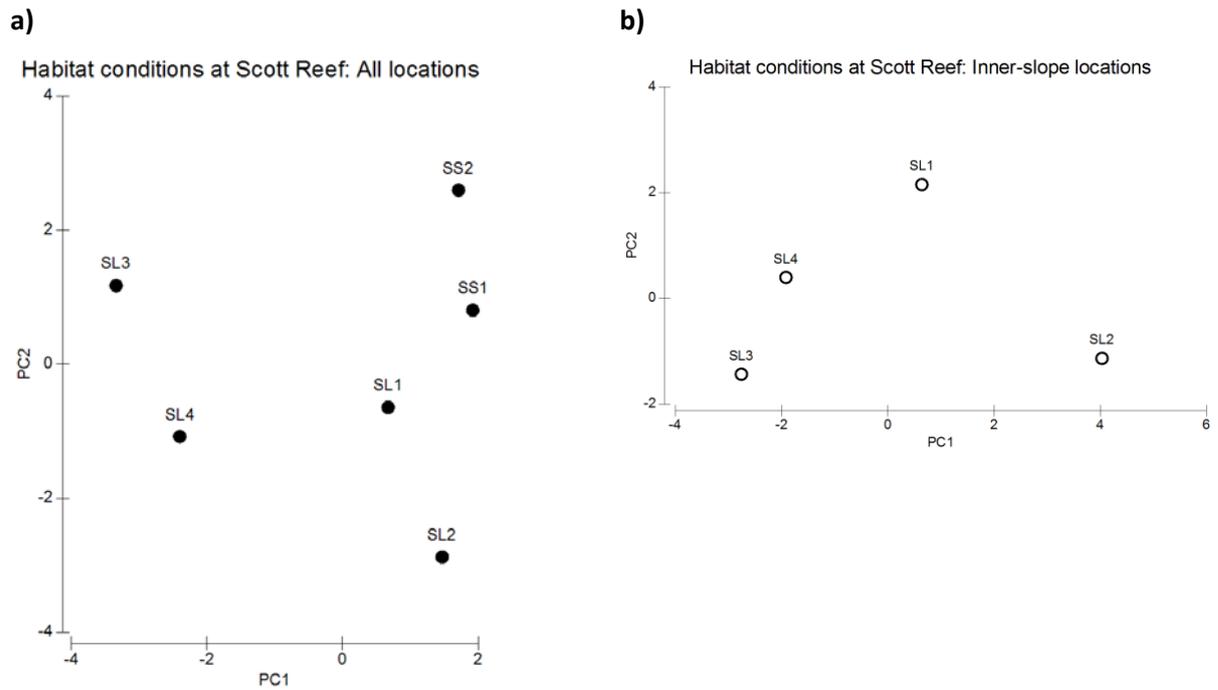


Figure 4.5 Similarity in routine habitat conditions at locations across Scott Reef. Principal components analyses (PCA) of a) 10 physical parameters at all locations, and b) and 14 parameters at the inner-slope locations. Parameters used are in Table 4.1 and results of analysis in table 4.3.

Table 4.3 Results of principal component analysis (PCA) of variation in routine habitat conditions among locations. Analyses were conducted on normalised data from 10 physical parameters quantified at all locations, and 14 parameters quantified at inner-slope locations. More detailed parameter descriptions are in Table 4.1.

a) Habitat conditions at Scott Reef: All locations

PC	Eigenvalues	%Variation	Cum.%Variation
1	5.22	52.2	52.2
2	3.72	37.2	89.3
3	0.589	5.9	95.2
4	0.383	3.8	99.1
5	9.48E-2	0.9	100.0

Eigenvectors

Variable	PC1	PC2	PC3	PC4
Cover of sand	0.423	-0.106	-0.033	-0.177
Summer sedimentation	0.419	-0.126	-0.180	-0.073
Winter sedimentation	-0.146	0.368	-0.770	0.252
Summer silt particles	-0.399	-0.204	-0.139	0.078
Summer sand particles	0.407	0.145	-0.005	-0.382
Summer coarse sand particles	0.269	0.295	0.432	0.705
Winter silt particles	0.069	-0.509	-0.098	0.145
Winter sand particles	0.009	0.518	0.045	-0.013
Winter coarse sand particles	-0.270	0.368	0.222	-0.480
Summer temp. range	0.386	0.158	-0.328	0.000

b) Habitat conditions at Scott Reef: Inner-slope locations

PC	Eigenvalues	%Variation	Cum.%Variation
1	9.31	66.5	66.5
2	2.7	19.3	85.8
3	1.99	14.2	100.0

Eigenvectors

Variable	PC1	PC2	PC3
Cover of sand	0.316	0.100	-0.150
Summer sedimentation	0.288	0.198	-0.247
Winter sedimentation	0.051	0.565	0.237
Summer silt particles	-0.321	-0.095	-0.098
Summer sand particles	0.327	0.010	-0.041
Summer coarse sand particles	0.234	0.278	0.375
Winter silt particles	-0.262	0.116	-0.405
Winter sand particles	0.281	0.004	0.364
Winter coarse sand particles	0.036	-0.530	0.340
Summer temp. range	0.288	0.240	-0.193
Max. summer current speed	0.264	-0.094	-0.405
Max. summer wave height	0.268	-0.236	-0.302
Turbidity	-0.305	0.223	-0.029
Chlorophyll concentration	-0.290	0.280	-0.051

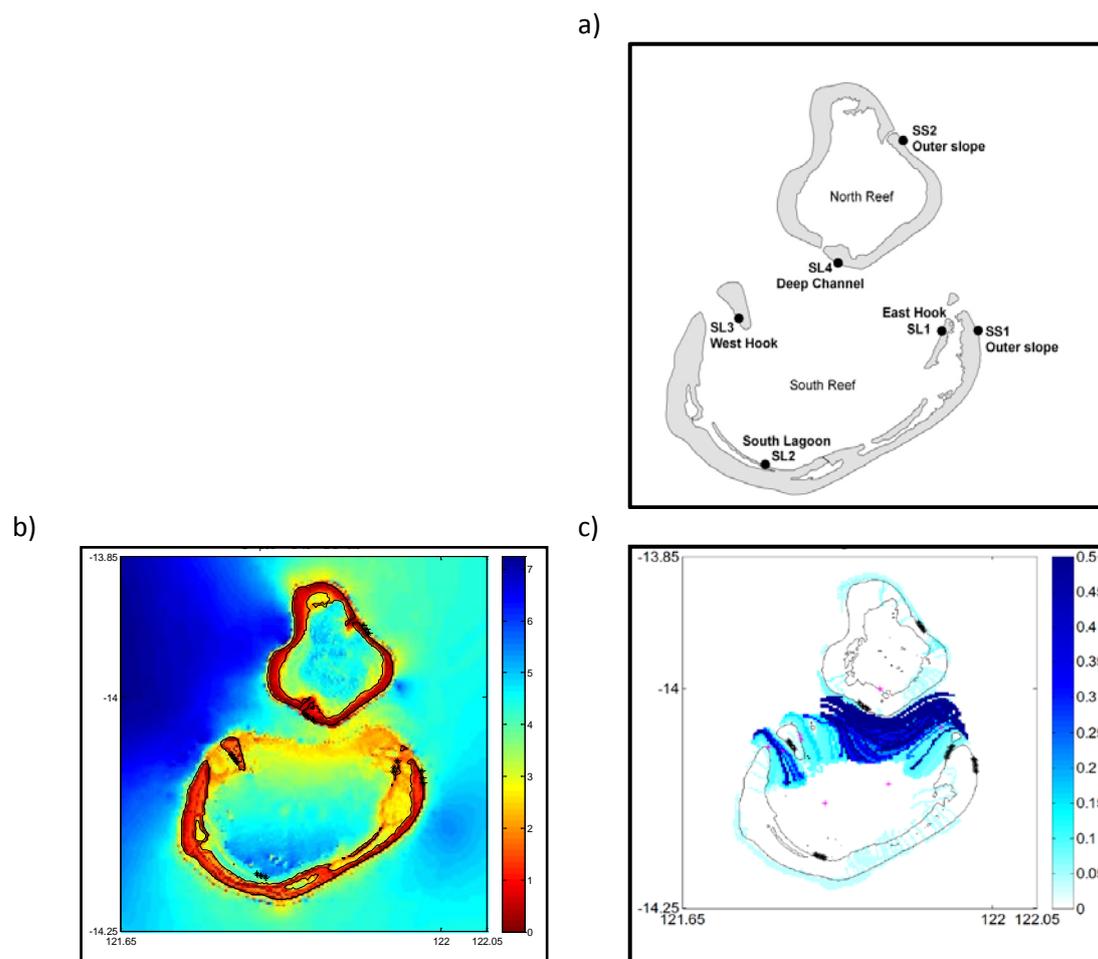


Figure 4.6 a) Study locations at Scott Reef. b) Diagrammatic representation of tidal mixing at locations across Scott Reef; red areas have the highest mixing. c) Diagrammatic representation of flow of cool water to locations across Scott Reef; dark blue areas receive the coolest water. Images b) and c) from (Bird et al. 2004).

4.4.4 Habitat conditions and acute disturbances

4.4.4.1 Cyclones and physical disturbance

Category 5 Cyclone Fay passed directly over Scott Reef in 2004 and damaged the reef structure and coral communities at many locations. Communities at the outer-slope locations (Figure 4.1) were most exposed to Cyclone Fay. Additionally, the less severe Category 3 Cyclone George passed Scott Reef in 2007, to which the West Hook and Deep Channel locations (Figure 4.1) were most exposed. Historically, tropical storms and cyclones are probably the most common disturbances that have affected the coral communities at Scott Reef. A generalized index of cyclone impact in recent decades suggests that several cyclones have had similar impacts to coral communities as Cyclone George in 2007, but none have been as severe as Cyclone Fay in 2004 (Figure 4.7a).

4.4.4.2 Sea-water temperature anomalies

Mass coral bleaching in 1998 was the most severe and widespread disturbance at Scott Reef since the start of monitoring in 1994, and its effects are still evident today. In addition to the mass-bleaching in 1998, there was a bleaching of moderate severity in April 2010 (Figure 4.7b). Colonies from a range of coral species were fully and partially bleached at locations across Scott Reef. Variation in exposure of communities to bleaching stress in 1998, and probably in 2010, were correlated to the degree of tidal mixing (Figure 4.6b) and exposure to cool oceanic water (Figure 4.6c) from around the Deep Channel (Bird et al. 2004). Based on these data, communities at the West hook (SL3) and Deep Channel (SL4) locations experience a high degree of mixing and exposure to cool water intrusions; the East Hook community experiences a moderate degree of mixing and exposure, and the South Lagoon (SL2) community the lowest mixing and exposure to cool water (Figure 4.6).

4.4.4.3 Disease

Starting around October 2009 and peaking in October 2010, an outbreak of 'white-syndrome' disease caused widespread mortality of some *Acropora* corals at two locations at Scott Reef (Figure 4.1; 4.7c). Most of the impact was restricted to the *Acropora* table corals (e.g. *A. hyacinthus*, *A. cytherea*), although branching and corymbose *Acropora* were also affected, and to the community at the South Lagoon. Outbreaks of white syndrome can be triggered by low water circulation, increased sedimentation and high water temperatures (Harvell et al. 2007), and are sustained by a high cover of susceptible species, of which characterised the South lagoon community. Since monitoring commenced in 1994, there has been a much lower incidence of disease at the South Lagoon community than during 2010. However, the incidence of disease has not been quantified and even qualitative estimates are unavailable prior to monitoring.

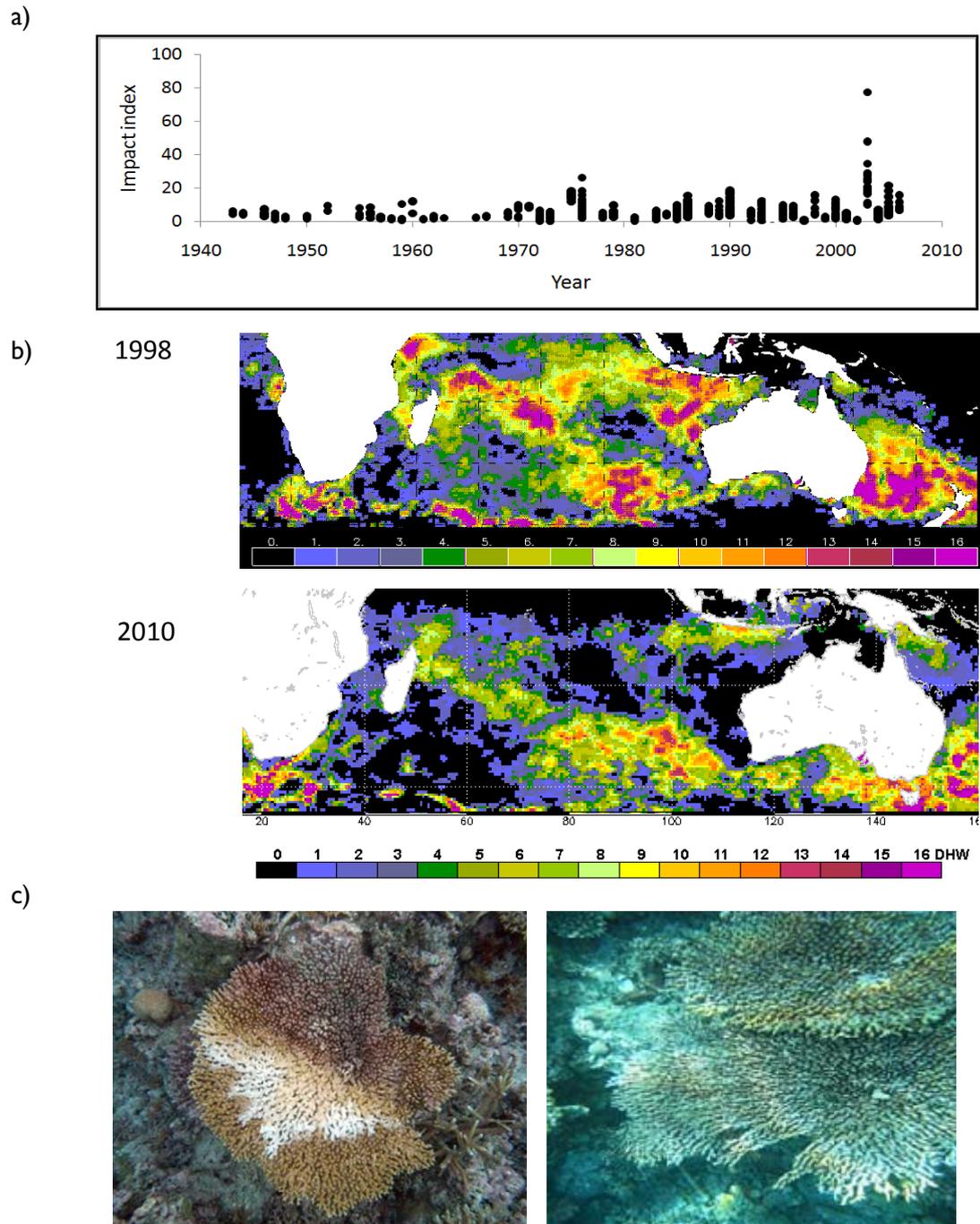


Figure 4.7 Acute disturbances to have impacted coral communities at Scott Reef during monitoring. a) History of cyclone disturbances, with exposure to Cyclone Fay in 2004 being the most obvious, followed by exposure to several additional cyclones of similar intensity to Cyclone George in 2007. b) Severity of temperature anomalies (DHW) at Scott Reef during the mass-bleaching in 1998 and the moderate bleaching in 2010. c) Spread of disease through dying and dead colonies of table *Acropora* at the South Lagoon location.

4.4.5 Frequency of acute disturbances

Over 17 years of monitoring benthic communities at Scott Reef have been exposed five major acute disturbances: one severe and widespread mass-bleaching (1998), one severe but more localised cyclone, and three moderate and localised disturbances (cyclone, disease, bleaching). In the 50 years before monitoring commenced, several cyclones are likely to have caused moderate and localised impacts to the coral communities, similar to Category 3 Cyclone George in 2007, but there is no evidence of a cyclone as severe as Category 5 Cyclone Fay 2004 (Figure 4.7a).

Table 4.3 Known history of community exposure to acute disturbances and impacts at Scott Reef in recent decades (1980 to 2010)

Year	Disturbance	Generalised impact
1998	Elevated water temperatures (DHW)	Severe and widespread
2004	Cyclone Fay (exposure index)	Severe and localised
2007	Cyclone George (exposure index)	Moderate and localised
2010	Elevated water temperatures (DHW)	Moderate and localised
2010	Whiteband disease	Moderate and localised

4.4.6 Habitat conditions and pre-bleaching community structure

Variation in routine habitat conditions influenced the structure and similarity (Figure 4.8) of coral communities at locations across Scott Reef, which was most obvious during the pre-bleaching years. Communities in the pre-bleaching years had not been exposed to severe and widespread disturbances for over a decade, based on historic sea-surface temperatures, cyclone activity and the abundance of corals most susceptible to common disturbances (Table 4.3).

The routine habitat conditions that best described the variation in community structure during the pre-bleaching years were their regimes of sedimentation, current speeds and wave heights (Table 4.3). Winter sediment deposition and particles sizes were more representative than those in summer because they were not skewed by the variable exposure of locations to summer storms. Additionally, communities were distinguished by whether sediment deposition was characterised by the smallest or largest particle sizes, which in turn was related to the maximum current speeds and the maximum wave heights during summer storms. Thus, the influence of routine habitat conditions on communities were most clearly characterised by low sediment deposition of the smallest particles sizes, and low current speeds and wave heights at the sheltered South Lagoon (SL2); by high sediment deposition of largest particle sizes, high current flow and wave heights at the West Hook (SL3) and Deep Channel (SL4) locations; and by intermediate conditions at the remaining locations (SL1, SS1, SS2, SS3)(Table 4. 3; Figure 4.1).

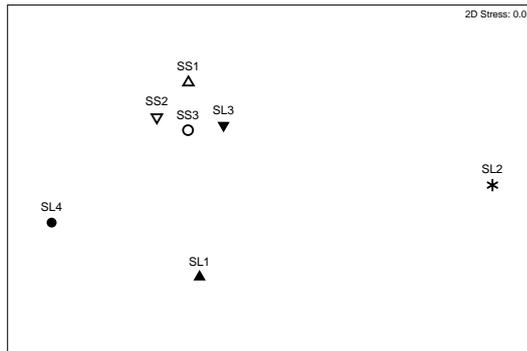


Figure 4.8 Similarities in pre-bleaching (1994 to 1997) structure among communities at Scott Reef. Non-metric multidimensional scaling (nMDS) of mean percentage cover (square-root) of 15 benthic groups averaged over sites and pre-bleaching years at each location. Locations are: outer-slope at South (SS1), North (SS2) and Seringapatam (SS3) Reefs, and inner-slope at East Hook (SL1), South Lagoon (SL2), West Hook (SL3) and Deep Channel (SL4). Study locations are illustrated in Figure 4.1.

Table 4.3 Habitat conditions that best explain the variation in pre-bleaching community structure among locations. Ten parameters were quantified at all locations and 14 parameters at the inner-slope locations (SL1, SL2, SL3, SL4). More detailed parameter descriptions are in Table 4.1.

Habitat conditions and pre-bleaching community structure : all locations	Habitat conditions and pre-bleaching community structure : inner-slope locations
Biota and/or Environment matching	Biota and/or Environment matching
<i>Parameters</i>	<i>Parameters</i>
1 Summer Temperature range	1 Summer Temperature range
2 Summer Sediment	2 Cover of Sand
3 Winter Sediment	3 Summer Silt
4 Cover of Sand	4 Summer Sand
5 Summer Silt	5 Summer Course Sand
6 Summer Sand	6 Winter Silt
7 Summer Course Sand	7 Winter Sand
8 Winter Silt	8 Winter Course Sand)
9 Winter Sand	9 Summer Sediment
10 Winter Course Sand	10 Winter Sediment
<i>Parameters best correlated to community structure</i>	<i>Parameters best correlated to community structure #</i>
# Corr. Parameters	Corr. Parameters
1 0.632 9	4 1.000 10-12,14
2 0.621 8,9	1 0.943 14
3 0.582 6,8,9	3 0.943 6,10,12
1 0.561 8	3 0.943 10,11,14
3 0.532 5,8,9	3 0.943 10,12,13
2 0.507 6,9	3 0.943 10,12,14
4 0.496 5,6,8,9	3 0.943 10,13,14
2 0.489 6,8	4 0.943 5,11,13,14
3 0.450 7-9	4 0.943 5,12-14
2 0.432 5,9	4 0.943 6,10,11,13
<i>Global Test</i>	<i>Global Test</i>
Sample statistic (Rho): 0.632	Sample statistic (Rho): 1
Significance level of sample statistic: 40%	Significance level of sample statistic: 41%
Number of permutations: 99 (Random sample)	Number of permutations: 99 (Random sample)
Number of permuted statistics greater than or equal to Rho: 39	Number of permuted statistics greater than or equal to Rho: 40

4.4.7 Established communities and the impact of mass bleaching

The pre-bleaching (1994-1997) communities across Scott Reef were characterised by several groups common to all locations, and differentiated by a few groups common at a few locations. All communities were characterised by a high cover of hard corals ($46 \pm 4\%$ S.E.), soft corals ($9 \pm 2\%$ S.E.) and turfing and coralline algae ($29 \pm 3\%$ S.E.) (Figure 4.9; Table 4.5). Among the hard corals, all communities were characterised by a moderate to high cover of encrusting corals, Pocilloporidae and massive *Porites* and Faviidae (Figure 4.9; Table 4.5), with the exception was the sheltered South Lagoon (SL2) community. In addition to the benthic groups common at all locations, communities at the outer-slope (SS1, SS2, SS3) and West Hook (SL3) locations were distinguished by a moderate to high cover of *Isopora* and branching *Acropora*.

Among the remaining inner-slope locations (SL1, SL4, SL2), there was greater variation in community structure. The community at East Hook (SL1) had a mix of benthic groups common at other locations, whereas the Deep Channel (SL4) and particularly the South Lagoon (SL2) communities were most unique. The Deep Channel (SL4) community was routinely exposed to the highest currents and wave heights, and was characterised by highest cover of encrusting corals, massive *Porites*, Faviidae, and particularly soft corals. Conversely, the South Lagoon (SL2) community had highest cover of foliose corals, branching and hispidose *Acropora*, and Fungiidae, plus a moderate cover of *Isopora*, corymbose *Acropora* and Pocilloporidae.

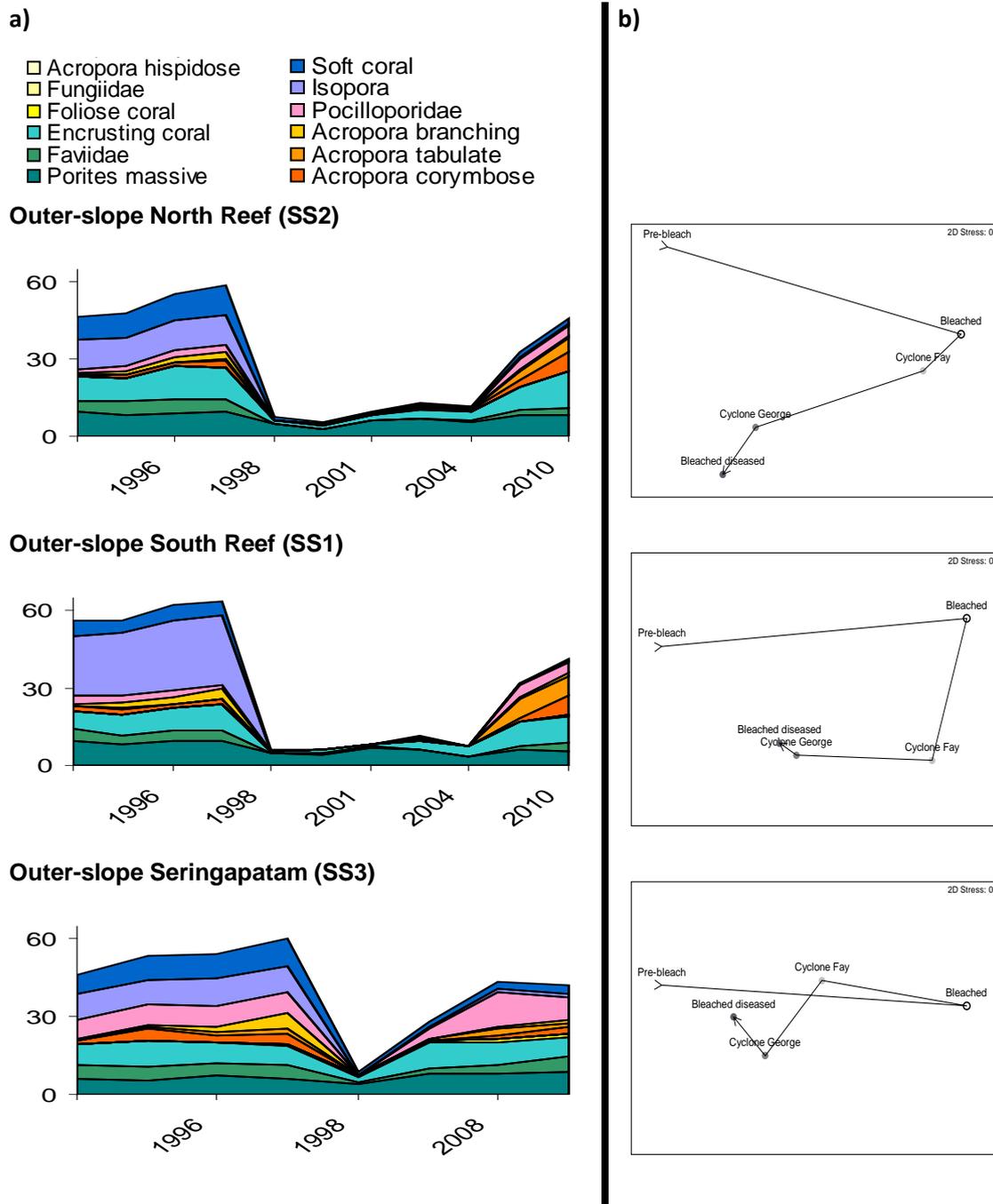


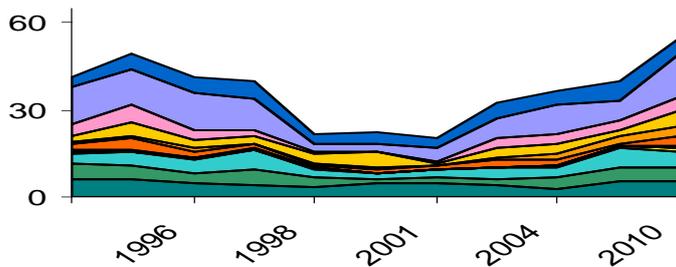
Figure 4.9 Changes in community structure through the monitoring period at locations across Scott Reef. a) Mean percentage cover of 15 benthic life-forms at each survey and location. b) Non-metric multidimensional scaling (nMDS) of temporal changes in mean percentage cover (square root) of 15 benthic life-forms between survey periods at each location. Locations are: outer-slope at South Reef (SS1), North Reef (SS2) and Seringapatam Reef (SS3), and inner-slope at East Hook (SL1), South Lagoon (SL2), West Hook (SL3) and adjacent to the Deep-Channel (SL4).

a)

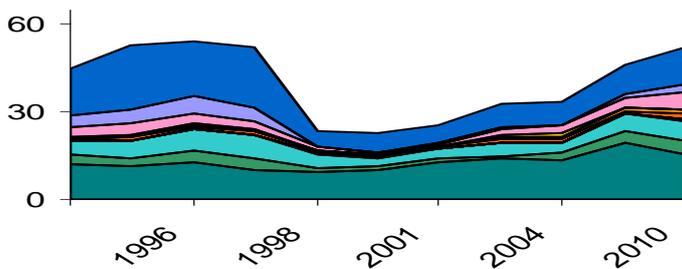
Figure 4.9 Continued

- | | |
|----------------------|----------------------|
| □ Acropora hispidose | ■ Soft coral |
| □ Fungiidae | ■ Isopora |
| □ Foliose coral | ■ Pocilloporidae |
| □ Encrusting coral | ■ Acropora branching |
| ■ Faviidae | ■ Acropora tabulate |
| ■ Porites massive | ■ Acropora corymbose |

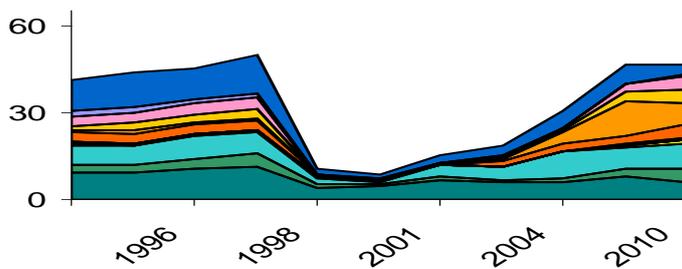
Inner-slope West Hook (SL3)



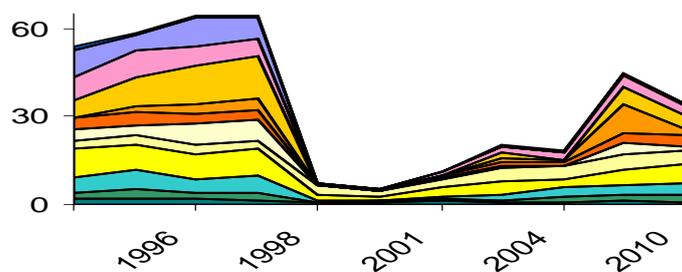
Inner-slope Deep Channel (SL4)



Inner-slope East Hook (SL1)



Inner-slope South lagoon (SL2)



b)

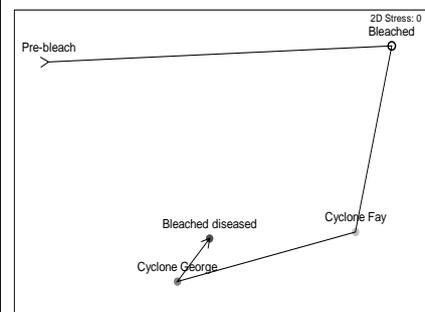
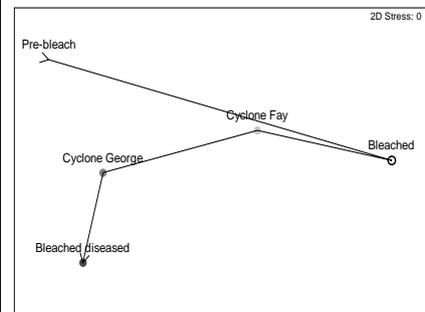
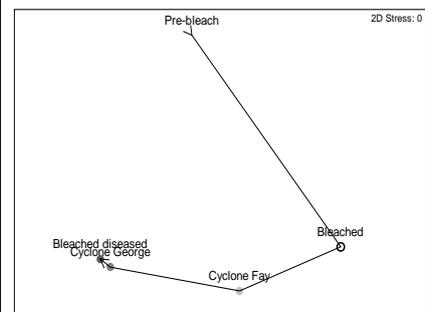
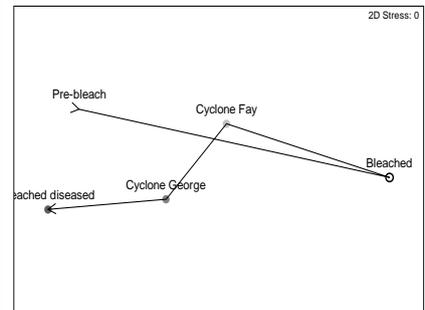


Table 4.5 Benthic life-forms that characterise communities within each period, and distinguish the changes in communities between periods. Life-forms that contribute most to characterising or distinguishing communities within and between periods are highlighted in dark grey; those that make a moderate contribution are highlighted in light grey, and those that make a low contribution have a white background. Whether life-forms made a high, moderate or low contribution was determined by considering their percentage (usually >5%) contribution to similarity within a period or dissimilarity between periods, the relative variance in their contribution, and their percentage cover. Cell values are percentage cover within a period, and changes in percentage cover between one period and the next. Cells are blank when a life-form makes a negligible contribution to characterising or distinguishing communities.

Life-form	Percentage cover in each period							Life-form	Change in percentage cover to next period						
	Inner-slope				Outer-slope				Inner-slope				Outer-slope		
	SL2	SL1	SL4	SL3	SS3	SS1	SS2		SL2	SL1	SL4	SL3	SS3	SS1	SS2
PRE-BLEACHING COMMUNITIES (1994 - 1997)								PRE-BLEACHING TO BLEACHED							
Acropora corymbose	3.8	3.1		2.6	3.2	1.5	1.7	Acropora corymbose	-3.5	-2.9		-1.6	-3.2	-1.5	-1.5
Acropora branching	10.9	2.4		2.7	2.5	2.1		Acropora branching	-10.7	-2.4	-0.6	-0.1	-2.5	-2.1	-1.3
Acropora hispidose	5.6							Acropora hispidose	-5.6						
Acropora tabulate	2.1							Acropora tabulate	-2.1			-0.3			
Encrusting coral	5.8	6.9	6.3	5.0	8.2	8.2	10.8	Encrusting coral	-5.1	-4.6	-2.5	-2.6	-5.7	-7.5	-9.3
Faviids	2.5	3.5	3.5	4.5	5.1	4.0	4.9	Faviids	-1.9	-2.7	-2.2	-2.0	-4.7	-3.7	-4.7
Foliose corals	8.6		4.5					Foliose corals	-6.9						
Fungiids	2.9							Fungiids							
Isopora	7.7	1.5		11.5	9.9	24.3	10.8	Isopora	-7.7	-1.5	-4.3	-8.3	-9.9	-24.3	-10.8
Millepora	1.4	1.5	2.2		3.8	2.1	3.2	Millepora	-1.3	-1.5	-2.1	-1.2	-3.8	-2.0	-3.2
Pocilloporidae	7.3	3.7	3.1	4.1	7.6	2.7	2.3	Pocilloporidae	-7.0	-3.5	-2.5	-3.6	-7.3	-2.7	-2.2
Porites Branching		3.3	2.8	1.7				Porites Branching		-3.3	-2.8	-1.7	-1.3	-0.7	-0.7
Porites Massive		9.9	11.6	5.4	5.9	9.2	9.0	Porites Massive		-4.8					
Soft Coral		11.1	19.3	5.4	9.2	5.8	9.7	Soft Coral		-9.0	-13.1	-1.8	-7.9	-5.5	-8.7
BLEACHED COMMUNITIES (1999 - 2001)								BLEACHED TO CYCLONE FAY							
Acropora corymbose	0.3		0.6	1.0				Acropora corymbose	1.4	1.4	0.5	1.1		0.4	0.3
Acropora branching	0.2			2.6				Acropora branching	0.7	0.4	0.8	0.3		0.2	0.1
Acropora hispidose								Acropora hispidose	0.5						
Acropora tabulate				0.0				Acropora tabulate	1.1	1.3	0.4	1.0	0.2	0.2	
Encrusting coral	0.7	2.3	3.8	2.3	2.4	0.6	1.5	Encrusting coral	1.9	3.3	0.4	1.0	8.1	3.0	2.2
Faviids	0.5	0.8	1.4	2.5				Faviids	0.5		0.2	1.5	1.6	-0.1	-0.1
Foliose corals	1.6	0.2						Foliose corals	1.3	-0.2	0.1	0.1	0.2	0.0	
Fungiids	3.0							Fungiids	1.5	-0.2		-0.1			0.0
Isopora				3.2				Isopora		0.1	0.2	3.4	0.3		0.1
Millepora								Millepora			0.2		1.0	-0.1	0.0
Pocilloporidae								Pocilloporidae	2.1	0.2	1.1	2.3	3.8	0.1	0.3
Porites Branching								Porites Branching				0.3			
Porites Massive	0.6	5.2	10.6	4.2	3.8	5.3	5.0	Porites Massive	0.1	0.7	3.4		4.0	-0.2	1.7
Soft Coral Tot		2.1	6.2	3.6	1.3	0.3	1.0	Soft Coral	0.3	2.4	1.9	1.9	0.7	0.0	0.1

Table 4.5 Continued.

Life-form	Percentage cover in each period							Life-form	Change in percentage cover to next period						
	Inner-slope				Outer-slope				Inner-slope				Outer-slope		
	SL2	SL1	SL4	SL3	SS3	SS1	SS2		SL2	SL1	SL4	SL3	SS3	SS1	SS2
SLOW RECOVERY AND CYCLONE FAY (2001 - 2004)								CYCLONE FAY TO CYCLONE GEORGE							
Acropora corymbose	1.6	1.6	1.1	2.1	0.3	0.4	0.5	Acropora corymbose	1.2	1.1		-1.4	0.5	1.0	2.2
Acropora branching	0.9		0.9	2.8				Acropora branching	4.8	2.9	-0.7	-0.9	0.2	0.5	
Acropora hispidose								Acropora hispidose	3.8	0.2					
Acropora tabulate	1.2	1.3						Acropora tabulate	8.9	10.3		1.1	2.8	7.1	3.5
Encrusting coral	2.5	5.6	4.2	3.8	10.5	3.6	3.6	Encrusting coral		1.8	1.6	2.6	-1.7	5.3	5.2
Faviids	1.1	1.1	1.5	2.6	2.0	0.3		Faviids	1.1	1.5	2.2	1.9	1.4	1.0	1.6
Foliose corals	2.9							Foliose corals	1.8	0.7	0.3	0.6	0.7		
Fungiids	4.4							Fungiids							
Isopora				6.6				Isopora	0.2		1.3	0.1	0.8	0.4	0.5
Millepora					1.0			Millepora	0.7	0.2	0.3	0.0			0.1
Pocilloporidae	2.4		1.7	2.7	4.1		0.4	Pocilloporidae	1.7	2.2	1.2	0.6	9.1	4.6	3.9
Porites Branching								Porites Branching							0.2
Porites Massive	0.8	5.9	14.0	3.7	7.8	5.1	6.8	Porites Massive	0.4	1.9	5.7	1.9	0.1	1.2	1.4
Soft Coral		4.6	8.1	5.5	2.0		1.1	Soft Coral		1.6	1.9	0.9	1.2	0.0	0.8
RECOVERY AND CYCLONE GEORGE								CYCLONE GEORGE TO MODERATE BLEACHING AND DISEASE							
Acropora corymbose	2.9	2.8	0.7		0.8	1.4	2.7	Acropora corymbose	1.1	1.9	1.5	3.1	1.7	5.2	4.5
Acropora branching	5.7	3.3		1.9				Acropora branching	-1.8	1.2	0.0	4.0	0.5	0.9	0.5
Acropora hispidose	4.3			2.4				Acropora hispidose	-2.8	0.4		0.1			
Acropora tabulate	10.1	11.6			3.1	7.3	3.5	Acropora tabulate	-8.5	-4.4	0.6	0.2	-1.4	0.3	1.8
Encrusting coral	3.1	7.5	5.8	6.4	8.8	8.9	8.8	Encrusting coral		0.7	1.2	-1.0		1.5	4.9
Faviids	2.2	2.6	3.8	4.5	3.4	1.3	1.7	Faviids	0.5	2.0			2.6	1.7	1.5
Foliose corals	4.7							Foliose corals	1.6			0.4	0.0	0.3	0.1
Fungiids	5.0							Fungiids	-0.3				0.1	0.2	
Isopora			1.8	6.7	1.1			Isopora		0.2	0.9	7.5	0.6	0.0	
Millepora								Millepora	-0.7	-0.1	-0.2	0.3	0.1	0.3	-0.1
Pocilloporidae	4.0	2.7	2.9	3.3	13.2	4.7	4.3	Pocilloporidae	-0.4	1.3	3.1	1.5	-4.8	-1.1	
Porites Branching								Porites Branching	0.2	-0.1	0.1				
Porites Massive		7.8	19.7	5.7	7.9	6.3	8.1	Porites Massive	-0.5	-1.6	-4.3	-0.4	0.5	-0.7	-0.1
Soft Coral		6.2	10.0	6.5	3.2		1.9	Soft Coral		-2.7	2.7	-0.8	0.0	0.2	0.0
MODERATE BLEACHING AND DISEASE															
Acropora corymbose	4.0	4.6	2.1	3.8	2.5	6.6	7.2								
Acropora branching	3.9	4.5		5.9		1.6									
Acropora hispidose	1.6			2.6											
Acropora tabulate	1.6	7.2	1.1		1.6	7.6	5.4								
Encrusting coral	3.5	8.1	7.0	5.4	8.0	10.4	13.8								
Faviids	2.6	4.6	4.4	5.1	6.1	3.1	3.2								
Foliose corals	6.3				1.1										
Fungiids	4.7														
Isopora			2.6	14.1	1.7										
Millepora															
Pocilloporidae	3.7	4.0	6.0	4.8	8.4	3.6	4.1								
Porites Branching															
Porites Massive		6.2	15.4	5.1	8.4	5.5	8.0								
Soft Coral	0.6	3.4	12.7	5.6	3.2		1.9								

Elevated water temperatures and mass coral-bleaching in 1998 impacted all coral communities, dramatically decreasing (by > 80%) the cover of hard and soft corals across Scott Reef. The relative decreases in coral cover among the locations ranged from approximately 50 to 90%, depending on the abundance of susceptible corals and the habitat conditions.

The relative decreases in mean cover were >90% for the most susceptible coral groups, which included the hispidose *Acropora*, branching *Porites*, *Millepora*, *Isopora* and Pocilloporidae (Figure 4.10). For all other groups, the relative decreases ranged between 70-90%, with the exception of the massive *Porites* that were least susceptible and decreased by approximately 50% (Figure 4.10). The susceptibility of groups and their initial cover influenced the variation in bleaching impact among localities, because the most susceptible groups (*Isopora*, *Acropora*, Pocilloporidae) were among the most abundant at some localities (SL2, SL1), whereas a higher abundance of more resistant corals (massive *Porites*, encrusting coral) resulted in comparatively smaller decrease in cover than at other localities (SL1, SL4).

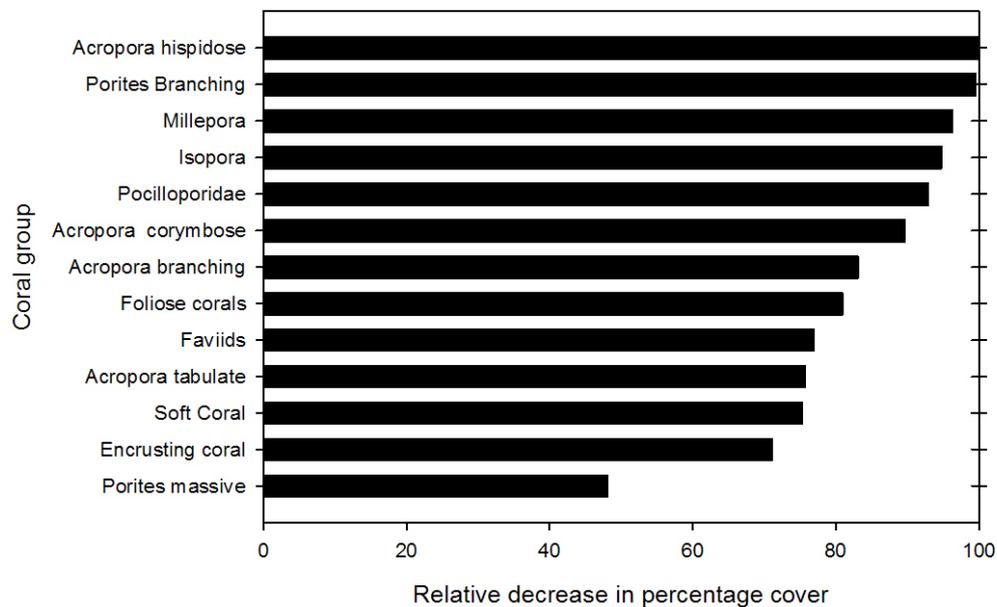


Figure 4.10. Susceptibility of corals to bleaching stress. Relative decrease in percentage cover of coral groups between 1997 and 1998.

In addition to the relative abundance of susceptible corals, variation in bleaching impact among localities was also driven by habitat conditions. Current speeds, tidal mixing and exposure to cool-water intrusions from the deep channel all influenced the degree to which localities were exposed to thermal stress (Figure 4.6). Consequently, the coral communities at West Hook (SL3) and adjacent to the Deep Channel (SL4) were least exposed to thermal stress and had the smallest decreases in coral cover (Figure 4.9; Table 4.5), including smaller relative decreases in cover of even the most susceptible groups (e.g. 70% reduction in *Isopora*). In contrast, the South Lagoon (SL2) community had the largest decreases in cover following the bleaching, including larger relative decreases in cover of the most resistant groups (e.g. 75% reduction in massive *Porites*).

4.4.8 Bleached communities and little short-term recovery (1999-2001)

The mass bleaching homogenised the coral communities across Scott Reef, as many of distinguishing groups were also the most susceptible. The most obvious change was the low cover of hard ($10 \pm 2\%$ S.E.) and soft ($2 \pm 1\%$ S.E.) corals, and the high cover of coralline and turfing algae ($80 \pm 3\%$ S.E.) following its colonisation of the newly-available space. In addition to the coralline and turfing algae, all post-bleaching communities were characterised by the coral groups most resistant to bleaching, particularly the massive *Porites* and encrusting corals, and the Faviidae at the inner-slope localities (Figure 4.9; Table 4.5). All other groups were in low abundance ($< 2\%$) at all localities, with the exception of the soft corals and *Isopora* at the West Hook (SL3) and Deep Channel (SL4) localities where they had been most abundant and were least exposed to thermal stress.

Three years after the mass-bleaching (2001), there had been no change in mean coral cover ($+0.05 \pm 0.1\%$) or community structure across Scott Reef (Figure 4.9). Cover of some coral groups and at some localities had continued to decline, while small increases in cover at other localities were driven primarily by the massive *Porites*. The massive *Porites* were the only coral group whose average cover across communities had increased by $> 1\%$, with the largest increase ($+ 4\%$) at the Deep Channel locality (SL4) where they had been most abundant and least exposed to thermal stress. In contrast, the massive *Porites* continued to decrease in cover ($- 4\%$) at the outer-slope locality at Seringapatam (SS3), as did all other coral groups. The Seringapatam locality had the largest ongoing decrease ($- 9\%$) in cover, in contrast to the largest increases ($+ 5\%$) at the East Hook (SL1) and South Lagoon (SL2) localities, due to massive *Porites*, and encrusting and foliose (SL2 only) corals. At the remaining localities, there was little change ($< 2\%$) in coral cover three years after mass-bleaching.

4.4.9 Slow recovery of communities and effects of Cyclone Fay (2002-2004)

From 2002-2004, increases in coral cover and a return to a pre-bleaching structure had commenced at some localities at Scott Reef, although this return was slowed by the localised effects of Cyclone Fay. In this period, the mean cover of hard ($20 \pm 3\%$) and soft ($3 \pm 1\%$) corals had increased, and there was a corresponding decrease in the cover of coralline and turfing algae ($68 \pm 5\%$) (Figure 4.2). Recovery was driven by the corals that had characterised the localities after the bleaching, which included the encrusting corals ($+ 3\%$) at all locations (but SL4) and small ongoing increases in the cover of massive *Porites* ($+2\%$) at some (SL4, SS2, SS3) locations (Figure 4.9; Table 4.5). Additionally, the changes in some localities were now driven by coral groups that were more susceptible to the bleaching and low in cover. In particular, there were moderate ($+1$ to 3%) increases in cover of soft corals, corymbose *Acropora* and Pocilloporidae at many locations. There had also been a relatively large increase ($+ 3\%$) in cover of *Isopora* at the West Hook community (SL3), where they had previously been abundant and were least impacted by bleaching. Among the localities, the rates of recovery varied according to both the relative abundances of these coral groups and their exposure to Cyclone Fay.

Category 5 Cyclone Fay passed over Scott Reef in 2004, but its impacts were limited to slowing the recovery of coral communities rather than causing large absolute reductions in coral cover. Indeed, there was a small increase in mean coral cover ($+2\% \pm 2$) at Scott Reef following Cyclone Fay, but the apparent lack of impact was a consequence of the low abundance of susceptible species and the variable exposure of localities. Mean changes in cover of all coral groups following Cyclone Fay were $<1\%$, and estimates of relative impacts among groups were confounded by the very low abundance ($< 0.5\%$) at the most exposed locations in 2003. Among the localities, small reductions ($< 3\%$) in coral cover occurred only at those with the highest abundance of susceptible species (SL2) or

at the outer-slope localities (SS1, SS2) that were most exposed to the path of the cyclone (location SS3 was not surveyed in 2004). The severity of the impact at the outer-slope locations was clearly visible in the coral communities, with physical damage to many of the hard and soft corals, even those least susceptible to physical disturbances. This included large relative decreases (-20 to -50%) in cover of massive *Porites* colonies.

With the exception of those most impacted by Cyclone Fay, localities had shifted towards their pre-bleaching structure (Figure 4.9). Most localities were now characterised by a low to moderate (1 – 4 %) cover of soft corals, Faviidae, Pocilloporidae and corymbose *Acropora*, in addition to the more abundant massive *Porites*, and encrusting corals. Additionally, localities were more increasingly distinguished by unique coral groups. A relatively higher cover of *Isopora* and branching corals distinguished the West Hook locality (SL3), foliose corals, fungiids and a range of *Acropora* distinguished the South Lagoon localities (SL2), and massive *Porites* and soft corals distinguished the Deep Channel locality (SL4) (Table 4.5). These were the same groups that distinguished these localities prior to the bleaching.

4.4.10 Recovery of communities and effects of Cyclone George (2005-2008)

More than seven years after the mass-bleaching, there was a rapid increase in coral cover and return to a pre-bleaching structure across Scott Reef, but which was slowed at some localities by the selective impacts of Cyclone George. In this period, the mean cover of hard ($38\% \pm 3$) and soft ($4\% \pm 1$) corals had increased more rapidly than in previous years, and there was again a comparable decrease in cover of coralline and turf algae ($50\% \pm 3$) (Figure 4.2). Most notably, recovery was driven by increases in the cover of Pocilloporidae ($+3\% \pm 1$) and particularly table *Acropora* ($+6\% \pm 1$ S.E.) at all locations across Scott Reef (but for table *Acropora* at SL4). Additionally, recovery was driven by ongoing increases in the cover of corymbose *Acropora*, Faviidae, encrusting corals and massive *Porites* at many localities. There were also ongoing increases in the cover of coral groups that distinguished different localities, such as increases in foliose corals (+2%), branching (+5%), hispidose (+4%) and particularly table (+9%) *Acropora* at South Lagoon (SL2), and soft corals (+2%), Faviidae (+2%) and particularly massive *Porites* (+6%) at the Deep Channel locality (SL4) (Figure 4.9; Table 4.5). Increases in cover of branching *Acropora* and *Isopora* were likely to have further distinguished changes in the West Hook (SL3) locality, but for the impact from Cyclone George.

Category 3 Cyclone George passed Scott Reef in 2007, causing localised and selective impacts to coral communities. Surveys were not conducted immediately before or after the cyclone, so moderate impacts to susceptible corals (*Isopora*, *Acropora*) were possibly masked by increases in cover around that time. Changes in coral cover indicated that West Hook locality (SL3) was worst affected, with some impact also evident at Deep Channel (SL4), although these were restricted to small (< -2%) decreases in cover of susceptible growth forms, particularly the branching *Acropora* (Figure 4.9).

The rapid increases in cover across a range of coral groups at most localities across Scott Reef caused a shift towards their pre-bleaching structure (Figure 4.9). The cover of hard corals was similar (>75%) to that prior to bleaching at all localities, but for the outer-slope community at South Reef (SS1; 60%). Localities were characterised by a larger number of common benthic groups, and further distinguished by groups common at only a few locations. Most localities (not SL3, SL4) were characterised by corymbose (1-3%) and table (3-12%) *Acropora*, in addition to a moderate to high cover of encrusting corals (3-9%), Pocilloporidae (3-13%) and Faviidae (2-5%) that had previously characterised all localities. Despite the impact of Cyclone George, localities continued to be distinguished by increases in cover of their characteristic groups, which were primarily a high abundance of foliose corals, fungiids, and branching, hispidose and table *Acropora* at the South Lagoon

(SL2); Faviidae, soft corals and particularly *Isopora* at West Hook (SL3); Faviidae, and particularly massive *Porites* and soft corals at the Deep Channel (SL4) (Table 4.5). Additionally, the outer-slope (SS1, SS2, SS3) localities were now characterised by a relatively high cover of encrusting corals, Pocilloporidae and massive *Porites*, and a low or variable cover of most other groups (Table 4.5).

4.4.11 Recovery and moderate impact of bleaching and disease (2009-2010)

Twelve years after mass-bleaching, coral cover had continued to increase at Scott Reef, but the rate of increase and the return to a pre-bleaching structure was slowed by the selective impacts of disease and moderate bleaching. Mean cover in 2010 had reached 43% ($\pm 3\%$) for the hard corals and 4% ($\pm 2\%$) for the soft corals, with a further decrease in turf and coralline algae ($40 \pm 3\%$) (Figure 4.2). In this period, there were moderate increases in the cover of corymbose *Acropora* (1-5%) at all localities, and of Faviidae and encrusting corals at most locations (Figure 4.9; Table 4.5). Among the other groups, there were both increases and decreases in cover according to their exposure and susceptibility to disease and bleaching. The largest decreases in cover were due to the outbreak of white band disease at the South Lagoon (SL2) community, which dramatically reduced (-9%) the cover of table *Acropora*. The table *Acropora* had by far the largest relative (-80%) decreases in cover, although there were also relative (30-60%) decreases in branching and hispidose *Acropora* at the South Lagoon community (Figure 4.9; Table 4.5). The disease outbreak also affected the East Hook community (SL1), but caused comparatively small absolute (-4%) and relative (-40%) decreases in cover of the table *Acropora*.

In addition to the spread of disease at two locations, elevated water temperatures caused selective bleaching of some corals and localities. The incidence of bleaching and the resulting decrease in cover were highest for the Pocilloporidae (-5%) at the at the outer-slope community at Seringapatam (SS3), where there was also a small decrease (-1%) in cover of table *Acropora*. A low proportion of other corals at other localities had also bleached, particularly the corals in the family Fungiidae and localities at the outer-slope locations (SS1, SS2), but reductions in cover were primarily restricted to the Pocilloporidae at the outer-slope community at Seringapatam.

The impacts of disease and bleaching slowed the return of some localities to a pre-bleaching cover and structure, while shifts away from a pre-bleaching structure in other localities were driven by the increased cover of unique coral groups. All localities were characterised by the same coral groups that had been typical prior to this disturbance, including a moderate to high cover of massive *Porites*, encrusting coral, corymbose *Acropora*, Faviidae and Pocilloporidae; table *Acropora* and soft corals also characterised many localities (Table 4.5). Additionally, the most unique localities (SL2, SL3, SL4) were increasingly distinguished by the same groups of corals that had distinguished them prior to disturbance. However, at the South Lagoon (SL2) community these distinguishing groups (e.g. branching, hispidose *Acropora*) were in lower abundance due to the impacts of bleaching and disease, where as the distinguishing groups (*Isopora*, massive *Porites* and soft coral) were in higher abundance at the West Hook (SL3) and Deep Channel (SL4) that were comparatively unaffected by disturbance.

Table 4.6 Benthic groups that most distinguish the structure of localities prior to mass-bleaching and more than a decade after the disturbance. Groups that contribute most to the dissimilarity are highlighted in dark grey, light grey are moderate contribution and white background are low contribution. Cells are blanks where groups make a negligible contribution to differences. Values are differences in percentage cover f between pre-bleaching years and 2010.

Benthic Group	SL1 Change	SL2 Change	SL3 Change	SL4 Change	SS1 Change	SS2 Change	SS3 Change	Average
<i>Acropora</i> corymbose	1.6		1.2	1.4	5.1	5.5		3.0
<i>Acropora</i> branching	2.1	-7.0	3.2	-0.5	-0.5	-0.5	0.9	-0.3
<i>Acropora</i> hispidose	0.4	-4.0	0.0					-1.2
<i>Acropora</i> tabulate	6.4		2.0	1.1	7.2	5.3	1.6	3.9
Encrusting coral	1.3	-2.3	0.5		2.3	3.0	8.0	2.1
Faviids				0.8		-1.7		-0.4
Foliose corals		-2.3	0.9				1.1	-0.1
Fungiids			0.2					0.2
<i>Isopora</i>	-1.1	-7.4	2.6	-1.9	-23.9	-9.9	1.7	-5.7
Millepora	-1.4	-1.2	-0.9	-1.8	-1.8	-3.2	0.9	-1.3
Pocilloporidae	0.3	-3.6		2.8		1.8	8.4	1.9
<i>Porites</i> Branching	-3.2		-1.5	-2.7	-0.7	-0.7	0.0	-1.5
<i>Porites</i> Massive	-3.8	-0.9		3.9	-3.7		8.4	0.8
Soft Coral	-7.7		0.2	-6.6	-5.3	-7.8	3.2	-4.0
Turf & Coralline	6.4	29.1	-7.6	3.1	25.2	17.5	41.3	16.4

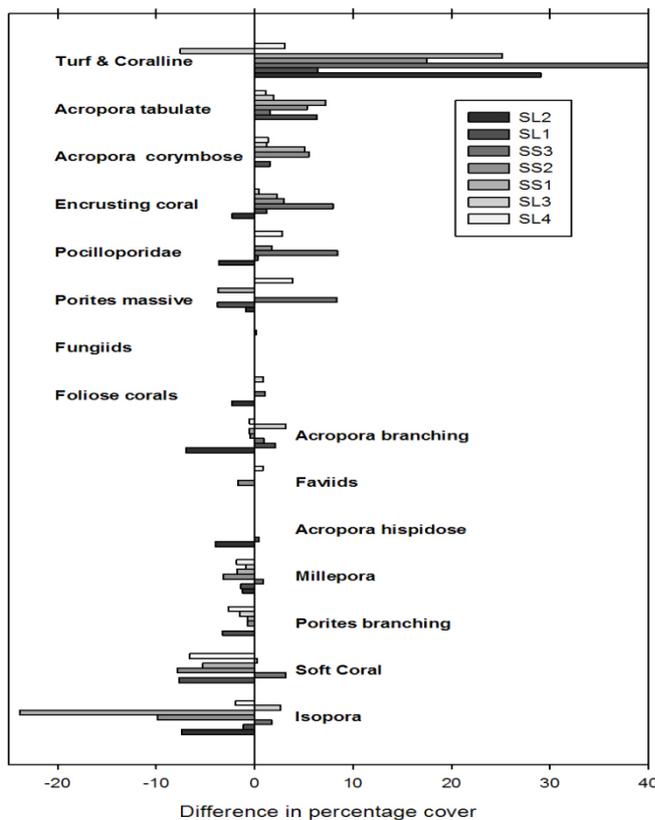


Figure 4.11 Differences in percentage cover between pre-bleaching (1994 to 1997) years and 2010 for each benthic group.

4.4.12 Recovery of coral communities at Scott Reef? Structure of coral communities in 2010 compared with pre-bleaching years

Cover of hard corals in 2010 was similar ($43 \pm 3\%$) to that prior to bleaching ($46 \pm 4\%$), but cover of soft corals was less than half ($4 \pm 2\%$) that in pre-bleaching years ($9 \pm 2\%$). The lower cover of hard and soft corals in 2010 was matched by a higher cover of turf and coralline algae in 2010 ($40 \pm 3\%$), compared to the pre-bleaching years ($29 \pm 3\%$). Determining whether communities had recovered from mass-bleaching required an assessment of both the cover and the relative abundance of different groups; at some localities coral cover was well below that in pre-bleaching years but the relative abundance of different groups was similar, while in other localities coral cover was similar to that pre-bleaching but the abundance of constituent groups differed from those prior to the bleaching. The degree of dissimilarity in structure between pre-bleaching years and in 2010 for each community depended on their regimes of disturbance, habitat conditions, and the groups of corals that drove the recovery. However, there was a consistent pattern of decreasing dissimilarity in the structure of communities through time, when compared to their pre-bleaching years (Figure 4.12).

The most obvious difference in structure between many pre-bleaching communities and those in 2010 was the cover of turf and coralline algae, and soft corals (Table 4.6; Figure 4.11). At the localities (SS3, SS2, SS1, SL2) worst affected by the mass-bleaching and subsequent disturbances (cyclone, disease, bleaching), the cover of coralline and turfing algae in 2010 was higher (+15 – 41%) than in the pre-bleaching years (Table 4.6; Figure 4.11). In contrast, the cover of turf and coralline algae were similar ($\pm 10\%$) to the pre-bleaching years at the remaining localities (SL4, SL3, SL1) that were less impacted by the mass-bleaching, but which were exposed to subsequent disturbances. The relative cover of soft corals in 2010 was much lower (9 to 35%) than in pre-bleaching years at all localities, with the exception of those at West Hook (SL3: 103%) and the Deep Channel (SL4: 65%) that were least impacted by the mass-bleaching and had the highest initial cover of soft corals. At these localities (SL3, SL4) there were small but consistent increases in cover each year after the mass-bleaching.

The relative cover of hard coral at localities in 2010 was similar (94 to 125%) to that in pre-bleaching years, with the exception (55 to 75%) of those localities (SL2, SS1) worst impacted by the mass-bleaching and subsequent disturbances. The reduced dissimilarity in the structure of communities through time, compared to their pre-bleaching state, was driven by groups that consistently characterised all the localities, which included the encrusting corals, massive *Porites*, *Pocillopora* and Faviidae (Table 4.6; Figure 4.11). In contrast, community structures in 2010 were distinguished from that in pre-bleaching years by a lower abundance of *Isopora*, and the absence of *Millepora* and branching *Porites* at localities where they had been moderately abundant (Table 4.6; Figure 4.11).

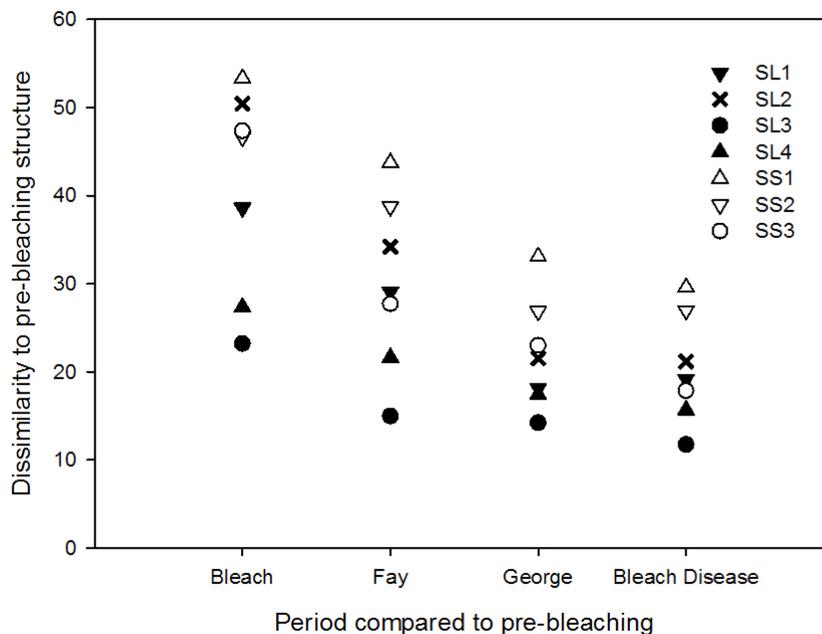


Figure 4.12 The dissimilarity between pre-bleaching structure of localities and that during subsequent monitoring periods. The lower the dissimilarity the more similar is the community structure to that prior to bleaching. Periods are bleached (1998-2001), recovery and Cyclone Fay (2002-2004), recovery and Cyclone George (2005-2008) and recovery and moderate disease and bleaching (2009-2010).

The South Lagoon community was severely affected by mass bleaching and by the most recent bleaching and outbreak of disease in 2010. In 2010, hard coral cover at SL2 (27%) was less than half its high cover prior to the bleaching (62%), but with a moderate dissimilarity to pre-bleaching structure (Figure 4.12) given the representation of groups that consistently characterised the community through time. The community was consistently characterised by *Acropora*, foliose corals, Pocilloporidae, Fungiidae and *Isopora*, but in 2010 the cover of all these groups was lower than in pre-bleaching years, particularly the *Isopora* and branching and hispidose *Acropora* (Table 4.6). The cover of table *Acropora* was similar to that prior to mass-bleaching, but would have been much higher if not for the decrease (-8%) due to disease in 2010. The only other locality to have not returned (75%) to its pre-bleaching cover of hard corals in 2010 was at the outer-slope at South Reef (SS1), and of all the localities its structure differed most from that prior to bleaching (Figure 4.12). This locality (SS1) was also severely impacted by mass bleaching and by cyclone disturbance, and in 2010 had a had a lower cover massive *Porites* (-4%), soft corals (-5%) and particularly *Isopora* (-24%), but a higher cover of corymbose (+5%) and tabulate (+7%) *Acropora* (Table 4.6).

The outer-slope localities at North Reef (SS2) and Seringapatam (SS3) had returned ($\pm 6\%$) to their pre-bleaching cover in 2010, but with contrasting dissimilarity to their pre-bleaching structure (Figure 4.12). The outer-slope community at North Reef (SS2) had a high dissimilarity to its pre-bleaching structure, due to the lower cover of soft coral (-5%) and particularly *Isopora* (-10%), and a higher cover (+5%) of corymbose and table *Acropora* (Table 4.6, Figure 4.11). In contrast, the outer-slope community at Seringapatam (SS3) had a low dissimilarity to its pre-bleaching structure, because of a higher cover of encrusting corals, Pocilloporidae and massive *Porites* in 2010; however, because these groups were also common prior to bleaching they contributed little to the differences in community structure.

The remaining localities (SL1, SL3, SL4) were least impacted by mass-bleaching in 1998, and in 2010 they had the highest relative cover (115-125%) of hard corals and lowest dissimilarity to pre-

bleaching structure (Figure 4.12). Over all the monitoring periods, the East Hook (SL1) community was characterised by a mix of corals groups, and was distinguished from its pre-bleaching structure in 2010 by a lower cover of massive *Porites* (-4%), branching *Porites* (-3%), and particularly soft corals (-8%), but a higher (+6%) cover of tabulate *Acropora*. By comparison, these groups of corals in similar abundance characterised the West Hook (SL3) and Deep Channel (SL4) localities in 2010 and prior to bleaching (Table. 4.6, Figure 4.11). These groups included the soft corals, massive *Porites*, branching and corymbose *Acropora* and particularly *Isopora* at West Hook (SL3), and encrusting corals, massive *Porites*, Faviidae and soft corals at the Deep Channel (SL4). The exception was a lower cover (-6%) of soft corals at the Deep Channel community in 2010, although the cover of soft corals during all periods was consistently higher at this locality than at any other.

4.6 Discussion

Changes in community structure at Scott Reef over 17 years of monitoring were driven by 1) routine habitat conditions (e.g. substrata, sedimentation, current speeds), 2) extreme conditions during acute disturbances (e.g. sea-water temperature, wave heights) and 3) the life histories (e.g. reproductive mode, growth rates, susceptibility to disturbances) of the dominant corals. These data clearly demonstrate that long-term studies (decades) of replicate localities over large spatial scales (10s of km) are required to understand the resilience of coral reefs to regimes of disturbance.

4.6.1 Routine habitat conditions

The role of routine habitat conditions in structuring coral communities has been well documented in both hard and soft corals (Fabricius et al. 2005)(Done 1982)(Woesik van and Done 1997). Environmental gradients at Scott Reef ranged from the outer-slope habitat that was exposed to the open ocean, to inner-slope locations adjacent to the deep channel or in the sheltered south lagoon protected from wave action. Much of the variation among locations was explained by their water temperatures, regimes of sedimentation and turbidity, and maximum current speeds and wave heights. This variation in habitat conditions was manifest in the structure of coral communities throughout the monitoring period, but particularly during the pre-bleaching years when they had not experienced major disturbances for more than a decade.

The South Lagoon (SL2) community had by far the most unique habitat conditions and coral community structure, and was distinguished by low rates of sedimentation of small particle sizes, relatively high turbidity, and low current speeds and wave heights. Consequently, the community at the South Lagoon was characterised by foliose corals, *Acropora* with fragile growth forms (table, branching, hispidose), corals of the families Pocilloporidae and Fungiidae, but with large fluctuations in their absolute cover due to disturbances. These corals are typically not well suited to high energy environments and the deposition of large sediment particles, but are able to tolerate low water flow and moderately high turbidity. However, the *Acropora* are least suited to low flow and high turbidity, and these conditions probably contributed to the spread of disease through the *Acropora* at the South Lagoon in 2010. The most dissimilar habitat conditions and community structure to that at the South Lagoon was at the Deep Channel location, which was distinguished by higher rates of sediment deposition of the largest particle sizes, high current flow and wave heights. Consequently, the community at the Deep Channel was characterised by massive *Porites* and Faviidae, encrusting corals, and particularly soft corals, but few corals with fragile growth forms.

4.6.2 Acute disturbances

Over 17 years of monitoring, coral communities at Scott Reef were exposed to multiple acute disturbances of varying severity and scale, which included temperature anomalies and mass-bleaching,

wave energy and cyclones, and disease outbreaks. The impacts from these acute disturbances were relatively homogeneous over spatial scales of less than a few kilometres, but far more variable over larger (> 5 km) spatial scales. In addition to the scale of impacts, there were consistent patterns of susceptibility among coral groups to these acute disturbances, with the fragile *Acropora* and Pocilloporidae generally being the most susceptible, and the encrusting corals and massive *Porites* and Faviidae least susceptible. Similar trends of susceptibility been reported in most studies of coral communities (Knowlton et al. 1981; Loya et al. 2001; Baird and Marshall 2002; Madin et al. 2008).

Variation in the spatial scale of impacts and in the susceptibility of corals decreased with the severity of the acute disturbance, which was most evident following the mass-bleaching in 1998. Mass-bleaching in 1998 was by far the most severe and widespread disturbances, and its impacts extended to the fish communities (Halford and Perret 2009) and are still evident in some benthic localities today. Reductions in coral cover following mass-bleaching were > 50% in all localities and for all coral groups. However, there was variation in bleaching impacts among localities and these were best explained by habitat. For example, the West Hook and Deep Channel locations experienced the greatest degree of tidal mixing and exposure to cool-water intrusions at the time of bleaching (Steinberg et al. 2006), and their communities had the lowest relative decreases in cover; conversely, the communities at the South Lagoon and at outer-slope at South Reef had a high abundance of susceptible coral groups (e.g. branching *Isopora* and *Acropora*) and the highest relative decreases in cover. Similar variation in impacts among localities, according to the degree of exposure and abundance of susceptible species were evident also for all subsequent acute disturbances and had important implications for the rates of community recovery.

The coral communities at Scott Reef were exposed to several additional acute disturbances following the mass-bleaching, but the impacts from these disturbances were more selective and localised. Consequently, major reductions in coral cover were restricted to a few coral groups at a few communities, usually slowing their rates of recovery from mass bleaching during no more than 2-4 years. These additional disturbances included two cyclones, of which the first and most severe was category 5 Cyclone Fay in 2004. This cyclone passed directly over Scott Reef and its impacts to the exposed outer-slope locations on the eastern side of Scott Reef were so severe that outcrops several meters in size were pushed onto the reef flat ((Gilmour and Smith 2006) and the cover of massive *Porites* decreased by approximately 50% following fragmentation and scouring by sediments. Despite the severity of the cyclone, there were only small reductions in coral cover at these outer-slope localities because there had been little recovery since the mass-bleaching. However, Cyclone Fay did kill many of the small colonies that otherwise would have contributed to future increases in cover and recruitment, and the outer-slope localities had slowest initial rates of recovery following the mass-bleaching. Category 3 Cyclone George passed Scott Reef in 2007, and its impacts were less severe and more selective. Cyclone George reduced the cover of only the *Acropora* with fragile growth forms at the West Hook and Deep Channel locations, and these impacts had little impact on the rates of recovery of localities from the mass-bleaching. Coral reefs have evolved to cope with frequent exposure to storms and cyclones, and communities usually recovery quickly from the selective impacts (Tanner et al. 1994; Connell 1997). All but the most severe cyclones tend to have impacts that are spatially patchy that injure rather than kill some colonies, so recovery is facilitated by the regrowth of survivors and the supply of recruits produced locally.

The most recent disturbances to have impacted the coral communities at Scott Reef and to have slowed their recovery from the mass-bleaching in 1998 was an outbreak of white syndrome disease and a moderate bleaching event in 2010. Both of these disturbances were extremely selective in their impacts, affecting only a few localities and groups of corals. The outbreak of white syndrome primarily affected the abundant table *Acropora* at the South Lagoon locality, but with some less severe impacts to other *Acropora* and to the table *Acropora* at the East Hook locality. Similarly, the bleaching event primarily affected the Pocilloporidae at the outer-slope localities, and the Fungiidae at the South Lagoon locality. The Pocilloporidae were worst affected, but the resulting decreases were matched by increases in cover before and after the bleaching and at the unaffected localities.

Most of the *Acropora* were not affected by the bleaching in 2010, in contrast to the mass-bleaching in 1998, whereas the Fungiidae were severely impacted by the bleaching in 2010 and not in 1998. Similar variation in susceptibility among coral groups between the bleaching events in 1998 and 2010 have been reported at other Indo-Pacific reefs, and the underlying cause for this variation is unknown.

4.6.3 Life histories of corals

The structure of many coral communities prior to the mass-bleaching and after recovery more than a decade later was often distinguished by only a few groups of corals. In particular, the soft corals and branching *Acropora* and *Isopora* (*I. bruegmanni*) had not returned to their pre-bleaching cover, whereas the tabulate *Acropora* were more abundant. The lack of recovery of these corals at many localities may be explained by the severity of the impact from the mass-bleaching and by their modes of reproduction. Reproduction in soft corals and branching *Acropora* can be driven more by asexual growth and fragmentation, than by the output of many sexually produced larvae dispersing over large distances. Similarly, reproduction in *Isopora* involves the production of brooded planulae that characteristically disperse only short distances. The recovery of these corals following mass-bleaching depended on local proliferation of survivors, more than the supply of larvae from other localities. Indeed, recovery of these corals has clearly been slowest at those localities worst impacted by the mass-bleaching, and fastest at those least impacted. For most other groups of corals, the production and dispersal of sexually-produced larvae facilitated their recovery within localities across Scott Reef. The influence of larval supply on the recovery and structure of communities following the mass-bleaching was most evident at the East Hook locality, which has the highest rates of recruitment and is supplied by several other localities. Consequently, the East Hook community recovered quickly from the mass-bleaching and was consistently characterised by the widest range of coral groups. Sexual reproduction and the dispersal of larvae among locations at Scott Reef underlies the recovery and diversity of communities. However, had the disturbance regime been so severe as to cause greater reduction in cover across all localities, then the persistence of the most susceptible coral groups may have been compromised. The isolation of Scott Reef from other reef systems in the region means it does not receive a sufficient supply of recruits from other coral reefs to aid recovery over ecological time scales. At other isolated reef systems exposed to a more severe regime of disturbances, the lack of larvae supply from other reef systems is likely to have contributed to the loss of the most susceptible corals and a prolonged shift to a more degraded state (eg, Graham et al. 2006; Ledlie et al. 2007).

4.7 Resilience of coral communities at Scott Reef

Through a regime of acute disturbances affecting coral communities across Scott Reef over more than a decade, the most severe and lasting impacts were from the mass-bleaching in 1998. Impacts from subsequent disturbances were far more selective and localised and had comparatively little effect at the scale of the entire Scott Reef system. Collectively, however, the impacts from these disturbances were more significant, slowing the recovery of the Scott Reef system following the mass-bleaching.

The coral communities at most localities had therefore reached a state similar to pre-bleaching within approximately a decade after the bleaching event. However, even small increases in the severity of the disturbance regime at Scott Reef, whether as a few additional disturbances of moderate severity or a single severe and widespread event, would have dramatically slowed the rate of return to a pre-bleaching state. For much of the post-bleaching period communities existed in a degraded state, compared to that prior to bleaching, with a low representation of coral groups that were most susceptible to disturbances. Indeed, for the coral communities at Scott Reef to return fully to their pre-bleaching state will require only moderate and localised disturbances for much of

the next decade. The habitat conditions and disturbance regime at Scott Reef during the period of monitoring exemplify conditions approaching a tipping point, beyond which communities are likely to exist in a prolonged state of reduced cover, diversity and structural complexity.

4.8 References

- 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
- Bird J, Steinberg C, Brinkman R, McAllister F (2004) Biological and Physical Environment at Scott Reef: 2003 to 2004, II: Physical Environment. Australian Institute of Marine Science
- Bythell JC, Hillis-Starr ZM, Rogers CS (2000) Local variability but landscape stability in coral reef communities following repeated hurricane impacts. *Marine Ecology Progress Series* 204: 93-100
- Christie CA, Bass DK, Neale SJ, Osborne K, Oxley WG (1996) Surveys of sessile benthic communities using the video technique. Long term monitoring of the Great Barrier Reef, Standard operational procedure no 2. Australian Institute of Marine Science, Townsville
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310
- Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16 (Suppl): 101-113
- Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1: 95-107
- Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247: 121-132
- Done TJ, DeVantier LM, Turak E, Fisk DA, Wakeford M, van Woesik R (2010) Coral growth on three reefs: development of recovery benchmarks using a space for time approach. *Coral Reefs Online First* 26 May 2010
- Fabricius KE, De'ath G, McCook L, Turak E, Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Marine Pollution Bulletin* 51: 384-398
- Gilmour JP, Smith LD (2006) Category 5 cyclone at Scott Reef, Northwestern Australia. *Coral Reefs* 25: 200-200
- Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences* 103: 8425-8429
- Halford AR, Perret J (2009) Patterns of recovery in catastrophically disturbed fish assemblages. *Marine Ecology Progress Series* 383: 261-272
- Harvell D, Jordan-Dahlgren E, Merkel S, Rosenberg E, Raymundo L, Smith G, Weil E, Willis B, Global Environment Facility C (2007) Coral disease, environmental drivers, and the balance between coral and microbial associates. *Oceanography* 20: 172-195
- Hoegh-Guldberg O (2004) Coral reefs in a century of rapid environmental change. *Symbiosis* 37: 1-31
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatzitolos ME (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318: 1737-1742
- Hughes TP (1989) Community structure and diversity of coral reefs: The role of history. *Ecology* 70: 275-279
- Jones GP, Syms C (1998) Disturbance, habitat structure and the ecology of fishes on coral reefs. *Australian Journal of Ecology* 23: 287-297
- Karlson RH, Hurd LE (1993) Disturbance, coral reef communities, and changing ecological paradigms. *Coral Reefs* 12: 117-125
- Knowlton N, Lang JC, Rooney MC, Clifford P (1981) Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. *Nature* 294: 251-252
- Ledlie MH, Graham NAJ, Bythell JC, Wilson SK, Jennings S, Polunin NVC, Hardcastle J (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs* 26: 641-653
- 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

- Madin JS, O'Donnell MJ, Connolly SR (2008) Climate-mediated mechanical changes to post-disturbance coral assemblages. *Biology Letters* 4: 490-493
- Ninio R, Meekan MG (2002) Spatial patterns in benthic communities and the dynamics of a mosaic ecosystem on the Great Barrier Reef, Australia. *Coral Reefs* 21: 95-103
- Smith LD, Gilmour JP, Heyward AJ (2008) Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. *Coral Reefs* 27: 197-205
- Steinberg C, Brinkman R, Choukroun S, McAllister F (2006) Biological and Physical Environment at Scott Reef (2006) II: Physical Environment. Australian Institute of Marine Science
- Tanner JE, Hughes TP, Connell JH (1994) Species coexistence, keystone species, and succession: A sensitivity analysis. *Ecology* 75: 2204-2219
- Woesik van R, Done TJ (1997) Coral communities and reef growth in the southern Great Barrier Reef. *Coral Reefs (Online First)* 16: 103-115

5. Long-term monitoring of fish communities

5.1 Summary

Scott Reef is one of only three emergent oceanic atoll systems in the north-east Indian Ocean between Indonesia and the tropical north-west coast of Australia. Here we show that the fish community at this important reef system has undergone significant change in composition through a 17 year period, and is now quite different to the assemblage that occurred on the reef prior to a mass coral bleaching there in 1998. The effect of the bleaching event in 1998 was most striking on species that used coral either for food such as butterflyfishes or for protection such as many planktivorous damselfishes. Following death of the coral from bleaching and subsequent overgrowth by algae, abundances of herbivores increased, as did numbers of detritivores, which probably benefited from the trapping of detritus by rubble and algal turfs. Fish assemblages on the reef underwent three distinct phases during the study:

- (1) a pre-bleached community dominated by habitat and dietary specialists (predominantly coral and plankton feeders)
- (2) an intermediate post-bleach community characterized by species that have a preference for the habitat types resulting from coral bleaching, either directly through the erosion of dead coral into rubble habitats or from the increase in area available for turf algae to
- (3) the most recent fish community characterized by fish that have more generalist diet and habitat requirements overlaid by mid-sized carnivorous species that have increased in number presumably due to the reduction of their main predators through the fishing of sharks.

The passage of Cyclone Fay directly over Scott Reef in early 2004, is likely to have caused additional changes to the composition of the benthic community and stalled the recovery of the fish community. Unlike benthic communities, for which disturbance due to bleaching and cyclones are the principal and obvious drivers of change in patterns in abundance and structure, we detected significant trends in fish assemblages during the 17 years of our study that had no clear or simple explanation. For example, we found that the numbers of larger, mobile reef fishes steadily increased during the study, particularly in the case of carnivorous species belonging to the families Lethrinidae, Lutjanidae and Serranidae. This increase in abundance was accompanied by an increase in fish species richness, and both trends were apparently unaffected by the major bleaching event or the passage of cyclones across the reef. One possibility is that these patterns were the result of increasing fishing pressure on Scott Reef by Indonesian fishermen that have targeted large predatory sharks over the last decade. Studies on other reef systems have shown that apex predator release can result in fundamental changes to the biomass and abundance of lower trophic levels in coral reef ecosystems, which might account for some of the changes recorded by our study. In particular, this might explain the increasing number of the carnivorous species that have been released from predation by sharks over the duration of the study.

5.2 Introduction

Predicting how biotic communities respond to changing environmental conditions is an important goal of ecology, and one that has become even more critical in the face of increasing environmental stressors associated with a changing global climate (Balmford and Bond 2005). With numerous ecosystems now exhibiting marked responses to a warming and more variable climate (IPCC 2007), a major challenge for the discipline of ecology is to understand the many competing mechanisms that determine population change and alter community structure. The terms “bottom-up” and “top-down” have been used by ecologists to describe how resource availability or the actions of consumers regulate the structure of biotic communities, respectively (Carpenter et al. 1985). While

there is still fundamental disagreement on whether communities are driven by bottom-up or top-down ecological forces (Strong 1992; Hughes 1994; Polis et al. 2000; Knowlton and Jackson 2008), these forces should not be viewed as exclusive and ecological theory should now be directed to understanding the synergistic role that top-down processes, such as predation, have in shaping the composition and diversity of many biotic communities (Terborgh and Estes 2010). Determining the relative impacts of these two types of processes is an important global challenge facing managers of both terrestrial and marine resources and isolating the conditions where these impacts may be large or small throughout biological systems is critical in order to meet this challenge. Fundamental to such efforts are the ecological insights into the wide variety of disturbances that effect systems that can be gained from large-scale experiments in complex natural systems.

Coral reefs are the most diverse ecosystem within the marine environment and accommodate thousands of species, including up to one-third of all known marine fishes within this “rainforest of the sea” (Moberg and Folke 1999; Bellwood et al. 2004; Hoegh-Guldberg et al. 2007; Knowlton and Jackson 2008). The reason that they are able to host so many species may be, in part, because they are dynamic environments that are subject to episodic disturbances that alter structural components of the environment to provide a diverse array of habitats (Connell 1978; Huston 1979; Huston 1985; Connell et al. 1997; Hughes and Connell 1999; McCulloch et al. 2003; Wilson et al. 2006; Mumby et al. 2007; Wilson et al. 2009). However, coral reefs are also one of the world’s most threatened ecosystems, often the first to exhibit a marked response following acute disturbances such as elevated water temperatures and intense tropical cyclones; and also through longer-term chronic disturbances such as heavy fishing, ocean acidification and eutrophication (Connell 1997; Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007; IPCC 2007; Veron 2008).

While species diversity tends to be greatest at intermediate frequencies and intensities of disturbance (Connell 1978), the ability of reefs to exhibit and maintain high levels of diversity and resilience may be compromised in the future due to climate change. A warming planet is predicted to result in more frequent coral bleaching and a greater frequency and intensity of tropical storms (Hoegh-Guldberg et al. 2007; IPCC 2007). This will result in shorter times available for reefs to recover between disturbance events (Hughes et al. 2003) and could ultimately lead to reefs undergoing phase shifts to alternate stable states where they are dominated by organisms other than corals (Norström et al. 2009), as has already occurred on some coral reefs of the Caribbean (Mumby et al. 2007).

The effects of disturbance on coral-dominated communities flow through to the assemblages of fishes that live on reefs. For many fish species, the typical response to coral loss is a net decline in abundance, indicative of increased mortality, reduced recruitment of new individuals and/or movement of fishes to alternate habitats (Wilson et al. 2006; Bonin et al. 2009). However, communities of coral reef fishes are composed of species with varying degrees of specialization for coral and other habitats and this gives rise to a variety of responses to disturbance-induced changes in the benthos (Jones and McCormick 2002; Wilson et al. 2006; Feary et al. 2007). For example, while species that are obligate associates of live coral, either due to dietary or habitat preferences, generally decline in abundance after disturbance, herbivorous species may increase in abundance as algae replaces cover of live corals (Sano et al. 1987; Jones et al. 2004; Garpe et al. 2006; Graham et al. 2006; Wilson et al. 2006; Cheal et al. 2008; Emslie et al. 2008; Munday et al. 2008; Pratchett et al. 2008).

Coral reef fishes play an essential key role in maintaining ecological processes and functioning of reef ecosystems (Bellwood et al. 2004). The removal of higher order predators through fishing can have significant effects on coral reef ecosystem structure through the release of, generally mid-sized, meso-predators (Prugh et al. 2009; Terborgh and Estes 2010). Examples of the trophic implications of predator removal have occurred on Kenyan reefs where the heavy fishing of triggerfish has led to the release of sea urchin populations and the subsequent consumption and degradation of reef building organisms and the competitive release of algae (McClanahan 2000). Evidence on the effect

the removal of predators has on reef systems can often be masked by the past removals of species or by other stressors linked to human activities (Knowlton and Jackson 2008).

The role of disturbance in coral reefs and the prediction of likely effects of climatic changes in the future can be difficult to assess due to the temporal scales at which these processes occur. Recovery of a coral reef from large scale (tens – hundreds of km) disturbance can take more than a decade (Ninio et al. 2000; Halford et al. 2004; Osborne et al. 2011; Sweatman et al. 2011) and this process is likely to be even longer in a situation where reefs are not part of an archipelagic system of habitats such as the Great Barrier Reef (GBR). At present, there are few studies that have monitored coral reefs at sufficient time scales to fully document patterns of recovery, particularly in the case of isolated coral reef systems such as atolls (Halford and Caley 2009).

The Scott Reef system is a remote group of shelf-edge atolls in the Indian Ocean between Timor and the north-west coast of Australia. The system is located in a zone of regular cyclonic activity, suggesting that these reefs have evolved over thousands of years to withstand and recover from natural episodes of disturbance (Moberg and Folke 1999). These atolls have a diverse array of flora and fauna (Bryce et al. 2009) and currently a relatively low intensity of mostly local human impacts, and are therefore high priorities for conservation. The apex predators of Scott Reef, however, have been subjected to high levels of fishing and shark numbers are chronically low compared to the nearest un-fished reefs (Meekan and Cappo 2004; Meekan et al. 2006). To some extent, resilience will depend on the connectivity of reef systems, since this will allow new individuals to be supplied from reefs unaffected by local disturbances (e.g. Williams and Speare 2002; Halford et al. 2004). At Scott Reef, genetic analyses of fishes and corals indicates that exchange with its neighbouring systems occurs only sporadically and there may be intervals of years, decades, or even longer periods between inputs of exogenous larvae into reef populations (Underwood et al. 2009). This genetic evidence implies that many communities at Scott Reef rely on their own reproductive output to respond to disturbances such as cyclones and coral bleaching events and that as a consequence, they may be less resilient than reefs within an inter-connected, archipelagic system such as the GBR. An absence of human settlement and the reproductive and physical isolation of Scott Reef means that its reef communities are insulated from the damaging interactive disturbances that typically effect more connected and/or coastal reefs (for example nitrification, pollution and freshwater runoff), thus making it an ideal study site to measure the impacts of benthic modification (bottom-up) against a background of predator removal from fishing (top-down).

AIMS initiated long-term monitoring of fish and benthic communities at Scott Reef in 1994. This database provides a unique opportunity to examine the resilience, recovery and restructuring of reef fish communities at decadal scales after widespread and pervasive disturbance events involving both coral bleaching (Smith et al. 2008; Halford and Caley 2009), cyclonic storms overlaid on a reef subjected to apex predator removal. The monitoring program recorded densities of fishes and the percentage contributions of benthic life-form groups in shallow waters (6 to 9 m) on fixed transects at sites nested within seven locations at Scott Reef. The results were subjected to general additive mixed modelling (GAMM) and multivariate analyses to address the following questions: (1) How do patterns of benthic cover and the abundance and species richness of reef fishes change in response to two major disturbances over a 17-year study period? (2) Do the abundances of functional groups of fishes show predictable patterns of decline and recovery in response to disturbance? (3) What are the key species and functional groups most responsible for any community changes in response to disturbance and are therefore essential for maintaining ecosystem resilience? (4) How do functional groups of fishes respond to bottom-up (habitat decline) and top-down (apex predator removal) processes and can these responses be used to derive the relative importance of these processes which are both implicated in driving coral reef decline?

5.3 Materials and Methods

The study was conducted at Scott Reef, an isolated offshore reef system consisting of North Scott, South Scott and Seringapatam Reefs, which rise sharply from a water depth of *ca* 450 m in the tropical north-eastern Indian Ocean (Figure 4.1). The reef system occupies an area of *ca* 800 km² and is biogeographically important as it intersects the Indonesian and north-west Australian faunal provinces (Jones 1973; Wilson and Allen 1987). The system is largely unaffected by many of the anthropogenic stressors of coral reefs close to the coast due to its isolation, distance from shore and the absence of human settlement. However, Scott Reef is an important site for fishing by Indonesians who target a range of reef organisms (mostly shark, trepang and trochus). Stocks of these animals are now chronically over-fished (Cappo et al. 2004; Meekan et al. 2006). To quantify temporal changes in reef fish communities at Scott Reef, seven locations were surveyed in the same period (October to January) during 12 surveys between 1994 and 2010 as part of the long-term monitoring programme (LTM) at the Australian Institute of Marine Science (Heyward et al. 1998). The 1998 survey was undertaken in November *ca* 8 months after a reef-wide coral bleaching event that began in March 1998 (Smith et al. 2008).

Three locations (SS1, SS2 and SS3) were sampled on the outer reef slope and four locations (SL1, SL2, SL3 and SL4) were sampled on the inner reef slope (Figure 4.1). Within each location, fish were sampled at three sites, separated by a distance of *ca* 250 m. At each site, five permanently-marked 50 m long transects were deployed parallel to the reef crest in water depths ranging between 6 - 9 m, each separated by a distance of 10 to 20 m. Each transect was censused by a diver on SCUBA who identified and recorded the number of fishes belonging to 10 non-cryptic families (Acanthuridae, Chaetodontidae, Labridae, Lethrinidae, Lutjanidae, Scaridae, Serranidae, Siganidae, Pomacentridae and Zanclidae). The smaller, more site-attached or territorial species from the family Pomacentridae were surveyed along a 50 x 1 m corridor within the transect, while the larger, more mobile species from all other families were surveyed along a 50 x 5 m corridor. Fishes were classified into seven trophic groups based on their diet and feeding behaviour. Species classified as corallivores included both obligate and facultative coral feeders (Pratchett 2005; Wilson et al. 2006). Herbivorous species were identified as by Green & Bellwood (2009) while detritivores (including epilithic algal matrix feeders), invertivores, planktivores, omnivores and piscivores followed Froese & Pauly (2009) and Wilson et al. (2003).

Benthic communities were recorded along each transect using diver-held video or digital cameras and the point sampling technique of Page et al. (2001) was used to calculate the percentage cover of taxonomic groups and life-form categories. Cover was estimated for eighteen categories considered more likely to be associated with the habitat and dietary requirements of reef fishes; tabulate *Acropora*, branching *Acropora*, corymbose and digitate *Acropora*, bottlebrush *Acropora*, *Montipora* and other encrusting, massive coral, *Isopora* brooders, Pocilloporidae, foliose, Fungiidae, macroalgae, algal turf/coralline (including abiotic, recent dead coral and bare substrate), algae other, sand/rubble, sponge, other coral and other.

For each sampling occasion the counts of fishes were summed to site level and converted to densities (number of fish, 250m⁻²) to account for the difference in transect width. For each transect the total number of species, density of each individual fish species and the total density of fishes was calculated. The percentage contribution of each benthic category was averaged to site level. Thus, for both the fish and benthic databases there were three replicates (sites) for each location, on each sampling occasion (year).

5.3.1 Long-term trends of fish fauna

Temporal trends in the densities of fish families were examined at the reef level and within each reef using generalized additive mixed models (GAMMs) (Pinheiro and Bates 2000; Zuur et al. 2009).

These models were used to examine the relationship between fish abundance and any long-term trend. Two models were developed; firstly trends of abundance at the reef level and secondly within each reef location. The relationship between the long term trend and abundance of Pomacentridae, non-Pomacentridae, functional categories of fishes and individual fish species and species richness were explored. As the predictor (independent) variables were either linear or non-linear, GAMMS were applied because these models can accommodate both types of variables.

GAMMS extends the generalized additive model (GAM) to include random effects to account for correlation among observations on the same sampling unit. For each model, the fixed components (covariates that are not influenced by the hierarchical structure in the data) were the temporal and spatial effect. The temporal effect is the long-term time trend, which was the number of months and years elapsed since initial start date. The spatial effect determined if abundance was different among the seven reef locations. For each reef location a smoothing term was applied and so a different long-term trend was modelled to each location. The random effects component accounted for spatial variation by allowing for the three levels of spatial variability – locations, sites nested within locations and transects within sites. Observations at each level shared the same spatial variability and were regarded as non-independent. The model also allowed for different variance structures per reef location, thus all tests were corrected for spatial autocorrelation.

Several models were developed for each measure, including linear regression, linear mixed-effects models and generalized additive models. Various measures of goodness of fit were applied to identify the 'best' model, these measures included R^2 , Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and the (restricted) log-likelihood test. For almost all measures the GAMMS were the best model, hence this model was selected. All models were analysed using the R (R Development Core Team 2007) function `gamm`. Estimated trends from the GAMMS and observed means for each measure were plotted against survey month and year to provide a visual presentation of the temporal patterns, also included in each plot were the lower and upper confidence from the model.

5.3.2 Multivariate analysis

Prior to analysis, the density of each fish species was $\text{Log}_n(x+1)$ transformed, then used to construct Bray-Curtis similarity matrices. The logarithmic transformation of the fish density data ensured that some account was taken of the numerous rare species and to down-weight the contribution of the more dominant species (Clarke and Warwick 2001). The relationship between the log_{10} of the standard deviations and log_{10} of the means of the densities of each fish species demonstrated that this was an appropriate transformation (Clarke and Warwick 2001). The Bray-Curtis distance matrix derived from mean transformed values was subjected to hierarchical agglomerative clustering with group average linking (CLUSTER) and an associated Similarity Profiles (SIMPROF) test (Clarke et al. 2008) and non-metric multidimensional scaling (nMDS) ordination.

SIMPROF in conjunction with CLUSTER was used to identify whether samples from particular years grouped together and thus did not differ significantly in their species composition. This analysis was a permutation test that determined whether any significant group structure existed within a set of samples for which there was no a priori grouping hypothesis (Clarke et al. 2008). When used in conjunction with CLUSTER analysis, a SIMPROF test was performed at each node of the dendrogram to ascertain whether the particular group of samples being subdivided contained significant internal differences, except in those cases when a test carried out at a broader division returned a non-significant result. This routine thus provided a sound basis for identifying those points in the clustering procedure at which further subdivision of samples was unwarranted. The null hypothesis that there were no significant differences among groups was rejected if the significance level (p) associated with the test statistic (π) was < 0.01 .

To confirm statistical differences in composition between particular year-group categories identified in the SIMPROF procedure, Analysis of Similarities (ANOSIM) tests were used. The species composition data were composed of the Bray-Curtis similarity matrices that were constructed from replicate data. For each ANOSIM test, the null hypothesis that there were no significant differences among groups was rejected when the significance level (P) was < 0.05 . The extent of any significant differences produced by this test was determined using the R -statistic value (Clarke 1993), which can range from +1, *i.e.* all samples within each group are more similar to each other than to any of the samples from other groups, to approximately zero, *i.e.* when the similarities within and between groups are the same. As these 2-way ANOSIM tests could still hide interactions between the main factor of interest, the influence of interactions were also examined using a Permutational Multivariate Analysis of Variance test (PERMANOVA; Anderson 2001; McArdle and Anderson 2001), forgoing some of the robustness of the non-parametric approach of ANOSIM for the more penetrative and informative general linear modelling of PERMANOVA. When pairwise ANOSIM comparisons detected that the compositions of fish assemblages differed significantly among locations and/or among year categories, similarity percentages (SIMPER) was used to identify the fish species that distinguished the components of such a priori groups (Clarke 1993). We tested for community dispersion (heterogeneity) among years with Permutational analysis of multivariate dispersions (PERMDISP; Anderson 2006) using Bray-Curtis as a distance measure. PERMDISP comprises a distance-based test of the homogeneity of multivariate dispersions among groups of a single factor.

The PRIMER v6 multivariate statistics package (Clarke and Gorley 2006) with the PERMANOVA+ for PRIMER add-on module (Anderson et al. 2008) was used for all multivariate analyses.

Redundancy Analysis (RDA) was used to explore the interaction between fish species and benthic groups at Scott Reef. To provide unbiased estimates of the variation partitioning based on RDA, the fish and coral data were transformed using Hellinger (Legendre and Gallagher 2001). Rare fish species, *i.e.* occurrence of five or less individuals at reef location, were removed from the analysis. For simplicity, only fish species with an RDA of greater than 0.35 (and less than -0.35) for first three components were shown on the graph. The above analyses were implemented using R (R Development Core Team 2009) Packfor package, with statistical significance determined by 9999 permutations.

5.4 Results

Between 1994 and 1997 coral cover at Scott Reef was relatively stable and averaged around 40% of the benthic community. In 1998 there was a reef-wide and pervasive bleaching event that resulted in a steep decline of live corals to approximately 10% cover of benthic habitats. This was followed by a rise in abundance of algae, which grew over the skeletons of the recently dead corals (Figure 5.1a; Smith et al. 2008). Mean coral cover then remained low ($< 20\%$) through to 2005, but recovered to approximately pre-disturbance levels (40%) by 2010. As corals returned, cover of algae declined.

Temporal trends in densities of damselfishes, all other larger, more mobile fishes and fish species richness were fitted by GAMM models with interactions between location and year. The trend in the mean densities of the damselfishes was non-linear ($p < 0.0001$) with values declining from 1995 through 1999 before returning to higher levels in subsequent years (Figure 5.1b). In contrast, the densities of larger and more mobile fishes (non-Pomacentridae) and numbers of fish species increased linearly throughout the entire 17 year study period (Figure 5.1c,d), with the trend being greater for non-pomacentrids ($p < 0.0001$) than number of species ($p < 0.001$).

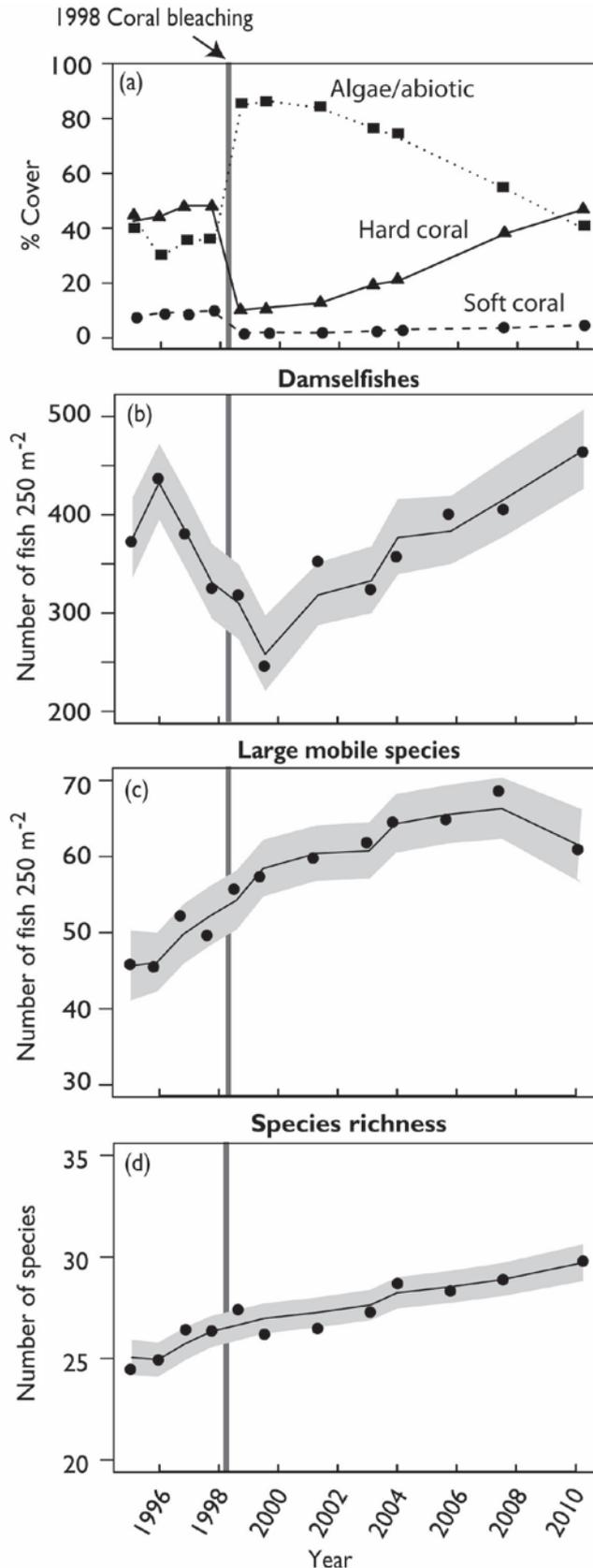


Figure 5.1. Benthic percentage cover (a) and mean densities of (b) pomacentrid and (c) non-pomacentrid (larger) fishes and (d) species richness of fishes at Scott Reef between 1994 and 2010. Solid lines are general additive mixed model (GAMM) fits, light grey shading indicates 95% confidence bands, circles are the observed mean densities and vertical grey bar indicates period of coral bleaching. All analyses were conducted at the transect level.

The composition of the fish community at Scott Reef changed throughout the study and a pronounced shift occurred following the 1998 bleaching (Figure 5.2a). The SIMPROF test of significant structure classified the samples into distinct pre-bleach, post-bleach, period of cyclones and late stage communities (phases). A nMDS ordination of the same data showed the trajectory of faunal change through time and indicated that the late stage post-bleach community in 2008 and 2010 was tracking away from earlier pre-bleach communities (Figure 5.2b). Species composition differed mostly among the four time periods (ANOSIM $R = 0.87$, $P < 0.001$) but also differed among locations (ANOSIM $R = 0.54$, $P < 0.001$). Pair-wise ANOSIM comparisons showed that the species composition of the fish faunas in each time period differed significantly from that in each other period (all $P < 0.001$), with R -statistic values ranging from 0.26 for the pre-bleach vs immediate post-bleach period comparison to 0.85 between the earliest (1994-97) vs the most recent period (Table 5.1). ANOSIM R values for comparisons between faunas of temporally contiguous periods were far less than those that were widely-separated.

Table 5.1. Pairwise R -statistic values from 2-way crossed ANOSIM (Location x Period) of the fish communities at Scott Reef between 1994 and 2010. Higher R values indicate greater dissimilarity between fish communities. The sequential increase in these values to their highest level between the earliest (pre-bleaching) and most recent communities indicates a progressive shift in the composition of fish communities at Scott Reef through time.

Period	Pre-bleaching	Post-bleaching	Cyclones
Post-bleaching	0.26***		
Cyclones	0.68***	0.43***	
Late stage	0.85***	0.80***	0.75***

*** $P < 0.001$. R values > 0.65 in bold.

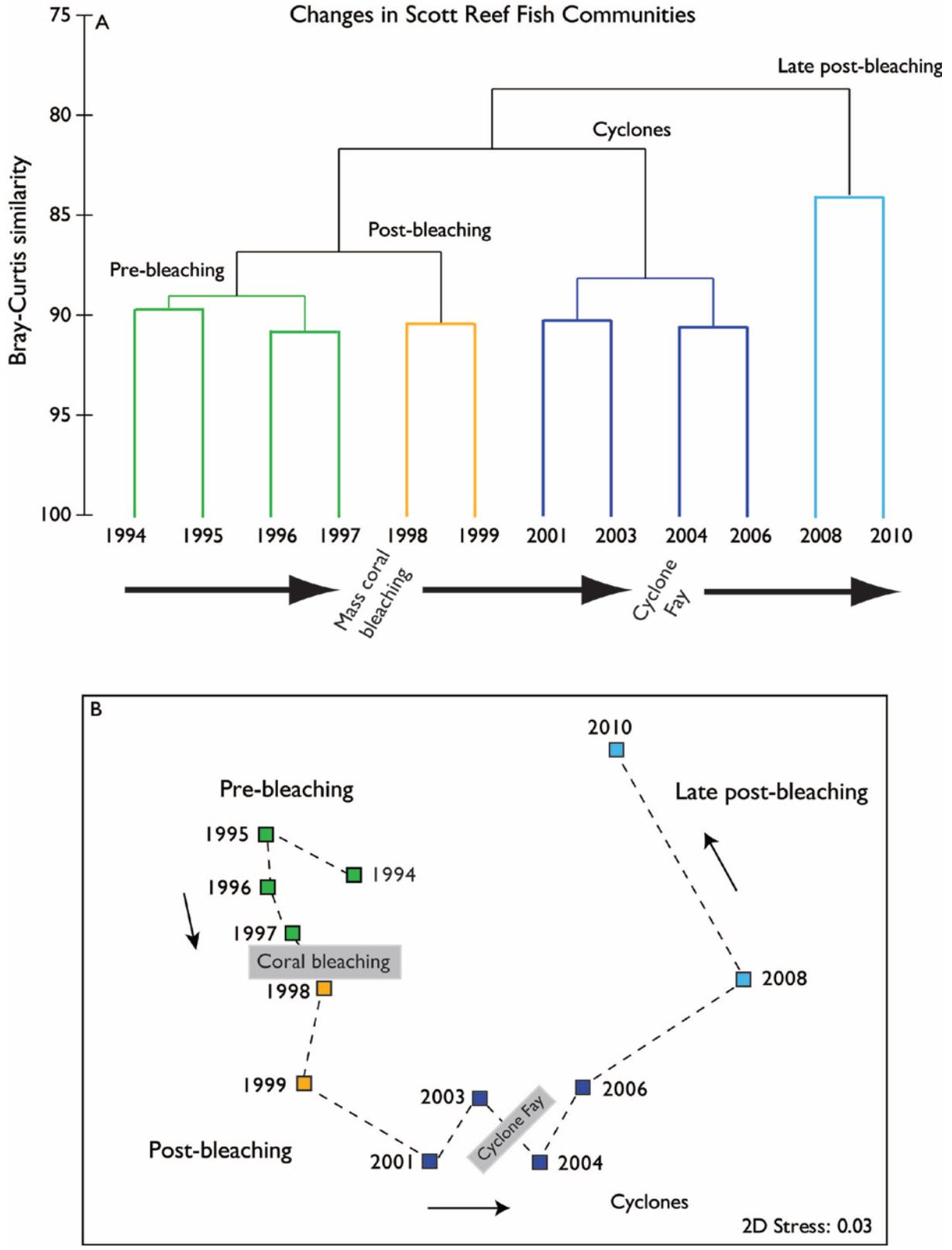


Figure 5.2. CLUSTER analysis (a), with SIMPROF of the species compositions of reef fish communities at Scott Reef between 1994 and 2010. Different coloured lines indicate groups that SIMPROF determined were significantly different from other groups and (b) Non-metric multidimensional scaling (nMDS) ordination showing the trajectory of change in the structure of fish communities at Scott Reef between 1994 and 2010. Points for each year of sampling are coloured according to the significant groups identified in the SIMPROF procedure.

Two-way PERMANOVA showed that the compositions of the fish faunas at Scott Reef were influenced significantly by location and time period and that there was a significant interaction between these factors (all $P < 0.0001$). The component of variation was far greater for location (35.5) than for either time period (15.1) or the interaction (2.1).

Trends in fish communities at Scott Reef were dominated by the response of fishes to the catastrophic bleaching event that removed *ca* 80% of all live coral cover in early 1998 (Smith et al. 2008). This response was most striking in species that are reliant on coral for food. Densities of this group declined from a high in 1996 to lows from 2001 through 2004 before a modest increase in the last two years of the study (Figure 5.3a). A similar decline in planktivores occurred following the bleaching event, although in contrast to coral feeding species, numbers of these fishes returned to pre-bleaching levels within 2-3 years of the event. Numbers of herbivores increased after the bleaching event as dead coral surfaces were overgrown by algae, and then returned to pre-bleaching levels by 2006. The abundance of detrital-feeding species also increased after the bleaching event, but have since declined and are lower in 2010 than in the pre-bleaching period. In contrast to these trophic groups, numbers of carnivores displayed no obvious response to the bleaching event and have increased linearly throughout the study.

Species that were characteristic throughout the study in each of the time periods included the surgeonfish *Ctenochaetus* spp. that consume detritus within the epilithic algal matrix (EAM) and the damselfishes *Pomacentrus lepidogenys*, *P. philippinus* and *P. vaiuli* (Table 5.2). The fauna of the early pre-bleaching period was distinguished from that in all other post-bleaching periods by greater numbers of the damselfishes *Chromis ternatensis*, *Amblyglyphidodon curacao* and *Amblyglyphidodon aureus*. The period of cyclonic disturbance was distinguished by higher densities of herbivorous species such as *Acanthurus nigrofuscus* and the territorial damselfish *Plectroglyphidodon lacrymatus*. The fauna in the most recent period (2008 to 2010) was distinguished by relatively greater contributions of the planktivores *Chromis xanthura* and the carnivorous species *Lutjanus decussates*, *Lutjanus gibbus* and *Monotaxis grandoculis* (Table 5.2). The damselfish species *Pomacentrus philippinus* and *Chromis margaritifer* also distinguished the late stage community from earlier communities.

The temporal trends for densities of the key fish species identified by the above SIMPER analysis were modelled with GAAMs and highlight contrasting trends among species belonging to the same trophic group (Figure 5.4). Mean densities of *Chaetodon punctofasciatus* and *C. trifasciatus*, which are both coral feeders, decreased following the 1998 bleaching event, with both species showing a recent increase in abundance (Figure 5.4a). In contrast, *C. vagabundus*, which also consumes coral polyps, exhibited constant increases through the bleaching to 2008. The mean densities of the herbivorous *Chlorurus sordidus* and *P. lacrymatus* increased following the 1998 bleaching through to 2004 before decreasing to 2010, whereas *Acanthurus nigricans* maintained an increasing trend in abundance through the bleaching event to 2010 (Figure 5.4b). Densities of the plankton feeding damselfish *Chromis ternatensis* decreased following the bleaching and remained low through 2004 before increasing to 2010, whereas numbers of *Pomacentrus philippinus* and *Chromis margaritifer*, also planktivores, increased immediately following the bleaching and maintained that trend so that these species are now in greater abundance than they were prior to the bleaching (Figure 5.4d).

Table 5.2. Species identified by SIMPER as typifying the fish assemblages of reefs in the six time-periods (shaded boxes) and those that distinguished between the fish assemblages for each pair of those periods (non-shaded boxes). For each pairwise comparison, the species that distinguish between the fauna of one period from that of another are indicated in superscript.

Period	Pre-bleaching	Post-bleaching	Cyclones	Late stage
Pre-bleaching 1996	<i>Pomacentrus lepidogenys</i> <i>Pomacentrus vaiuli</i> <i>Pomacentrus philippinus</i> <i>Chromis ternatensis</i> <i>Ctenochaetus</i> spp. <i>Plectroglyphidodon lacrymatus</i> <i>Chrysiptera rex</i> <i>Chromis margaritifer</i> <i>Pomacentrus moluccensis</i>			
Post-bleaching	<i>Chromis ternatensis</i> ^{pre} <i>Chromis lepidolepis</i> ^{pre} <i>Amblyglyphidodon curacao</i> ^{pre} <i>Amblyglyphidodon aureus</i> ^{pre} <i>Monotaxis grandoculis</i> ^{post} <i>Acanthurus nigrofuscus</i> ^{post} <i>Scarus schlegelii</i> ^{post} <i>Zebbrasoma veliferum</i> ^{post} <i>Scarus dimidiatus</i> ^{post} <i>Chaetodon trifasciatus</i> ^{pre}	<i>Pomacentrus lepidogenys</i> <i>Pomacentrus philippinus</i> <i>Ctenochaetus</i> spp. <i>Pomacentrus vaiuli</i> <i>Plectroglyphidodon lacrymatus</i> <i>Chlorurus sordidus</i> <i>Zebbrasoma scopas</i> <i>Chromis ternatensis</i> <i>Chrysiptera rex</i> <i>Scarus niger</i>		
Cyclones	<i>Chromis ternatensis</i> ^{pre} <i>Chromis weberi</i> ^{cyclones} <i>Amblyglyphidodon curacao</i> ^{pre} <i>Amblyglyphidodon aureus</i> ^{pre} <i>Pomacentrus moluccensis</i> ^{pre} <i>Acanthurus nigrofuscus</i> ^{cyclones} <i>Monotaxis grandoculis</i> ^{cyclones} <i>Scarus schlegelii</i> ^{cyclones} <i>Chaetodon punctatofasciatus</i> ^{pre} <i>Zebbrasoma veliferum</i> ^{cyclones} <i>Plectroglyphidodon lacrymatus</i> ^{cyclones}	<i>Chromis ternatensis</i> ^{post} <i>Amblyglyphidodon curacao</i> ^{post} <i>Amblyglyphidodon aureus</i> ^{post} <i>Chrysiptera rex</i> ^{cyclones} <i>Chromis xanthurus</i> ^{cyclones} <i>Chromis margaritifer</i> ^{cyclones} <i>Lutjanus gibbus</i> ^{cyclones} <i>Monotaxis grandoculis</i> ^{cyclones} <i>Pomacentrus philippinus</i> ^{cyclones}	<i>Pomacentrus philippinus</i> <i>Pomacentrus lepidogenys</i> <i>Chrysiptera rex</i> <i>Pomacentrus vaiuli</i> <i>Ctenochaetus</i> spp. <i>Plectroglyphidodon lacrymatus</i> <i>Chromis margaritifer</i> <i>Chromis xanthurus</i> <i>Chlorurus sordidus</i> <i>Acanthurus nigricans</i> <i>Scarus niger</i>	
Late stage	<i>Chromis weberi</i> ^{late} <i>Chromis ternatensis</i> ^{pre} <i>Amblyglyphidodon aureus</i> ^{pre} <i>Amblyglyphidodon curacao</i> ^{pre} <i>Amblyglyphidodon leucogaster</i> ^{pre} <i>Chromis xanthurus</i> ^{late} <i>Lutjanus gibbus</i> ^{late} <i>Monotaxis grandoculis</i> ^{late} <i>Acanthurus nigrofuscus</i> ^{late} <i>Acanthurus nigricans</i> ^{late} <i>Chromis margaritifer</i> ^{late} <i>Chrysiptera rex</i> ^{late} <i>Pomacentrus philippinus</i> ^{late}	<i>Chromis lepidolepis</i> ^{late} <i>Chromis ternatensis</i> ^{late} <i>Amblyglyphidodon curacao</i> ^{post} <i>Amblyglyphidodon aureus</i> ^{post} <i>Chromis weberi</i> ^{late} <i>Chromis xanthurus</i> ^{late} <i>Plectroglyphidodon lacrymatus</i> ^{post} <i>Lutjanus gibbus</i> ^{late} <i>Chaetodon trifasciatus</i> ^{late} <i>Monotaxis grandoculis</i> ^{late} <i>Dascyllus reticulatus</i> ^{late} <i>Pomacentrus philippinus</i> ^{late} <i>Chromis margaritifer</i> ^{late}	<i>Chromis ternatensis</i> ^{late} <i>Chromis weberi</i> ^{cyclones} <i>Chromis lepidolepis</i> ^{late} <i>Plectroglyphidodon lacrymatus</i> ^{cyclones} <i>Lutjanus gibbus</i> ^{late} <i>Chaetodon trifasciatus</i> ^{late} <i>Dascyllus reticulatus</i> ^{late} <i>Plectroglyphidodon dickii</i> ^{late} <i>Chromis xanthurus</i> ^{late} <i>Monotaxis grandoculis</i> ^{late} <i>Acanthurus nigrofuscus</i> ^{cyclones}	<i>Pomacentrus philippinus</i> <i>Pomacentrus lepidogenys</i> <i>Pomacentrus vaiuli</i> <i>Chrysiptera rex</i> <i>Chromis margaritifer</i> <i>Ctenochaetus</i> spp. <i>Plectroglyphidodon lacrymatus</i> <i>Chlorurus sordidus</i> <i>Chromis xanthurus</i> <i>Chromis ternatensis</i>

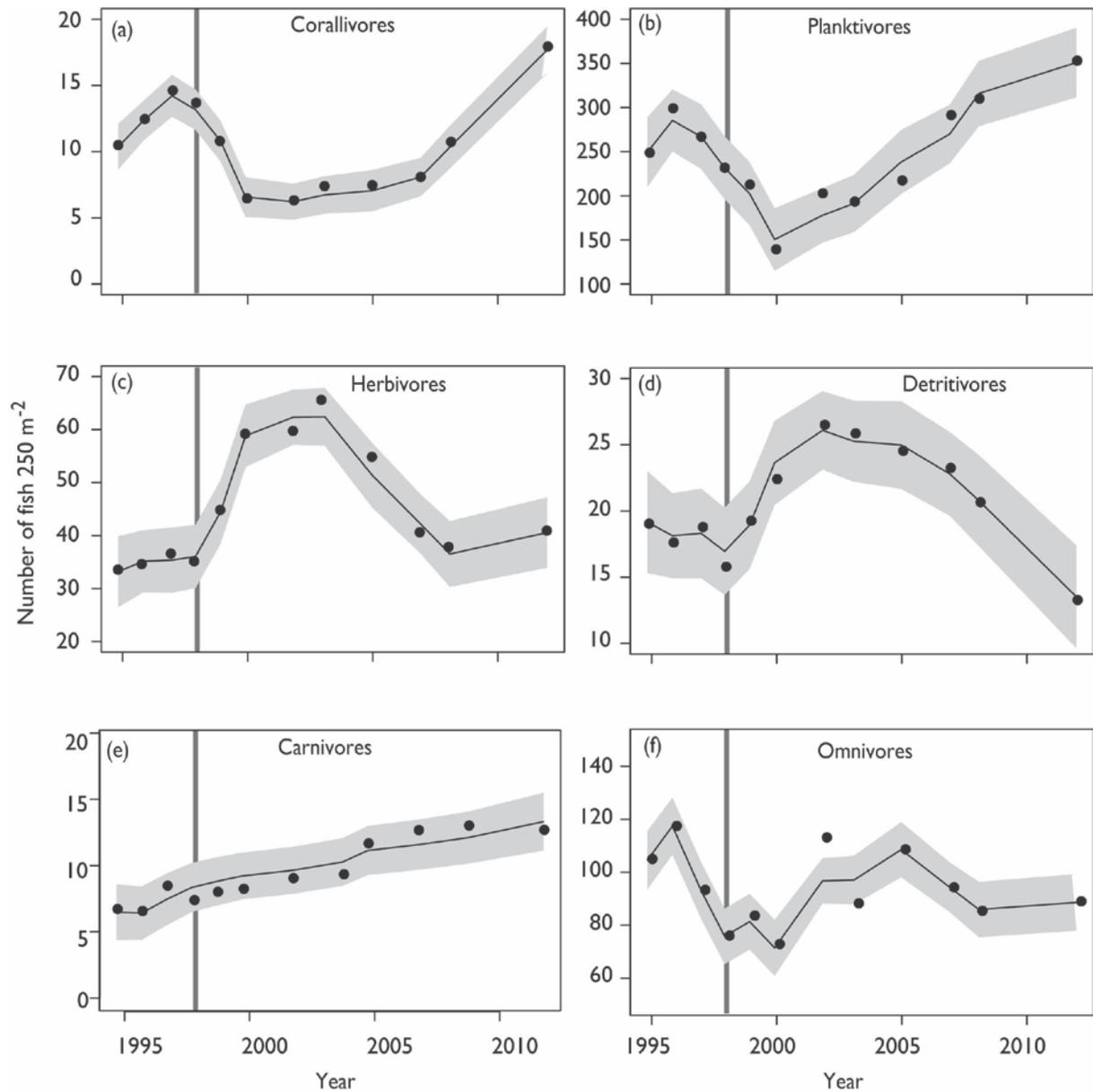


Figure 5.3. Mean (\pm 95% C.I.) densities of functional groups of fishes at Scott Reef between 1994 and 2010. Solid lines are general additive mixed model (GAMM) fits, light grey shading indicates 95% confidence bands, circles are the observed mean densities and vertical grey bar indicates period of coral bleaching. All analyses were conducted at the transect level.

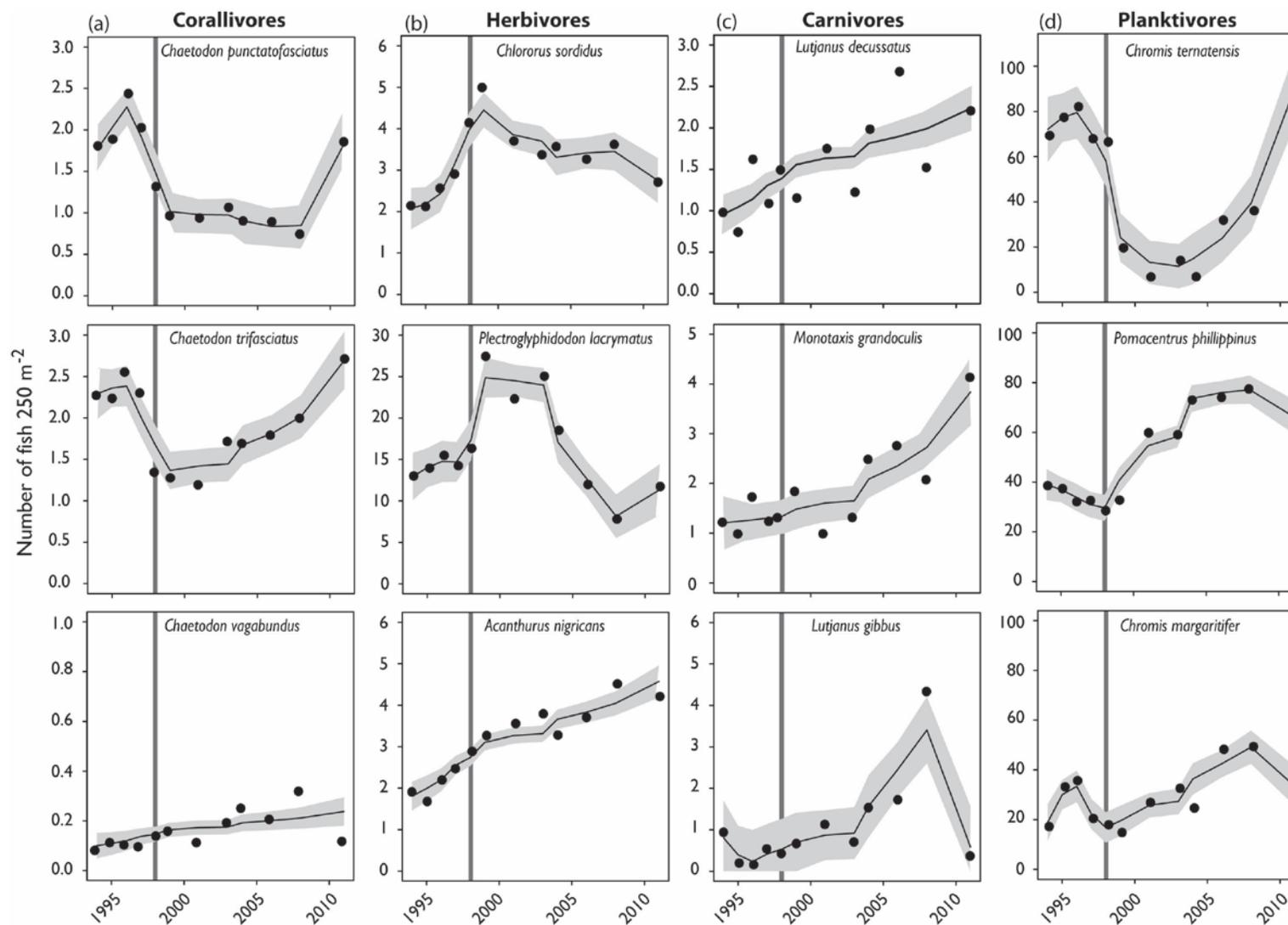


Figure 5.4. Mean (\pm 95 C.I.) densities of fish species identified by SIMPER as distinguishing particular time periods at Scott Reef between 1994 and 2008. Solid lines are general additive mixed model (GAMM) fits, light grey shading indicates 95% confidence bands, circles are the observed mean densities and vertical grey bar indicates period of coral bleaching. All analyses were conducted at the transect level.

5.4.1 Relationship between fish and the benthos

When data from both fish and benthic transects were analysed together in the RDA, selected benthic variables explained 57.2% of fish community variation (Figure 5.5). The first RDA axis captured 17.9% of total community variation, and described the fish faunal division largely in terms of fungiid and foliose coral variation which were very strongly correlated with the first axis ($R > \pm 0.8$). Massive corals, bottlebrush *Acropora* and branching *Acropora* were also closely associated with this axis ($R > \pm 0.5$). Axes 2 and 3 of the RDA captured 8.6% and 5.7% of fish faunal composition, respectively, and principally reflected variation in *Isopora* (brooding coral) and the algae-turf coralline group. Certain fish species were very closely aligned with particular benthic groups. The damselfish *Chromis ternatensis* was most abundant on transects where cover of the brooding coral *Isopora* was high, whereas the detritus feeding surgeonfish group *Ctenochaetus* spp. occurred in greatest densities where cover of algal turf/coralline algae was high (Figure 5.5). The two butterflyfish species *Chaetodon melannotus* and *Chaetodon ornatissimus* exhibited a close association with soft coral cover, which, at least in the case of the first species accounts for it feeding predominantly on soft coral (Pratchett 2005).

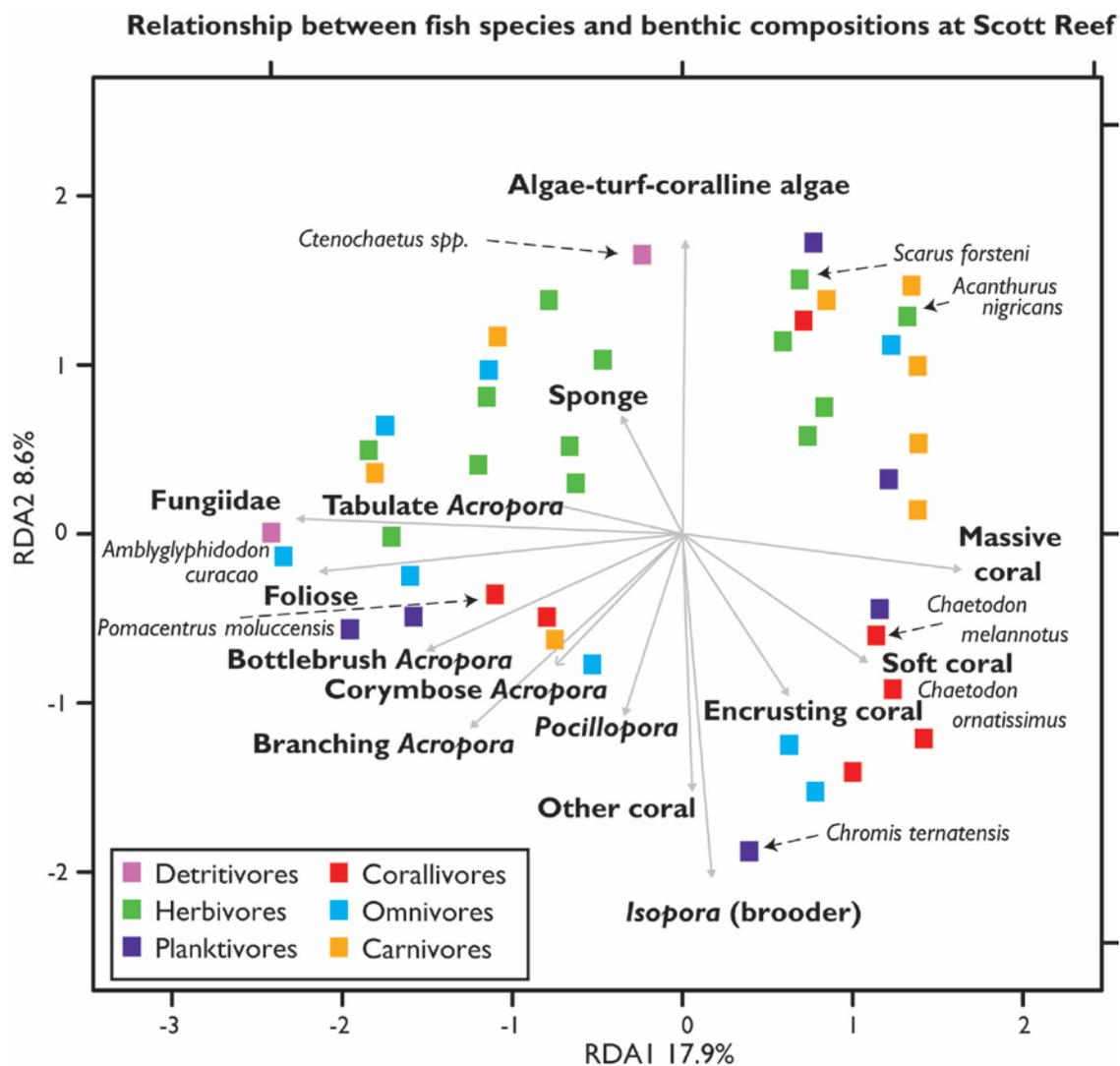


Figure 5.5. RDA correlation biplot showing the relationship between fish species and benthic composition at Scott Reef. Coloured squares represent fish species with greatest fits and are coloured according to their trophic classification. Predictor variables (arrows) point to the benthic groups that are most highly correlated with those fish species.

5.5 Discussion

5.5.1 Reassembly of fish communities in response to disturbance

Fish communities at Scott Reef have undergone significant change in composition through a 17 year period, and are now quite different to those that occurred on the reef prior to a mass coral bleaching in 1998, which reduced live coral cover by at least 75% (Smith et al. 2008). Fish assemblages on the reef underwent three distinct phases during the study from (1) a pre-bleached community dominated by habitat and dietary specialists (predominantly coral and plankton feeders) through (2) an intermediate post-bleach community characterized by species that have a preference for the habitat types resulting from coral bleaching, either directly through the erosion of dead coral into rubble habitats or from the increase in area available for turf algae to (3) the most recent fish community characterized by mid-sized carnivorous species and also fish that have generalist diet and habitat requirements. The effect of the bleaching event in 1998 was most striking on the obligate associates of live coral, species that used coral either for food such as butterflyfishes (Cole et al. 2008) or for protection such as many planktivorous damselfishes (Wilson et al. 2008). Following death of the coral and overgrowth by algae, abundances of herbivores increased, as did numbers of detritivores, which probably benefitted from the trapping of detritus by rubble and algal turfs. There was a lag of 12-18 months in the response of some trophic groups to the bleaching, likely to be roughly equivalent to the time taken for the structure of the dead coral to decompose to rubble and for effects on those species that used live coral as a habitat for recruits to flow through to adult populations (Halford and Caley 2009).

The fact that the ANOSIM *R*-statistic values were greatest for the comparison between faunas of the pre-bleaching and most recent communities (0.85) and least for comparisons between faunas of temporally contiguous periods (< 0.30), is strong evidence that the reef fish faunas at this isolated system are undergoing continuous successional change, but are now comprised of a suite of species that differs to those at the reef prior to the 1998 coral bleaching. This result implies that an earlier suggestion that fish communities at Scott Reef in 2003 were returning to pre-bleaching structures by Halford & Caley, (2009) has not been realised. The reasons for this may include destructive waves generated by the passage of Cyclone Fay directly over Scott Reef in early 2004 (Smith et al. 2006), which may have caused additional changes to the composition of the benthic community and hindered the recovery of the fish community towards a pre-bleach structure. In any event, our long-term (17 year) data set revealed a sequence of ongoing increases and decreases in the abundance of functionally significant groups of fishes that may not be readily apparent in short and medium-term studies (e.g. Sano et al. 1984).

In highly connected reef systems, such the GBR, studies of the effect of catastrophic loss of coral cover on fish communities report high levels of resilience with assemblages returning close to pre-disturbance structures within 10 to 20 years (Bohnsack 1983; Connell 1997; Sano 2000; Williams and Speare 2002; Halford et al. 2004). At other isolated atolls similar to Scott Reef, fish communities have shown both evidence of recovery from the 1998 bleaching event (Sheppard et al. 2008), while others have shown little or no recovery (Graham et al. 2006). Some of these differences may simply reflect the duration of the study and extent of the disturbance event, with communities showing a high degree of resilience reflecting in part, the ability of longer-lived fishes to move among habitats in response to disturbance. However, a study of cryptobenthic fish communities on the GBR has also identified a phase shift from a pre-bleach to a post-bleach fish community (Bellwood et al. 2006a) that has persisted for at least five years after the disturbance event. Thus, a significant increase in the number of dietary and habitat generalist species in post-bleaching fish assemblages has now been recorded for both isolated (present study) and connected (GBR) (Bellwood et al. 2006a) reef systems. The high Pearson correlation value from the RELATE analysis of matrices derived from pomacentrid and non-pomacentrid fishes suggests that the pattern of change for both short and long lived reef fishes are similar. Continued monitoring at Scott Reef is required to determine whether

the late post-bleach fish community identified in the present study is a transitional rather than a stable state.

5.5.2 Characteristics of pre-bleached and post-bleached communities

A review of the effects of coral bleaching on reef fishes (Pratchett et al. 2008) has highlighted that coral cover and topographic complexity are the critical components of coral reef habitats that shape their fish communities. Multivariate linkage trees (LINKTREE) has clearly demonstrated that the pre-bleach fish community at Scott Reef was correlated with greater cover of soft corals, branching *Isopora* and corymbose and digitate *Acropora* corals, each of which suffered massive mortality in the subsequent coral bleaching (Gilmour et al. 2009). The pre-bleached fish community at Scott Reef was characterized by the presence of coral-dwelling fishes that feed mainly on coral or plankton such as *Chromis ternatensis*, *Pomacentrus lepidogenys* and *Chaetodon punctatofasciatus*. Trends in abundance of pomacentrids at Scott Reef closely followed the progressive changes in cover of live hard coral. Coral dependency for pomacentrids is high compared to other coral reef fishes and ca 20% of all pomacentrid species on the GBR rely on coral either for food or shelter (Munday et al. 2007).

The intermediate post-bleach fish community between 2001 and 2004 was distinguished from that in 2008 by greater contribution of algae and reduced contributions of tabulate *Acropora*, pocilloporids, massive and encrusting corals and sponges. It is not surprising that the fish species that distinguished this community (e.g. *Plectroglyphidodon lacrymatus*, *Ctenochaetus* spp. and various labrids) are not as reliant on live coral and feed predominantly on algae that they farm and defend aggressively (Ceccarelli et al. 2001) or graze within it to consume the detrital material that comprise their diet (Wilson et al. 2003). The decrease in numbers of *P. lacrymatus* in the late post-bleach period (after 2005) presumably reflects the gradual erosion of the dead branching corals utilised as algal farm sites by this territorial herbivore and the increase in tabulate *Acropora* which appears difficult for this species to defend.

The greater and more consistent densities of *Chromis xanthurus*, *Chromis margaritifer* and *Chrysiptera rex* in the late stage community of 2008 to 2010, played an important role in distinguishing the reef fish fauna of this period. These three planktivorous damselfishes are not associated with live coral and utilise a wide variety of reef microhabitats. Such generalist species are predicted to be more resilient to changing resource availability than specialists with a narrower trophic niche such as *C. ternatensis* (Wilson et al. 2008). Dead coral or rubble-associated fishes also increased in numbers following disturbance at reefs in Papua New Guinea (Jones et al. 2004).

Regime shifts of disturbed reef ecosystems to communities characterised by macroalgal dominance may not be as common as first thought (Bruno et al. 2009) and other alternate states of reefs are also likely (Bellwood et al. 2004; Norström et al. 2009), particularly in the case of Indo-Pacific reefs (Green and Bellwood 2009). Herbivorous reef fishes are hypothesized to play an important role in avoiding or reversing other alternate states on coral reefs and avoiding coral-algal phase shifts by limiting the establishment and growth of algal communities that impede coral recruitment (Bellwood et al. 2004; Bellwood et al. 2006b; Hughes et al. 2007; Bellwood and Fulton 2008) and therefore coral reef resilience (Nystrom and Folke 2001; Bellwood et al. 2004). Bellwood et al. (2006a) stressed the importance of identifying and protecting groups of fishes involved in the resilience and regeneration of disturbed reef systems, thus the high numbers of herbivorous fishes in the post-bleaching period at Scott Reef, will presumably play an important role in the longer-term resilience of Scott Reef.

5.5.3 Patterns of diversity and abundance of fishes at Scott Reef

Although the separation of the reef fish faunas at Scott Reef into distinct pre- and post-bleaching communities parallels the results of Bellwood et al. (2006a) on the GBR, our results contrast, to some degree, with the abundance and diversity metrics presented by their study. On the GBR, there was a gradual increase in abundance of cryptobenthic fishes following the 1998 bleaching, however, there was no discernible trend for species richness. The use of a range of traditional community metrics and species composition data in the present study highlights that while the increases in the abundance and species richness of fishes could be interpreted as a sign of the resilience of the coral reef ecosystem (*sensu* Kokita & Nakazono 2001; Booth & Beretta 2002; Halford et al. 2004), the changes in community and functional composition reveal a response to the coral bleaching that shows that ecosystem processes have probably been modified. This reinforces the cautions of both Jones & Syms (1998) and Bellwood et al. (2006a) of the importance of choosing the most appropriate measure of community structure to evaluate the resilience of coral reef ecosystems and enable comparisons with other published studies of disturbance.

5.5.4 Release of meso-predators at Scott Reef

Unlike benthic communities, for which disturbance due to bleaching and cyclones are the principal and obvious drivers of change in patterns in abundance and structure, we detected significant trends in fish assemblages during the 17 years of our study that did not respond clearly to the impacts of these disturbance events. For example, we found that the numbers of larger, mobile reef fishes steadily increased during the study, particularly in the case of carnivorous species belonging to the families Lethrinidae, Lutjanidae and Serranidae. This increase in abundance was accompanied by an increase in the number of fish species recorded in our transects. These trends were apparently unaffected by the major bleaching event or the passage of cyclones across the reef.

One possibility is that these patterns were the result of increasing fishing pressure on Scott Reef by Indonesian fishermen that have targeted large predatory reef fish and sharks over the last decade. Stocks of some of these species are now chronically over-fished (Cappo et al. 2004). Studies on other reef systems (Sandin & Pacala 2005; DeMartini et al. 2008) have shown that apex predator release can result in fundamental changes to the biomass and abundance of lower trophic levels in coral reef ecosystems, which might account for some of the changes recorded by our study. In particular, this might explain the increasing number of carnivorous species over the duration of the study. This hypothesis could be tested by comparing trends and composition of reef fish assemblages at Scott Reef with those of the Rowley Shoals, where there is very little or no fishing pressure and stocks of predatory fishes remain in pristine condition.

There is thus a clear line of evidence in the present study that the fish communities of this isolated reef system are operating under synergistic top down (predator removal) and bottom up (benthic habitat availability) forces that are influencing the functional composition of this reef fish community. The very low abundances of apex predators, most likely due to fishing (Meekan and Cappo 2004; Meekan et al. 2006), has resulted in the likely release from predation of the meso-predator group of mid-sized carnivores that have increased linearly in abundance throughout the 17 year period of this study and which SIMPER determined were species that distinguished the most recent community from all others. In contrast, environmental bottom up forcing has controlled the concaved pattern of change in the abundance of smaller damselfish, many of which have life-cycles closely linked to benthic structure such as coral.

While relatively few coral reef fishes are at risk of global extinction due to climatic disturbance, the entire fish community is vulnerable at reefs where they are influenced by both fisheries exploitation and factors related to climate change (Graham et al. 2010). Furthermore, fish species involved in maintaining ecosystem functions are those more susceptible to fishing than climate disturbance

(Graham et al. 2010). Scott Reef is currently subjected to factors related to global climate change, such as coral bleaching and frequent and intense storms, and also to the effects of fishing, such as the extraction of shark species from the apex predator community within the system. As populations of marine species within the Scott Reef system are likely to be self recruiting (Underwood et al. 2009; Underwood et al. 2011), the progressive increase in meso-predatory reef fish species serves to highlight the urgent need to undertake further ecosystem based research to inform managers before the damaging impact of a more permanent shift in ecosystem function occurs, such as a trophic cascade (Terborgh and Estes, 2010).

5.6 References

- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32-46
- Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62: 245-253
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods PRIMER-E, Plymouth
- Balmford A, Bond W (2005) Trends in the state of nature and their implications for human well-being. *Ecology Letters* 8: 1218-1234
- Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* 429: 827-833
- Bonin MC, Srinivasan M, Almany GR, Jones GP (2009) Interactive effects of interspecific competition and microhabitat on early post-settlement survival in a coral reef fish. *Coral Reefs* 28: 265-274
- Bryce CW, Whisson C, Fromont J, Huisman J, McKinney DW, Morrison S, Moore G, Titelius M, Hass C, Morrison P, Kernohan (2009) A marine biological survey of Mermaid Reef (Rowley Shoals), Scott and Seringapatam Reefs. Western Australian Museum, Perth, Western Australia
- Cappo M, Meek MR, Perry M, McCauley R, Harvey ES (2004) Traditional fishing puts the bite on sharks. *Australasian Science* 25: 29-32
- Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. *Bioscience* 35: 634-639
- Cheal AJ, Wilson SK, Emslie MJ, Dolman AM, Sweatman H (2008) Responses of reef fish communities to coral declines on the Great Barrier Reef. *Marine Ecology-Progress Series* 372: 211-223
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117-143
- Clarke KR, Gorley RN (2006) PRIMER v6: User manual tutorial. PRIMER-E, Plymouth
- Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology* 366: 56-69
- Clarke KR, Warwick RM (2001) *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*, 2nd edn. PRIMER-E, Plymouth Marine Laboratory, Plymouth
- Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries* 9: 286-307
- Connell JH (1978) Diversity in tropical rain forests and coral reefs - high diversity of trees and corals is maintained only in a non-equilibrium state. *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
- Emslie MJ, Cheal AJ, Sweatman H, Delean S (2008) Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. *Marine Ecology-Progress Series* 371: 177-190
- Feary DA, Almany GR, Jones GP, McCormick MI (2007) Coral degradation and the structure of tropical reef fish communities. *Marine Ecology-Progress Series* 333: 243-248
- Froese R, Pauly D (2009) FishBase. World Wide Web electronic publication. Available from www.fishbase.org
- Garpe KC, Yahya SAS, Lindahl U, Ohman MC (2006) Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Marine Ecology-Progress Series* 315: 237-247
- Gilmour JP, Travers MJ, Underwood JN, McKinney DW, Gates EN, Fitzgerald KL, Birrell CL (2009) Long-term monitoring of shallow-water coral and fish communities at Scott Reef. *AIMS*

- SRRP Technical Report - Project I. Report to the Browse Joint Venture Partners. Australian Institute of Marine Science, Perth, Western Australia
- Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 103: 8425-8429
- Green AL, Bellwood DR (2009) Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience. A practical guide for coral reef managers in the Asia Pacific Region. Australian Research Council Centre of Excellence for Coral Reef Studies and the School of Marine and Tropical Biology, James Cook University of North Queensland
- Halford A, Cheal AJ, Ryan D, Williams DM (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology* 85: 1892-1905
- Halford AR, Caley MJ (2009) Towards an understanding of resilience in isolated coral reefs. *Global Change Biology* 15: 3031-3045
- Heyward, A., A. Halford, et al. (1998). Temporal and spatial patterns of coral and fish assemblages at Scott Reef, 1994-1997, Australian Institute of Marine Science: 57.
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50: 839-866
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatzioiols ME (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318: 1737-1742
- Hughes TP (1994) Catastrophes, Phase-Shifts, and Large-Scale Degradation of a Caribbean Coral-Reef. *Science* 265: 1547-1551
- 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, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301: 929-933
- Hughes TP, Connell JH (1999) Multiple stressors on coral reefs: A long-term perspective. *Limnology and Oceanography* 44: 932-940
- Huston M (1979) General Hypothesis of Species-Diversity. *American Naturalist* 113: 81-101
- Huston MA (1985) Patterns of species diversity on coral reefs. *Annual Review of Ecology and Systematics* 16: 149-177
- IPCC (2007) Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Switzerland, Geneva
- Jones GP, McCormick MI (2002) Numerical and energetic processes in the ecology of coral reef fishes. In: Sale PF (ed) *Coral reef fishes; dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, pp 221-238
- Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences of the United States of America* 101: 8251-8253
- Jones HA (1973) Marine geology of the northwest Australian continental shelf. Bureau of Mineral Resources. *Geology and Geophysics Bulletin* 136
- Knowlton N, Jackson JBC (2008) Shifting baselines, local impacts, and global change on coral reefs. *Plos Biology* 6: 215-220
- McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology* 82: 290-297
- McClanahan TR (2000) Recovery of a coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. *Biological Conservation* 94: 191-198
- McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J, Barnes D (2003) Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. *Nature* 421: 727-730

- Meekan M, Cappo M (2004) Non-destructive Techniques for Rapid Assessment of Shark Abundance in Northern Australia, Report prepared for the Australian Government Department of Agriculture, Fisheries and Forestry Australian Institute of Marine Science
- Meekan M, Cappo M, Carleton J, Marriott R (2006) Surveys of Shark and Fin-fish abundance on reefs within the MOU74 Box and Rowley Shoals using Baited Remote Underwater Video Systems. Report for the Australian Government Department of Environment and Heritage. Australian Institute of Marine Science
- Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. *Ecological Economics* 29: 215-233
- Mumby PJ, Hastings A, Edwards HJ (2007) Thresholds and the resilience of Caribbean coral reefs. *Nature* 450: 98-101
- Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. *Fish and Fisheries* 9: 261-285
- Ninio R, Meekan M, Done T, Sweatman H (2000) Temporal patterns in coral assemblages on the Great Barrier Reef from local to large spatial scales. *Marine Ecology-Progress Series* 194: 65-74
- Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternate states on coral reefs: beyond coral-macroalgal phase shifts. *Marine Ecology Progress Series* 376: 295-306
- Osborne K, Dolman AM, Burgess SC, Johns KA (2011) Disturbance and the Dynamics of Coral Cover on the Great Barrier Reef (1995-2009). *PLoS One* 6
- Page CA, Coleman G, Ninio R, Osborne K (2001) Surveys of benthic reef communities using underwater video. Australian Institute of Marine Science, Townsville, Queensland
- Pinheiro JC, Bates DM (2000) Mixed effects Models in S and S-PLUS. Springer
- Polis GA, Sears ALW, Huxel GR, Strong DR, Maron J (2000) When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution* 15: 473-475
- Pratchett MS (2005) Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. *Marine Biology* 148: 373-382
- Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR (2008) Effects of climate-induced coral bleaching on coral-reef fishes - Ecological and economic consequences *Oceanography and Marine Biology: An Annual Review*, Vol 46, pp 251-296
- Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS (2009) The Rise of the Mesopredator. *Bioscience* 59: 779-791
- Sano M, Shimizu M, Nose Y (1984) Changes in structure of coral reef fish communities by destruction of hermatypic corals: observational and experimental views. *Pacific Science* 38: 51-80
- Sano M, Shimizu M, Nose Y (1987) Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. *Marine Ecology Progress Series* 37: 191-199
- Smith LD, Gilmour JP, Heyward AJ (2008) Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. *Coral Reefs* 27: 197-205
- Strong DR (1992) Are trophic cascades all wet - differentiation and donor-control in speciose ecosystems. *Ecology* 73: 747-754
- Sweatman H, Delean S, Syms C (2011) Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends. *Coral Reefs* 30: 521-531
- Terborgh J, Estes JA (2010) Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, D.C.
- Underwood JN, Smith LD, van Oppen MJH, Gilmour JP (2009) Ecologically relevant dispersal of corals on isolated reefs: implications for managing resilience. *Ecological Applications* 19: 18-29
- Veron JEN (2008) A Reef in Time. The Great Barrier Reef from Beginning to End. The Belknap Press of Harvard University Press, London, England

- Williams DM, Speare PJ (2002) Long-term (17 y.) Impacts of crown-of-thorns outbreak and loss of live coral cover on reef fish communities (Central Great Barrier Reef) 9th International Coral Reef Symposium, Bali, Indonesia
- Wilson BR, Allen GR (1987) Major components and distribution of marine fauna Fauna of Australia. Australian Government Publishing Service, Canberra, pp 43-68
- Wilson SK, Bellwood DR, Choat JH, Furnas MJ (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes Oceanography and Marine Biology, Vol 41, pp 279-309
- Wilson SK, Burgess SC, Cheal AJ, Emslie M, Fisher R, Miller I, Polunin NVC, Sweatman HPA (2008) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology* 77: 220-228
- Wilson SK, Dolman AM, Cheal AJ, Emslie MJ, Pratchett MS, Sweatman HPA (2009) Maintenance of fish diversity on disturbed coral reefs. *Coral Reefs* 28: 3-14
- Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology* 12: 2220-2234
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R* (Statistics for Biology and Health). Springer, New York

6. Size structure of hard corals

6.1 Summary

The size-frequency distributions of selected hard coral genera were recorded at 6 long-term monitoring locations across Scott Reef between 1996 -2010. The most obvious change in colony abundance and size-structure was the widespread death of corals following the mass-bleaching in 1998. Coral populations have been recovering at an increasing pace since this time.

There was evidence of a sudden increase in the larval supply of corals to all Scott Reef locations in 2008, after ten years of low recruitment following the 1998 bleaching. Since the recovery of larval supply in 2008, a dramatic increase in the number of small *Acropora* colonies can be seen at all locations in the most recent size-frequency survey conducted in October 2010, with a strong correlation between relative larval supply and 0-2 cm recruits at each location. This rapid increase in colony numbers indicates that changes in larval supply can drastically alter the rate of recovery in fast-growing species such as *Acropora*.

Two smaller-scale disturbances were recorded at Scott Reef between 2008 and 2010. Importantly, recent incidence of disease in tabulate *Acropora* at locality SL2 has dramatically changed the size-frequency distribution of *Acropora*. Previously, corals at this locality displayed a bimodal distribution dominated by large colonies, but in 2010 there were very few large colonies and an increase in small colonies due to recruitment. The recent dramatic loss of adult *Acropora* at this location may decrease larval supply to this and other locations at Scott Reef. In May 2010, a bleaching event affected vulnerable species at certain localities on Scott Reef. Pocilloporidae were most affected by recent bleaching, and the loss of between 59-76% of *Pocillopora* colonies is evident in the size-frequency data at the outer reef slope locations SS1 and SS2, along with smaller reductions at the 4 lagoon locations. The size-structure of massive *Porites* was recorded in 2010 for the first time since 2003. The slow-growing massive *Porites* were least affected by the 1998 bleaching, but there has been little change in size-structure of this family compared with faster-growing genera, such as *Acropora* and *Pocillopora*. The abundance and size-structure of massive *Porites* colonies in 2010 were similar to that prior to mass-bleaching at most locations.

6.2 Introduction

Size-frequency distributions can provide more information on the status and prognosis for coral populations than cover alone, as coral cover is biased by large colonies and is not suited to detect changes in numbers of recruits or juvenile corals. The use of size-frequency data can illuminate more of the demographic processes behind the decline, recovery or stability of a coral reef in response to environmental conditions (Connell 1973; Meesters et al. 2001). For example, it can show the life history strategies of species groups, indicate stages of recovery, identify periods of good or poor recruitment and the increase or decrease of certain size classes through disturbance, partial or whole colony mortality and fragmentation (Ebert et al. 1993; Bak and Meesters 1999; Edmunds and Elahi 2007; McClanahan et al. 2008). At Scott Reef the size-frequency distributions of four dominant groups of scleractinian corals (*Acropora*, *Isopora*, *Pocillopora*, and massive *Porites*) were quantified over 14 years, through five disturbance events; the mass bleaching of 1998, Cyclone Fay in 2004 and Cyclone George in 2007, and bleaching and disease outbreaks in 2010. The effect of these disturbances and subsequent recovery has been different for each of the coral groups studied.

6.3 Methods

The size frequency of four dominant groups of scleractinian corals, *Acropora*, *Pocillopora*, *Isopora*, and *Porites* was measured at Scott Reef in 1996, 1998, 1999, 2003-2006, 2008 and 2010. The locations studied were the 6 Reef slope locations at Scott Reef SL1 - SL4, SS1 and SS2. Ten permanent transects were surveyed at each location. Coral colonies larger than 10cm were measured in belt transects 1m x 20m, and colonies smaller than 10cm were measured in belt transects of 25cm x 20m (Figure 6.1). Counts of colonies <10cm were standardised to 20m² to match the area in which the large colonies were measured. Measurements were made of the longest linear dimension, and have been grouped here into size classes: 0-2cm, 3-5, 6-10, 11-15, 16-20, 21-30, 31-50, 50-100, and >100cm.

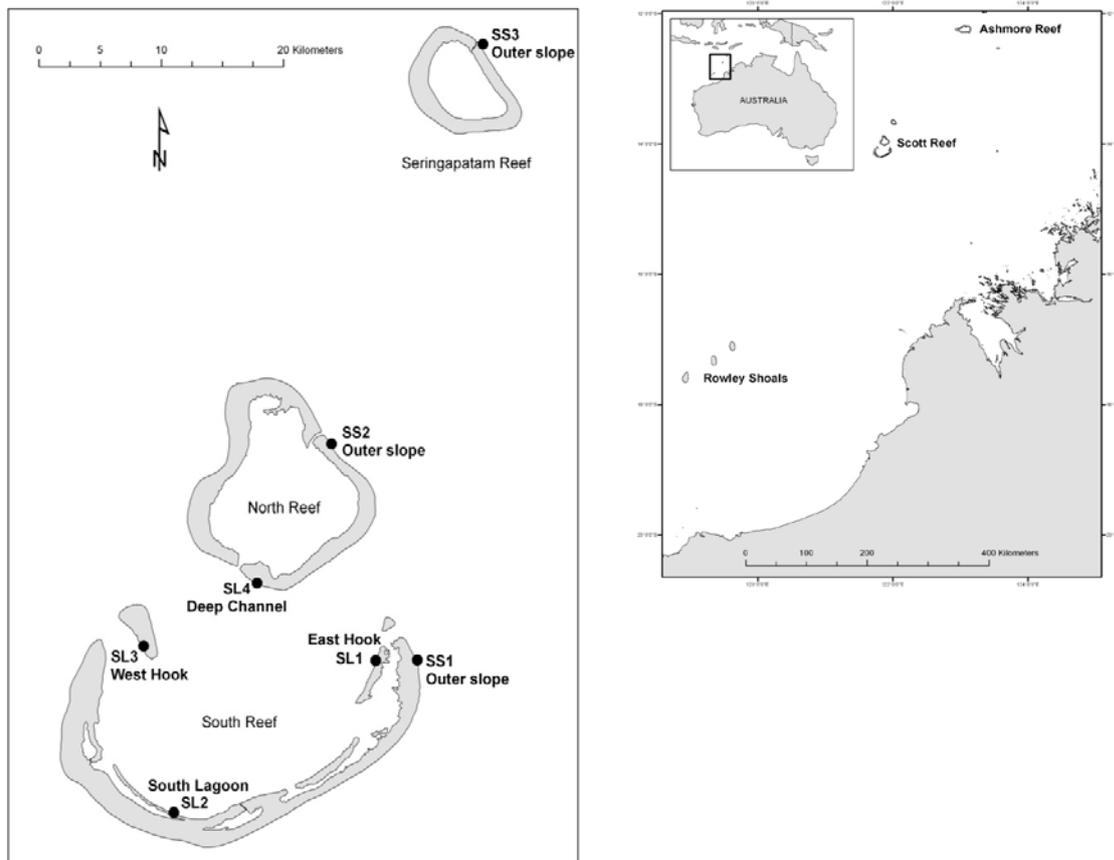


Figure 6.1 Position of Scott Reef off north-western Australia and its study locations. Locations are on the outer- (SS1, SS2, SS3) and inner-slope, with further distinction among inner-slope locations according to their proximity to East Hook (SL1), the Southern Lagoon (SL2), the West Hook (SL3) and the Deep Channel (SL4).

6.4 Results and Discussion

The coral communities of Scott Reef have been slowly recovering since the mass bleaching in 1998. The effect of this disturbance and the speed and dynamics of recovery were different for each of the coral groups due to differences in life-history traits such as growth rate and form, reproductive mode, and susceptibility to disturbance. Recovery of the coral communities at each of the locations also differed and was dependant on the severity of the bleaching (least severe at SL3 and SL4), exposure to cyclones (outer slope reefs SS1 and SS2), water quality (lowest at SL2), and larval supply

(highest at SL1). By 2008, scleractinian coral cover had returned to near pre-bleaching levels at most locations. In the 2010, size-frequency data reflect the: 1) recent recovery of larval supply in 2008 to pre-bleaching levels after 10 years of low larval supply following the 1998 bleaching; 2) the outbreak of disease in large *Acropora* colonies mostly at location SL2. 3) small-scale bleaching event in May 2010 that affected vulnerable coral groups such as Pocilloporidae, mostly at the outer reef locations SS1 and SS2.

6.4.1 *Acropora*

Acropora is the dominant coral genera at Scott Reef. Although the 1998 bleaching heavily reduced colony numbers across the reef, *Acropora* communities have now recovered to levels within or higher than pre-bleaching years at most locations. The fast growth rate of *Acropora* compared to many massive species allows it to quickly occupy space freed by disturbance (Smith et al. 2008). However, *Acropora* is also relatively vulnerable to various disturbances. In the most recent survey period, two main changes are seen in the size structure of the *Acropora* communities. The first is the effect of the return of high levels of larval supply in 2008. *Acroporidae* larval supply was drastically reduced following the 1998 bleaching and remained below 3% of pre-bleaching levels until 2004, was at 15% in 2006, and had returned to pre-bleaching levels by 2008. The effect of this increase in supply can be seen in the 2010 size-frequency data, where the number of colonies in small size classes has increased dramatically across the reef (Figure 6.2). The locations that show the highest increase in 0-2 cm colonies in 2010 are the locations that received the highest larval supply in 2009. SS2 had the highest larval supply in 2009 and the number of 0-2cm *Acropora* recruits counted on the transects at this location increased from 203 in 2008 to 4369 in 2010. Location SL1 had the second highest larval supply in 2009 and the second greatest increase in recruits, SL4 had the least larval supply and subsequently the lowest change in recruits in 2010. The increase in recruits has changed the shape of the size-frequency distributions. In 2010, size structure of *Acropora* was strongly skewed to the right (dominated by small size classes), which is typical of corals with fast growth rates and high recruitment (Meesters et al. 2001). The strong correlation between settlement rates and recruit cohorts at the location scale suggest that rate of recovery for *Acropora* following the 1998 bleaching would have been significantly faster if larval supply had not been so severely depressed until 2008.

A disease outbreak in the adult colonies of *Acropora* in 2009 also had a significant effect on the size structure of *Acropora* communities at some locations. Most of the effect was seen at SL2, where the total number of adult *Acropora* colonies (>15cm) decreased by 81% from 1454 to 267 between 2008 and 2010 (Figure 6.3). The number of small colonies at SL2 increased during this period either through new recruitment or partial mortality. There was also a smaller reduction in the large *Acropora* colonies at SL1, where a disease outbreak was observed. The loss of large *Acropora* colonies at SL2 changed the size-frequency distribution of this community dramatically (Figure 6.2). Previously, the community was dominated by large adults, but almost all of the large colonies have disappeared since the outbreak of disease, and the distribution at SL2 is now right skewed (dominated by small colonies). The loss of brood-stock at this location may reduce *Acropora* larval supply to other areas of Scott Reef during subsequent spawning events.

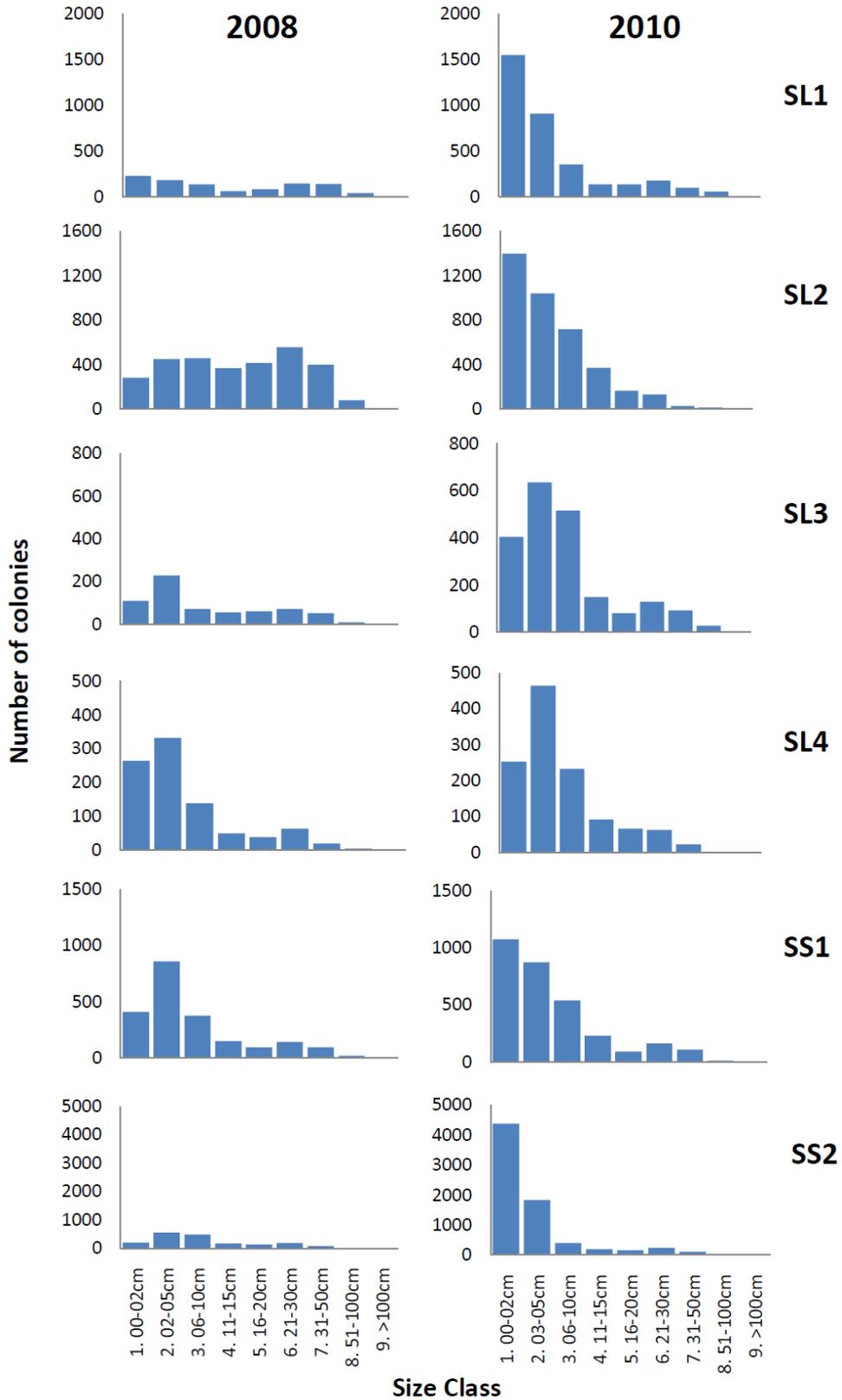


Figure 6.2 Size-frequency distributions of *Acropora* communities at each location in 2008 and 2010. An increase in the abundance of small colonies between 2008 (left graphs) and 2010 (right graphs) can be seen at all locations.

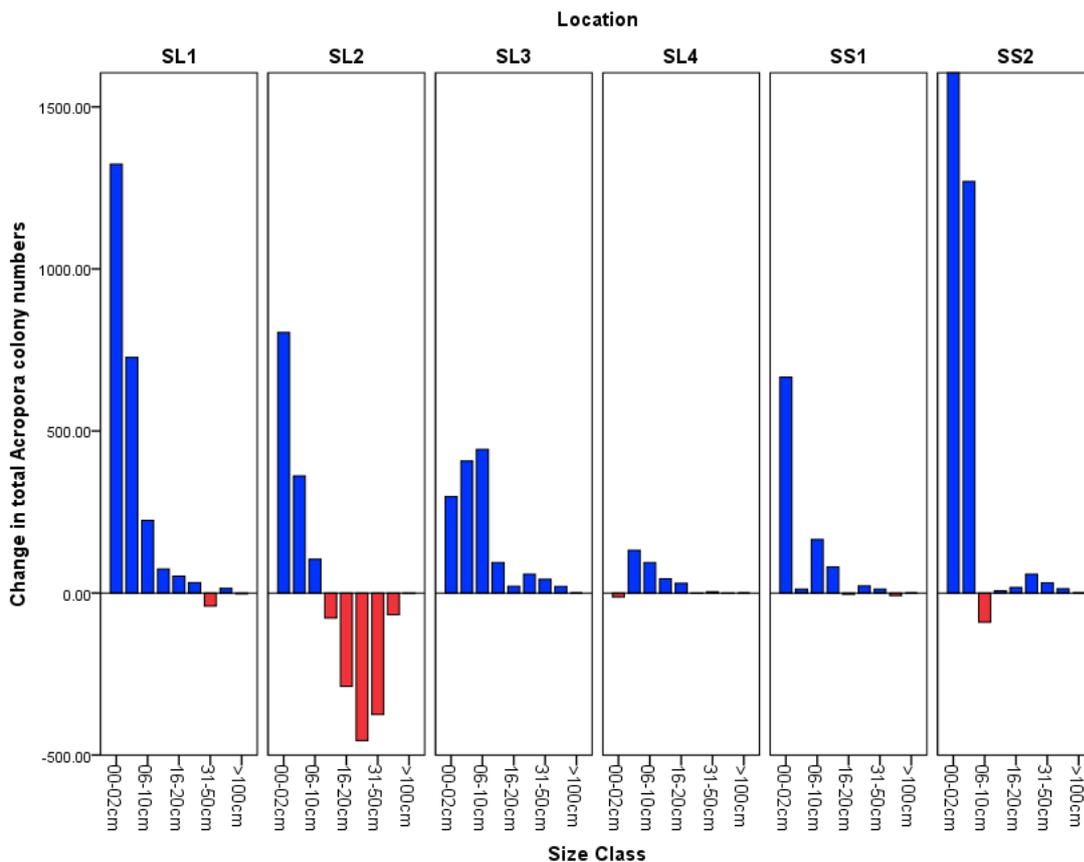


Figure 6.3 Change in the total number of *Acropora* colonies of each size class between 2008 and 2010 at each location. Evidence of a significant loss of large *Acropora* colonies can be seen at SL2. Negative change is indicated by red bars.

6.4.2 *Isopora*

The brooding *Isopora* corals were most affected by the bleaching and at some locations have not yet recovered; only those communities least affected by the bleaching have recovered. For example, communities at SL3 and SL4 were least affected by the mass-bleaching, and some *Isopora* survived to return the communities to their pre-bleaching structure by 2010. Indeed, the community at SL3, which had the highest number of *Isopora* colonies remaining after the 1998 bleaching, had large numbers of recruits by 2004, and in 2010 had a greater abundance of colonies across all size classes than in the pre-bleaching years (Figure 6.4). In contrast, the abundance of *Isopora* colonies has remained low at the locations worst affected by the bleaching. For example, at SS2 the *Isopora* accounted for half the total coral cover (approx. 30% cover), until 1998 when the bleaching completely devastated the local community. No *Isopora* colonies were seen on our size-frequency transects at SS2 until 2005, and in 2010 there were still very few colonies. This provides evidence of self-seeding of *Isopora* communities over small spatial scales (< few km) and of density-dependent effects of high coral cover on the abundance of small colonies during the pre-bleaching years. Between 2008 and 2010, the abundance of *Isopora* continued to increase at SL3 community, remained similar at some communities, and decreased in abundance at some communities (SL2, SS1) due to disease and/or bleaching (Figure 6.5).

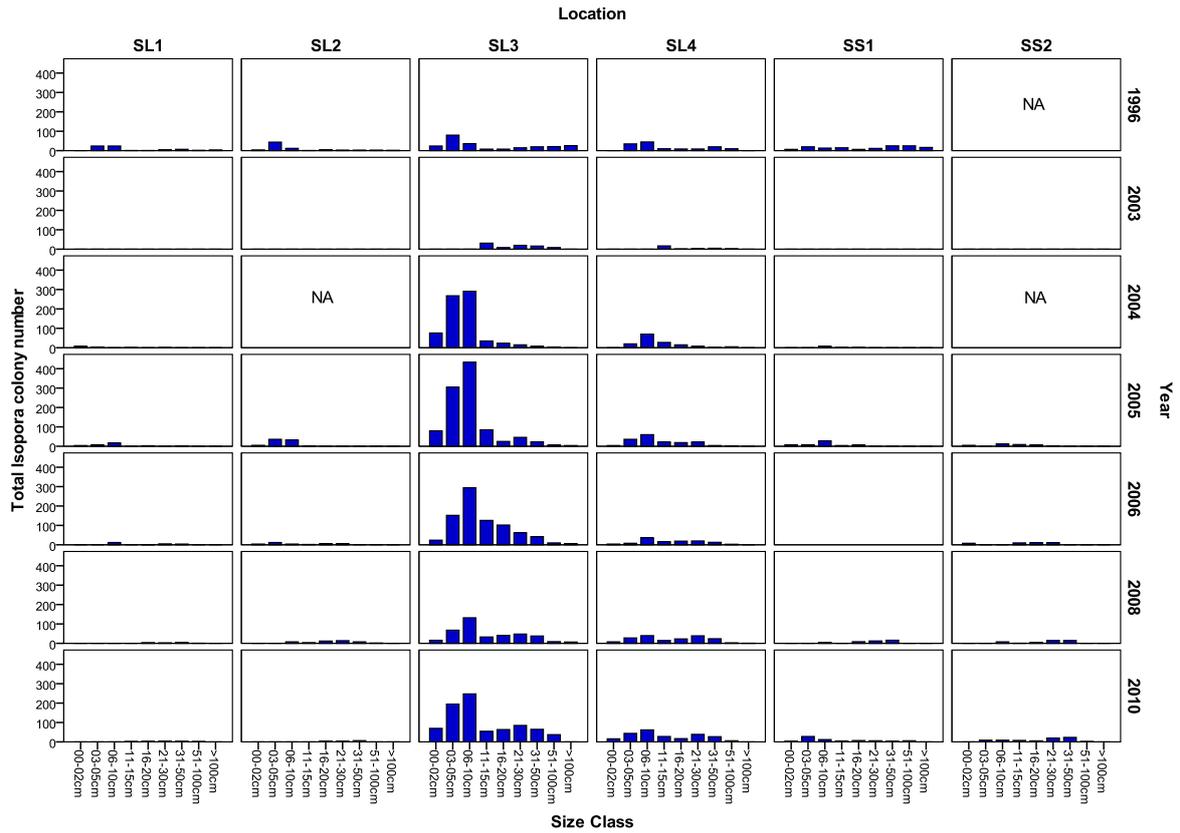


Figure 6.4 Total number of *Isopora* colonies in each size class at each location at Scott Reef. Graphs marked with 'NA' are locations not surveyed in that year.

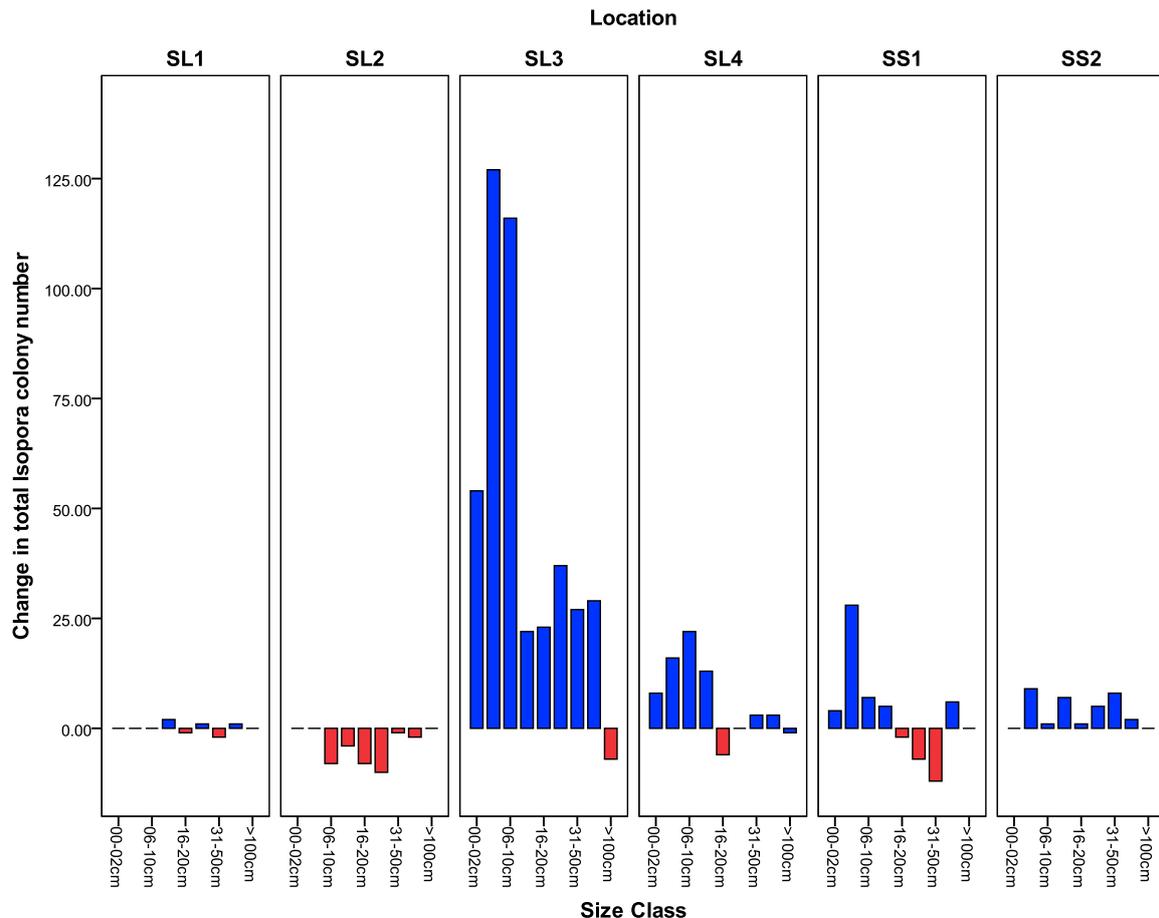


Figure 6.5 Change in the total number of *Isopora* colonies between 2008 and 2010 at each location at Scott Reef. Negative change is indicated by red bars.

6.4.3 *Pocillopora*

The abundance of *Pocillopora* increased relatively quickly following the mass bleaching in 1998. *Pocillopora* can quickly recolonise communities following disturbance, due to their fast growth rate (Harriott 1999), frequent reproduction and high larval retention (Preece and Johnson 1993). However, they are also highly vulnerable to thermal stress and bleaching (Loya et al. 2001; Smith et al. 2008) and were worst affected by the recent bleaching in May 2010. The impact of the bleaching in 2010 on the *Pocillopora* was most evident at the two outer reef locations (SS1, SS2) where the number of colonies of all size classes decreased significantly between 2008 and 2010 (Figure 6.6); 76% of colonies were lost at SS1 and 59% at SS2. A decrease in the abundance of the largest size classes also occurred at the other lagoon locations (SL1-4).

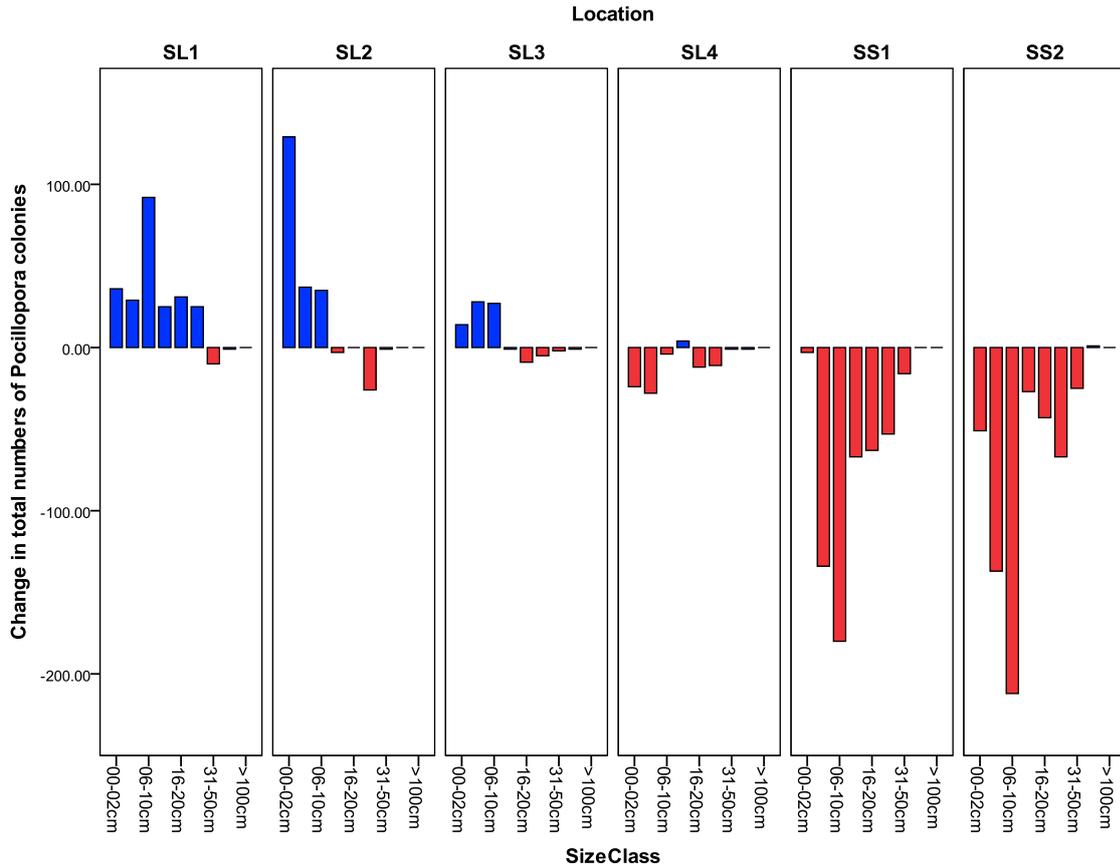


Figure 6.6 Change in total number of *Pocillopora* colonies between 2008 and 2010 on the long-term monitoring size-frequency transects. Negative change is indicated by red bars.

6.4.4 *Porites*

Before 2010, the most recent survey of size-structure of massive *Porites* colonies was in 2003. The massive *Porites* were least affected by the mass bleaching in 1998 and their communities have changed little throughout the monitoring period. Massive *Porites* have a comparatively low susceptibility to thermal bleaching (Loya et al. 2001), but also slow growth and low reproductive output. At SL1, only the smallest colonies were lost in the 1998 bleaching and numbers have remained relatively stable since. Massive *Porites* were uncommon at SL2 prior to the bleaching, and in 2010 there were only 4 colonies counted on the transects. In contrast at SS2 many size classes had increased significantly since 2003. At SL3, SL4 and SS1 there was a decrease in colonies following the 1998 bleaching, but by 2010, these communities had returned to a similar pre-bleaching structure (Figure 6.7). Between 2003 and 2010, there was relatively little difference in the abundance and size structure of communities at most locations (Figure 6.8).

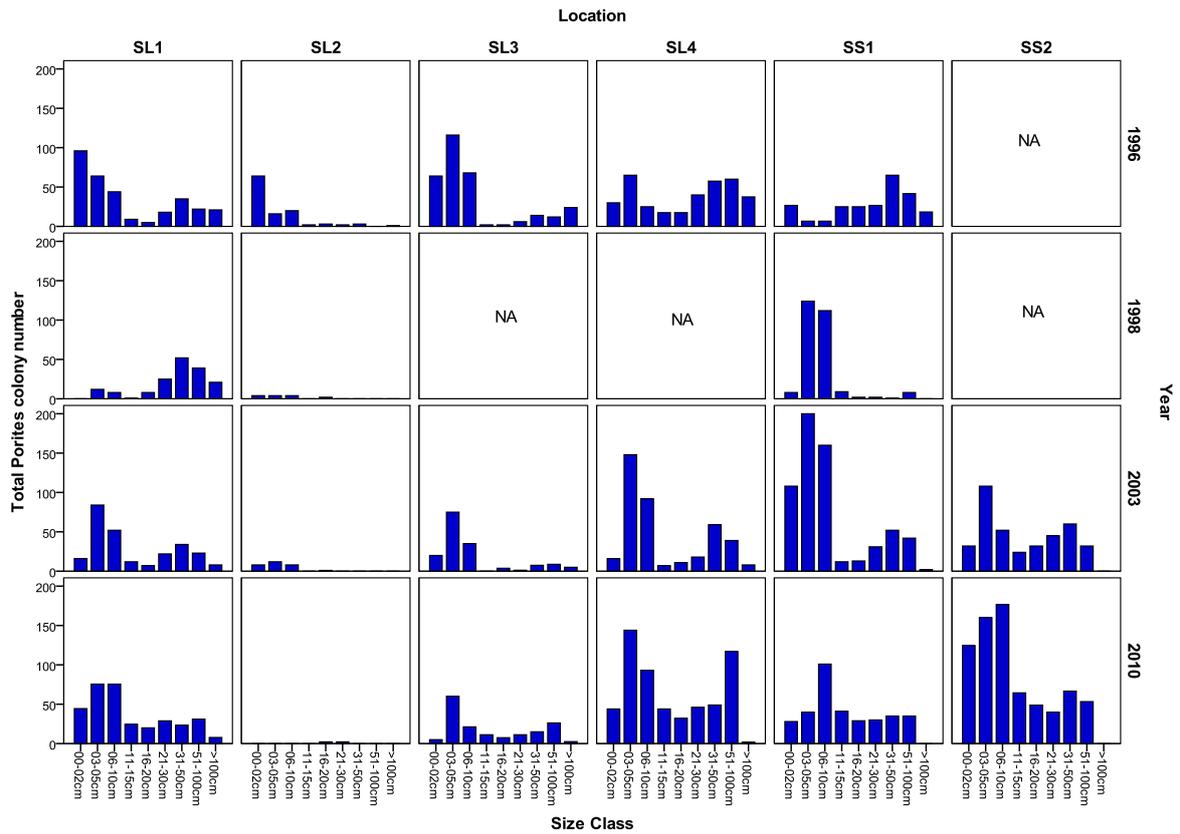


Figure 6.7 Total numbers of *Porites* colonies in each size class at each Scott Reef Location. Graphs marked with 'NA' are locations not surveyed in that year.

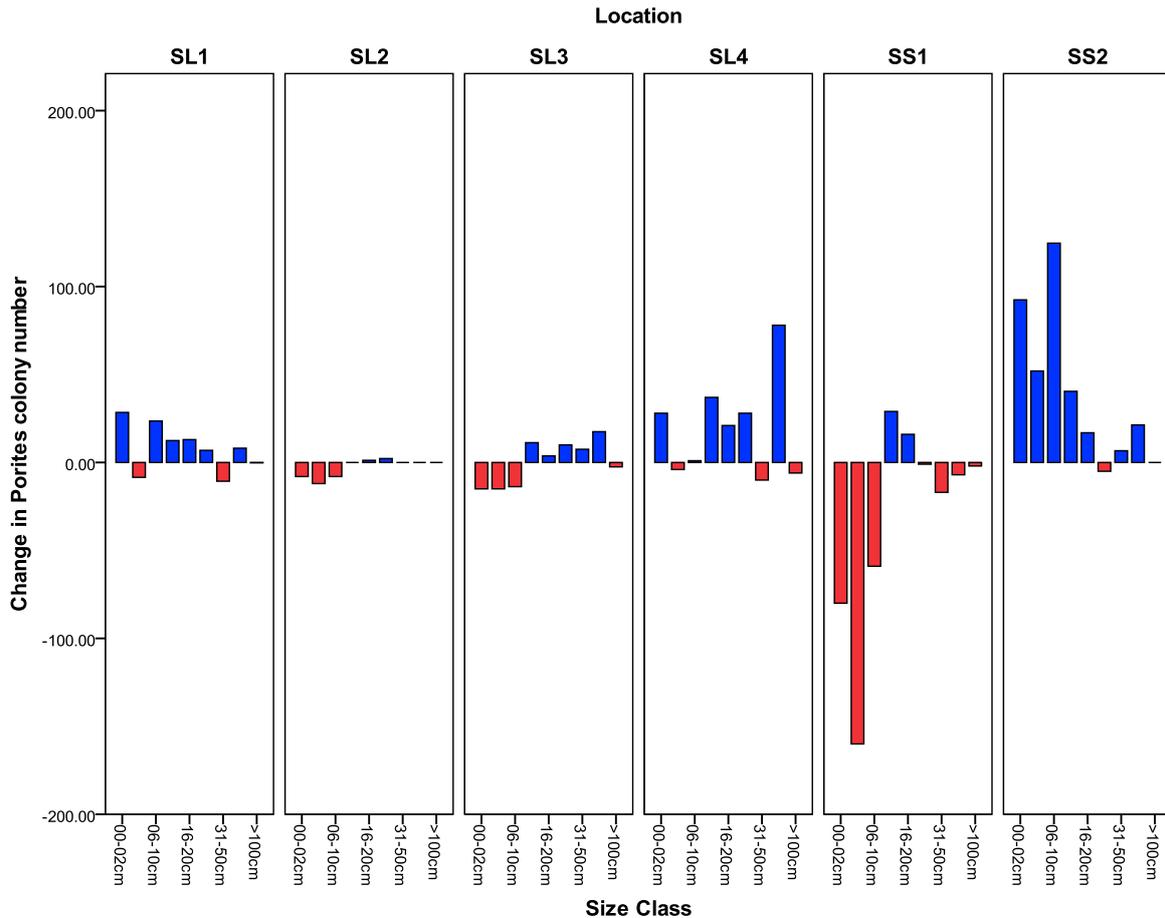


Figure 6.8 Change in total number of *Porites* colonies between 2003 and 2010 on the long term monitoring size-frequency transects. Negative change is indicated by red bars.

The size structure of the broadcast spawning *Acropora* and massive *Porites*, and the brooding *Isopora* and *Pocillopora*, reflected their exposure and susceptibility to disturbances, their modes of reproduction and their rates growth and survival. Additionally, the abundance of juvenile size classes correlated strongly with annual variation in larval supply, while variation in larval supply correlated strongly with the abundance of large adult colonies. Changes in the size structure of communities also complemented data on percentage cover and provided additional insights into community dynamics and resilience.

6.5 References

- Bak RPM, Meesters EH (1999) Population structure as a response of coral communities to global change. *American Zoologist* 39: 56-65
- Connell JH (1973) Population ecology of reef-building corals. In: Jones OA, Endean R (eds) *Biology and Geology of Coral Reefs*, pp 205-245
- Ebert TA, Schroeter SC, Dixon JD (1993) Inferring demographic processes from size-frequency distributions: Effect of pulsed recruitment on simple models. *Fisheries Bulletin* 91: 237-243
- Edmunds PJ, Elahi R (2007) The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastraea annularis*. *Ecological Monographs* 77: 3-18
- Harriott VJ (1999) Coral growth in subtropical eastern Australia. *Coral Reefs* 18: 281
- 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
- McClanahan TR, Ateweberhan M, Omukoto J (2008) Long-term changes in coral colony size distributions on Kenyan reefs under different management regimes and across the 1998 bleaching event. *Marine Biology* 153: 755-768
- Meesters EH, Hilterman M, Kardinaal E, Keetman M, de Vries M, Bak RPM (2001) Colony size-frequency distributions of scleractinian coral populations: Spatial and interspecific variation. *Marine Ecology Progress Series* 209: 43-54
- Preece AL, Johnson CR (1993) Recovery of model coral communities: complex behaviours from interaction of parameters operating at different spatial scales
- Smith LD, Gilmour JP, Heyward AJ (2008) Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. *Coral Reefs* 27: 197-205

7. Globally unique patterns of coral reproduction at Scott Reef

7.1 Summary

Mass spawning of corals at Scott Reef occurs biannually, with a primary event in autumn (March/April) and a smaller event occurring in spring (October/November). The highly synchronous nature of both spring and autumn spawning events at Scott Reef appears to be globally unique – on other reef systems where biannual spawning events occur, they are generally more protracted. The participation by corals in the mass spawning in autumn and spring was inferred from samples collected from hundreds of colonies of 76 species at 6 locations across Scott Reef and the Rowley Shoals from 2008 to 2010. Among the sampled corals, 33 species spawned only during the autumn event, 5 spawned only in spring, and 30 spawned in both seasons. For most species of biannual spawners, a larger percentage (60 to 99%) of colonies spawned in autumn than spring. However, a relatively high percentage (54-96%) of colonies of at least three *Acropora* species (*A. cytherea*, *A. millepora* and *A. monticulosa*) spawned in spring. Individual colonies appeared to spawn consistently in autumn or spring, with little evidence of two annual gametogenic cycles. Among 24 species of *Acropora* and non-*Acropora* corals, there was roughly a two-fold variation in mean polyp fecundity (4-10 eggs per polyp) and egg size (250 to 600 µm). There was considerable variability in fecundity and egg size between seasons in some species of biannual spawners, but no consistent trends in either trait were evident during the days before spawning. All of the species of broadcast spawning corals participated in one of the two mass spawning events, with the exception of the massive *Porites* that may spawn at several times through the year. Species of brooding corals (*Isopora bruggemanni*, *Seriatopora hystrix*) are likely to release sperm and planulae larvae over several months through the year, around the two mass spawning events.

7.2 Introduction

Understanding the timing of coral spawning and the degree of connectivity among communities is critical for the placement of marine protected areas and effective management of coral reefs (Underwood et al. 2009). Patterns of reproduction in coral communities are associated with either the spawning of eggs and sperm for external fertilization, or the internal brooding of larvae (Harrison and Wallace 1990). 'Mass' coral spawning involves the synchronous release of eggs and sperm by a high proportion of multiple species of corals in a single night each year, and has been documented around the world (Guest 2004; Penland et al. 2004; Guest et al. 2005; Carroll et al. 2006; Harrison 2011; Baird et al. 2009). Although a majority of coral species participate in mass spawning, some abundant and functionally important species brood and release fully-developed planulae larvae following internal fertilisation and embryogenesis (Harrison et al. 1984; Richmond and Hunter 1990). Patterns of reproduction in coral communities vary according to their species composition, location and prevailing environmental conditions (Baird et al. 2009). The phenomenon of mass coral spawning was first described on the Great Barrier Reef (GBR), on the east coast of Australia, where subsequent work has provided great insights into these patterns of reproduction. By comparison, there has been far less research into reproduction by corals on the west coast of Australia.

To date, there are few descriptions of coral reproduction on Western Australian (WA) reefs (Baird et al. 2009, Baird et al. 2011). This gap in knowledge is more critical because existing data highlight the unique patterns of reproduction displayed by WA coral communities, which contrast with those of the better studied communities on the GBR. In contrast the established times of mass-spawning

on the GBR during spring (October/November) each year, the peak in reproductive activity in WA occurs in autumn (March/April) (Simpson et al. 1991, Babcock et al. 1994, Gilmour et al. 2009). North of Ningaloo Reef, there are two peaks in reproductive activity: March/April and October/November (Gilmour et al. 2009), while at Ningaloo Reef and further south only one spawning season has been detected (Simpson 1991, Rosser and Gilmour 2008). This pattern appears consistent between inshore and offshore reefs (Rosser and Gilmour 2008).

Two spawning events a year have been documented on north-west Australia atolls (Gilmour et al. 2009), but the reproductive cycles of abundant species are unknown. The main reef systems off north-west Australia include Ashmore (Ashmore, Cartier and Hibernia Reefs), the Scott Reef system (North, South, and Seringapatam Reefs) and the Rowley Shoals (Mermaid, Clerke and Imperieuse Reefs). These are located more than 250 km from the mainland and span five degrees of latitude, with Ashmore Reef northern-most ($12^{\circ} 17'S$), then Scott Reef ($14^{\circ} 04'S$), and the Rowley Shoals further to the south ($17^{\circ} 52'S$). Each system consists of three or more reefs, with similar diversity and cover of coral communities (Veron and Marsh 1988). Scott Reef is the largest of the reef systems, has the most diverse coral communities, and is the focus of this study.

This study further investigates the patterns of reproduction by coral communities on reef atolls off north-western Australia to determine:

1. whether communities consistently spawn in autumn and spring, and whether the autumn spawning is the primary event;
2. the exceptions to the general pattern spawning in autumn and spring, for particular years or groups of corals;
3. the proportion of species and colonies that participate in the autumn and spring spawning;
4. whether individuals consistently spawn during the same season, switch between seasons, or twice a year;
5. whether there is a difference in fecundity and/or egg size among species, and among colonies within species that spawn during autumn or spring.

7.3 Methods

7.3.1. Study site

Scott Reef is an isolated reef system located 270 km off mainland of north-west Australia ($S14^{\circ} 04'$, $E121^{\circ} 46'$) and consists of North and South Scott and Seringapatam Reefs. Surveys of coral reproduction and recruitment were conducted at six locations across Scott Reef that were representative of the major shallow-water habitats (Heyward et al. 1997). Within each location were three long-term monitoring sites separated by a distance of 300 m. Reproductive surveys were conducted at one or more of these replicate sites.

7.3.2. Sampling methods

Replicate colonies of the dominant spawning and brooding corals were sampled from all six locations several weeks (2 to 5 weeks) around the predicted dates of mass spawning in autumn (March to May) and spring (October/November), in 2008 and/or 2009 and 2010. Colonies were identified to species and three branches collected to allow visual examination of eggs within the polyps. Only sexually mature (>20 cm diameter) colonies were sampled and branches were selected from the colony centre to avoid any sterile colony margins. Species that were among the most abundant at

Scott Reef or which displayed unique reproductive cycles were sampled in October 2008 and then again every autumn and spring until 2010, with a total of 244 colonies tagged through the sampling period. At the time of sampling, the spawning corals were examined in situ to rank their stages of egg development, based on size and pigmentation of visible eggs within polyps. The presence of planulae within brooders was also recorded. The time of spawning was inferred from egg scores (Harrison et al. 1984; Guest et al. 2005), according to the following criteria:

- Score 1- Large pigmented (red or pink) eggs were clearly visible within polyps, indicating that colonies will participate in the next spawning event within a month;
- Score 2- Large unpigmented (white or cream) eggs were clearly visible within polyps, indicating colonies will spawn following within two months;
- Score 3- Small unpigmented (white or cream) eggs were visible within polyps, indicating colonies are unlikely to spawn for several months;
- Score 4- No eggs were visible within polyps, indicating that colonies had recently spawned, or will not spawn for many months.

7.3.3. Sample processing

Colony samples were stored in a solution of 10% formalin and 90% seawater. Spawning corals were decalcified in 10% HCl and 10% formaldehyde (37%), with a gradual increase of acid from 5% to 10% over a period of days-weeks. Brooding corals were decalcified in 10% formic acid. Following decalcification, the tissue samples of spawning and brooding corals were stored in 70% ethanol.

Tissue samples of the spawning corals were used to estimate the number and size of eggs within polyps. For each colony, five polyps were dissected from each of the three branches or sections. The polyps were chosen from the middle of each section to avoid the growing tips of the branch. All eggs within each polyp were measured and counted, and if no eggs were present, a further 10 polyps were randomly selected and checked to confirm the results. The number of polyps dissected and eggs measured varied from this design in some species of massive corals, according to their polyp structure. The eggs within each polyp were measured under a Leica MS205 stereo microscope; maximal and medial diameters were measured using Leica Application Suite version 3.1 software. The geometric mean for each oocyte was calculated as the square root of the maximal x medial diameter (Wallace 1988).

For the brooding corals *Isopora bruggemanni* and *Seriatopora hystrix*, and the massive *Porites* spp., reproductive cycles were investigated by staging eggs and sperm through histological techniques. The decalcified tissues were dehydrated through graded ethanol, cleared in chloroform and embedded in paraffin wax. Samples were sectioned at 6 microns, mounted on slides and stained in Harris' Haematoxylin and Young's Eosin. The stages of development for eggs and sperm were ranked according to Szmant-Froelich et al. (1985) and Vargas-Angel et al. (2006).

7.4 Results

7.4.1 Patterns of mass spawning in autumn and spring

A total of 76 species of spawning and brooding corals were sampled at Scott Reef or the Rowley Shoals over three years. *In situ* scores of egg development prior to the predicted dates of spawning were recorded for 3,257 colonies, in addition to laboratory measurements of 78,980 eggs from 1,182 colonies. Histological analysis was used to investigate gametogenesis and planulation in a further 617 colonies from 4 species (Appendix 7.1).

The hard coral communities mass spawned at Scott Reef and Rowley Shoals during autumn and spring each year. The month of spawning was determined by the full moon dates within each season, but usually occurred in March and October, between approximately 1900 and 2300 hours, 7 to 9 nights after the full moon (Table 7.1). However, the timing of the full moon in late February and early October caused split-spawning during 2010, whereby a similar proportion of species and colonies spawned in either March or April during autumn, and October or November during spring.

The main mass-spawning occurred during autumn each year, although a significant proportion of species and colonies also participated in the spring spawning. By comparison, a small number of species spawned only during spring. Of the 76 species sampled at Scott Reef and the Rowley Shoals during one or more periods, 33 spawned only in autumn, 5 spawned only in spring, 30 spawned in both seasons; no spawning was inferred for the remaining 8 species (Table 7.2). Of the 21 species of *Acropora* for which spawning could be inferred more reliably from replicate ($n > 20$) colonies, 4 (19%) spawned only in autumn, 1 (5%) only in spring, and 16 (76%) in both seasons (Table 7.3). However, the incidence of biannual spawning and participation in the spring spawning may be lower for the non-*Acropora* species.

All the species that spawn twice a year had a larger proportion of colonies spawning in autumn than in spring, providing further confirmation that autumn is the main period of reproduction (Table 7.3). For most (76%) species of biannual spawners, a larger percentage (60 to 99%) of colonies spawned in autumn than spring. However, a relatively high percentage (54-96%) of colonies spawned in spring for a least three *Acropora* species (*A. cytherea*, *A. millepora* and *A. monticulosa*). Patterns of spawning for colonies were consistent among years, with little evidence of individuals spawning twice a year or switching their season of spawning. Most (98%) of the 211 tagged colonies from 15 species of *Acropora* spawned either in autumn or spring over consecutive years. However, results suggested that 5 colonies of 4 species spawned over consecutive seasons, during spring 2008, autumn 2009 and spring 2009.

Table 7.1 Times of mass spawning at Scott Reef and the Rowley Shoals. The date and month of spawning was inferred from egg sizes and *in situ* egg scores, plus observations of spawning during some seasons. NAFM: Nights after the full moon.

Year	Season	Month	Full moon	NAFM	Spawn date	Comment
2007	Spring	Sept	26	9		
		Oct			5	Inferred
2008	Autumn	Mar	21	8	30	Inferred
	Spring	Oct	14	8	22	Observed
2009	Autumn	Mar	11	8	19	Inferred
	Spring	Oct	4	8	12	Observed
2010	Autumn	Feb	28	9		
		Mar	30	8	9	Observed
		Apr			7	Inferred
	Spring	Sept	23			
		Oct	23	9	2	Inferred split-spawning
		Nov		7	30	Inferred split-spawning

Species	Autumn	Spring
<i>Acropora abrolhosensis</i>		
<i>Acropora aculeus</i>		
<i>Acropora acuminata</i>		
<i>Acropora anthocercis</i>		
<i>Acropora austera</i>		
<i>Acropora carduus</i>		
<i>Acropora cerealis</i>		
<i>Acropora clathrata</i>		
<i>Acropora cytherea</i>		
<i>Acropora desalwii</i>		
<i>Acropora digitifera</i>		
<i>Acropora donei</i>		
<i>Acropora florida</i>		
<i>Acropora gemmifera</i>		
<i>Acropora grandis</i>		
<i>Acropora granulosa</i>		
<i>Acropora horrida</i>		
<i>Acropora humilis</i>		
<i>Acropora hyacinthus</i>		
<i>Acropora intermedia</i>		
<i>Acropora latistella</i>		
<i>Acropora listeri</i>		
<i>Acropora loripes</i>		
<i>Acropora lutkeni</i>		
<i>Acropora microclados</i>		
<i>Acropora microphthalma</i>		
<i>Acropora millepora</i>		
<i>Acropora mille/hya</i>		
<i>Acropora monticulosa</i>		
<i>Acropora munted</i>		
<i>Acropora muricata</i>		
<i>Acropora nasuta</i>		
<i>Acropora polystoma</i>		
<i>Acropora robusta</i>		
<i>Acropora samoensis</i>		
<i>Acropora samo/gemm</i>		
<i>Acropora spicifera</i>		
<i>Acropora subglabra</i>		
<i>Acropora subulata</i>		
<i>Acropora tenuis</i>		
<i>Acropora valenciennesi</i>		
<i>Acropora valida</i>		
<i>Acropora vauhani</i>		
<i>Diploastrea heliopora</i>		
<i>Echinopora lamellosa</i>		
<i>Favia danae</i>		
<i>Favia matthaii</i>		
<i>Favia pallida</i>		
<i>Favia stelligera</i>		
<i>Favites abdita</i>		
<i>Favites russelli</i>		
<i>Galaxea astreata</i>		
<i>Galaxea fascicularis</i>		
<i>Goniastrea aspera</i>		
<i>Goniastrea edwardsi</i>		
<i>Goniastrea favulus</i>		
<i>Goniastrea pectinata</i>		
<i>Goniastrea retiformis</i>		
<i>Isopora brueggemanni</i>		
<i>Isopora palifera</i>		
<i>Lobophyllia hemprichii</i>		
<i>Merulina ampliata</i>		
<i>Montipora encrusting spp.</i>		
<i>Mycedium mancaoi</i>		
<i>Platygyra daedalea</i>		
<i>Platygyra ryukyuensis</i>		
<i>Porites massiva sp.</i>		
<i>Seriatozpora hystrix</i>		

Table 7.2 Species participating in mass spawning events during autumn and/or spring. Participation was inferred from a combination of *in situ* egg scores and laboratory analysis of egg sizes. Grey cells indicate that spawning could be inferred for less than 10 colonies during a season.

Table 7.3. Proportion of colonies spawning during autumn and spring for species of *Acropora* sampled with replication (n > 20). * denotes species know have participated in a split-spawning during March and April in autumn 2010.

Species	N	Autumn N	Spring N	Autumn %	Spring %
<i>Acropora carduus</i>	21	21	0	100	0
<i>Acropora cerealis</i>	43	43	0	100	0
<i>Acropora cytherea</i>	58	27	31	47	53
<i>Acropora digitifera</i> *	89	87	2	98	2
<i>Acropora florida</i> *	35	21	14	60	40
<i>Acropora gemmifera</i> *	97	74	23	76	24
<i>Acropora humilis</i> *	115	114	1	99	1
<i>Acropora hyacinthus</i> *	66	43	23	65	35
<i>Acropora lutkeni</i>	32	21	11	66	34
<i>Acropora microclados</i> *	58	43	15	74	26
<i>Acropora microphthalma</i> *	70	66	4	94	6
<i>Acropora millepora</i>	49	2	47	4	96
<i>Acropora monticulosa</i>	30	3	27	10	90
<i>Acropora nasuta</i> *	63	62	1	98	2
<i>Acropora polystoma</i> *	58	53	5	91	9
<i>Acropora samoensis</i>	36	33	3	92	8
<i>Acropora spicifera</i> *	253	252	1	99	1
<i>Acropora subglabra</i>	30	30	0	100	0
<i>Acropora tenuis</i> *	148	94	54	64	36
<i>Acropora valida</i>	29	29	0	100	0

7.4.2 Exceptions to generic patterns of biannual spawning

In 2010, spawning was split over consecutive months in autumn (March/April) and spring (October/November) (Table 7.1). Spawning was split for the entire community, with no evidence of a species spawning predominantly during one of two months within each season. A similar a percentage (45% and 40%) of colonies spawned over consecutive months within each season for all of the 18 species sampled with replication (n > 20) during 2010.

All of the species of broadcast spawning corals participated in one of two distinct mass-spawning events during autumn and spring, with the exception of the massive *Porites*. Excluding the split-spawning in 2010, most (70%) colonies spawned synchronously during a single month in autumn or spring, whereas the massive *Porites* colonies were dioecious spawners that released their gametes over several months of the year. Histological analysis identified most stages of development for eggs and sperm during each month of sampling, indicating the potential for colonies to spawn more than once from February to October, and potentially multiple times throughout the year (Table 7.4, Figure 7.1).

Table 7.4. Developmental stages of eggs and testes within massive *Porites* colonies sampled around the times of mass-spawning from 2008 to 2010.

Season	Year	Month	Replicates	Egg Stages				Testes Stages			
				I	II	III	IV	I	II	III	IV
Autumn	2009	February	16	2	2	0	1	4	3	1	0
	2009	March	19	3	0	2	0	3	1	0	0
	2010	March	24	3	3	3	1	3	4	3	2
	2009	April	18	0	0	0	0	1	0	0	0
	2010	May	18	0	0	0	1	0	0	0	0
Spring	2008	October	8	3	6	2	0	1	2	2	0
	2009	October	17	2	7	2	3	2	2	0	1
	2010	October	18	1	2	3	0	1	0	1	3

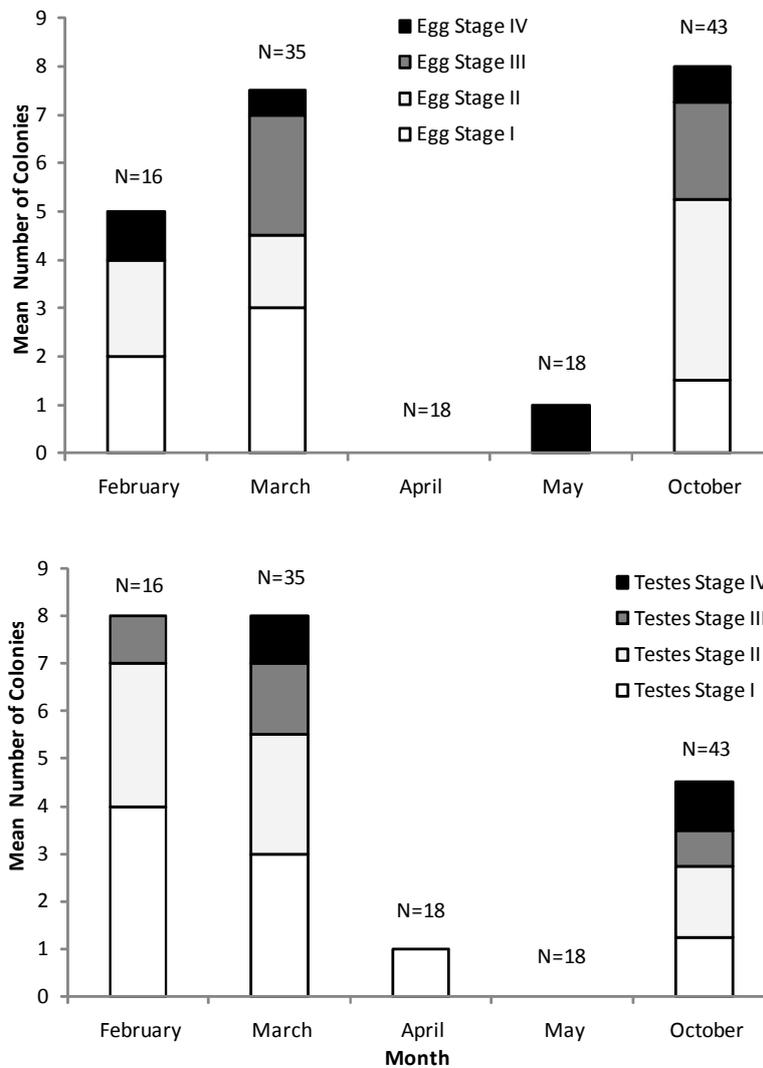


Figure 7.1. Developmental stages of eggs (above) and testes (below) within massive *Porites* colonies sampled around the times of mass-spawning from 2008 to 2010. N is the total number of colonies sampled in each month.

In contrast to the spawning corals, brooding corals had cycles of gametogenesis that resulted in the release of planulae larvae over multiple months. Gametogenic cycles of brooding corals were investigated in histological analysis of two of the most abundant species: *Isopora brueggemanni* and *Seriatopora hystrix*. Both species contained eggs and sperm in most developmental stages during each month of sampling (Table 7.5, Figure 7.2) and planulae were present during both the autumn and spring sampling. The presence of planulae and various stages of gamete development suggest populations are spawning and releasing planulae over several months from spring to autumn, and perhaps also into winter.

Table 7.5. Developmental stages of eggs, testes and planulae within brooding corals sampled around the times of mass-spawning from 2008 to 2010.

Season	Species	Month	N	Planulae	Egg Stage				Testes Stage			
					I	II	III	IV	I	II	III	IV
Autumn	<i>Isopora brueggemanni</i>	Feb	12	0	5	5	3	1	8	5	3	1
		March	41	0	11	17	14	6	18	11	5	0
		April	19	2	2	3	5	2	6	3	2	1
		May	24	3	4	4	11	5	5	8	4	0
	<i>Seriatopora hystrix</i>	Feb	19	5	6	7	5	3	5	2	0	0
		March	32	3	8	13	16	7	8	8	7	0
		April	13	3	0	2	3	3	0	3	2	0
		May	41	8	7	9	11	11	3	1	0	0
Spring	<i>Isopora brueggemanni</i>	Oct	50	29	9	15	18	16	5	10	8	3
	<i>Seriatopora hystrix</i>	Oct	56	15	9	19	16	15	3	0	2	2

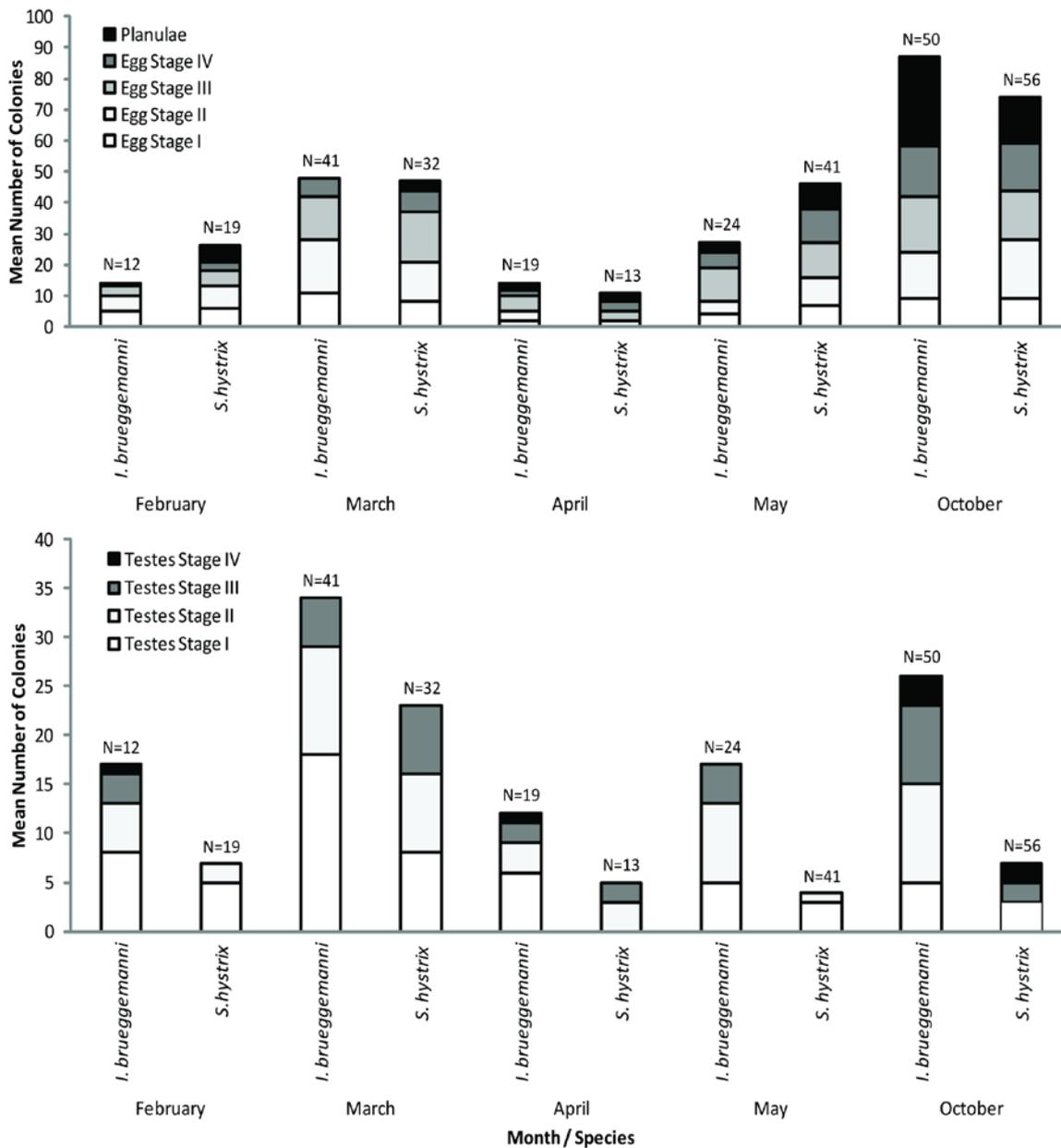


Figure 7.2. Developmental stages of eggs, testes and planulae within brooding corals sampled around the times of mass-spawning from 2008 to 2010.

7.4.3 Variation in polyp fecundity and egg sizes among species, years and spawning season

Over three years, colonies were sampled between 1 and 30 days before the predicted dates of spawning in autumn and spring. Within each species, comparisons of fecundity and egg sizes among years and seasons may therefore be confounded by the different times of sampling prior to spawning; for example, fecundity may decrease and/or egg size increase closer to the time of spawning within the sampling period. However, for species sampled most intensively, there was no obvious variation in fecundity or egg size in the month before spawning, with neither a clear pattern of increase or decrease through time.

Polyp fecundity and mature egg sizes varied widely among species. Among 24 species of *Acropora* and non-*Acropora* corals, there was roughly a two-fold variation in mean polyp fecundity and egg size, which ranged from between 4 to 10 eggs per polyp (Figure 7.3) and 250 to 600 μm (Figure 7.4). Encrusting *Montipora* spp. had the highest fecundity, but other non-*Acropora* corals were generally less fecund than *Acropora* species. Differences in fecundity and egg size did not vary in a consistent way and were not correlated (Figure 7.5). For example, species with the largest eggs did not also have lower (or higher) fecundity; species with the smallest eggs did not have higher fecundity.

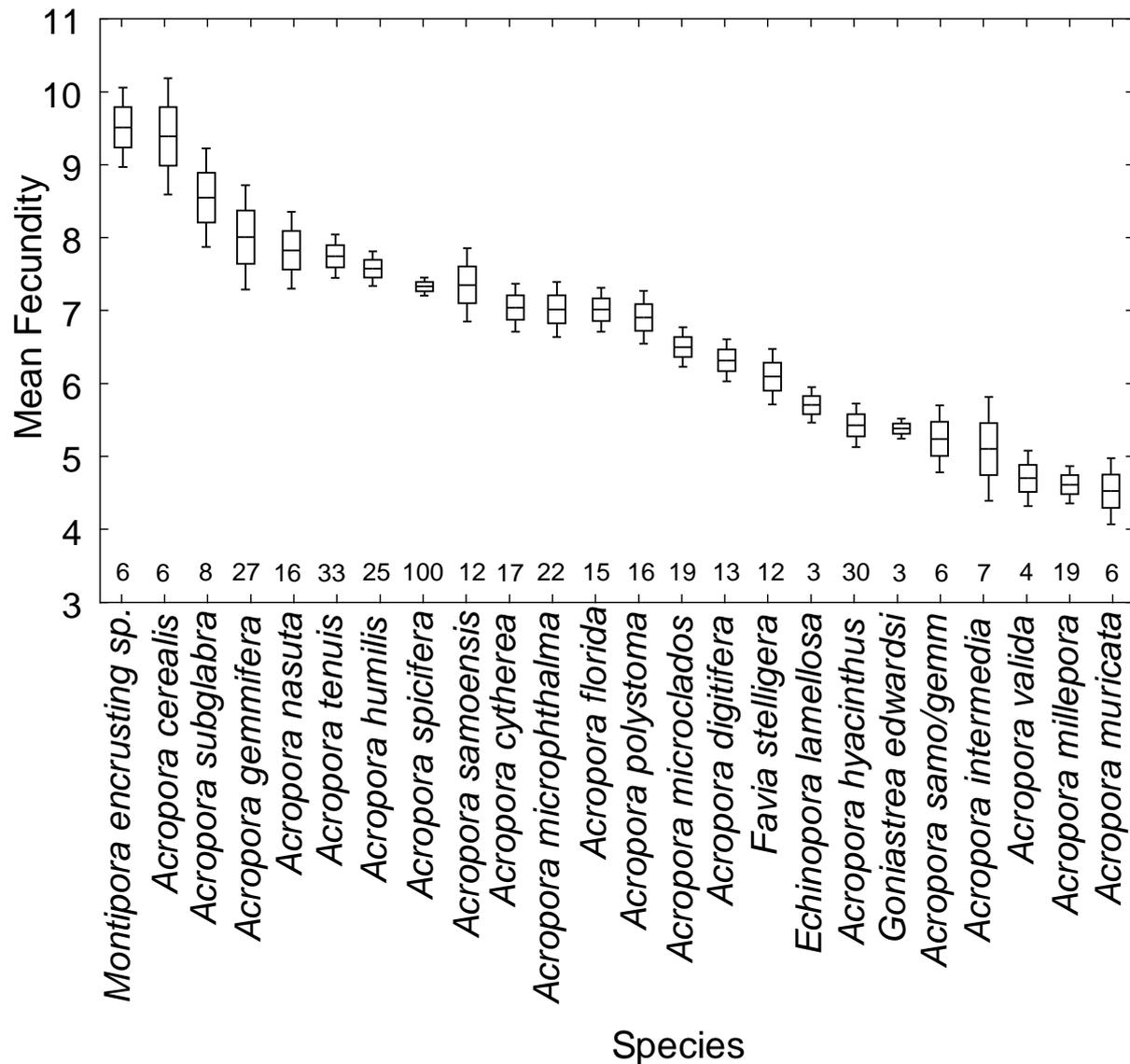


Figure 7.3. Mean fecundity for 24 species with mature eggs, in order of decreasing mean fecundity (number of eggs per polyp). Boxes represent 1 SE, and whiskers are 95% CI. Along the x-axis are the numbers of colonies with mature eggs used for each species. For each colony, 5 polyps were examined from each of three branches or sections (15 polyps per colony).

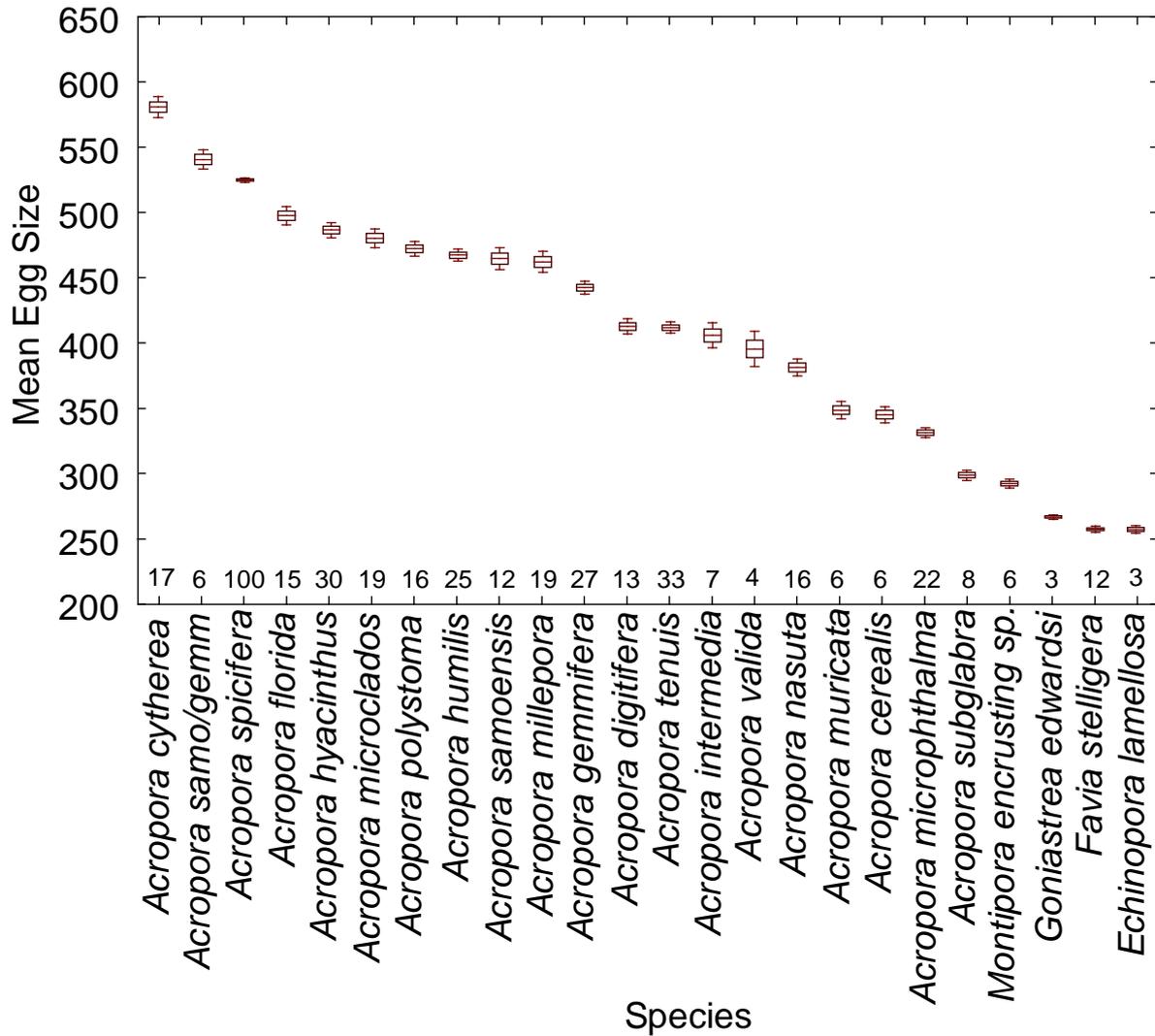


Figure 7.4. Mean mature egg size (in μm) for 24 species, in order of decreasing mean egg size. Boxes represent 1 SE, and whiskers are 95% CI. The numbers of colonies with mature eggs used for each species are shown on the x-axis. For each colony, 5 polyps were examined from each of three branches or sections (15 polyps per colony).

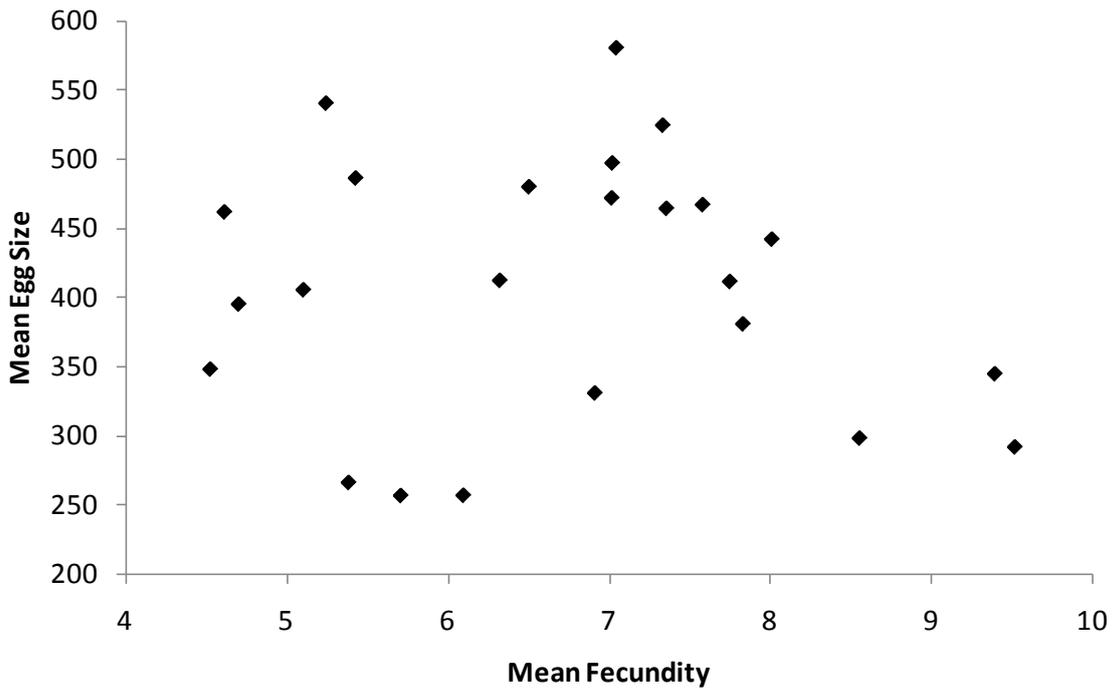
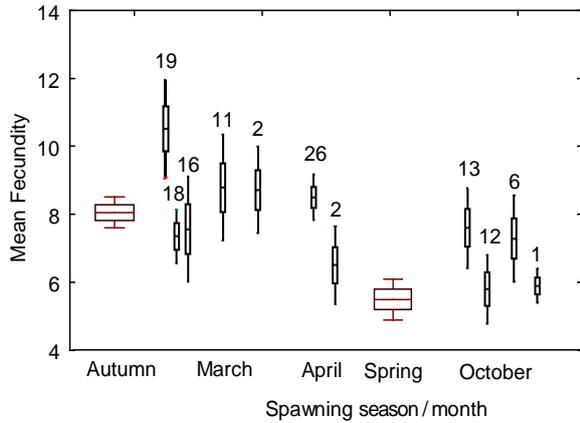


Figure 7.5. Bivariate plot of fecundity (mean number of eggs per polyp) and egg size (μm) for each species represented in Figures 3 and 4.

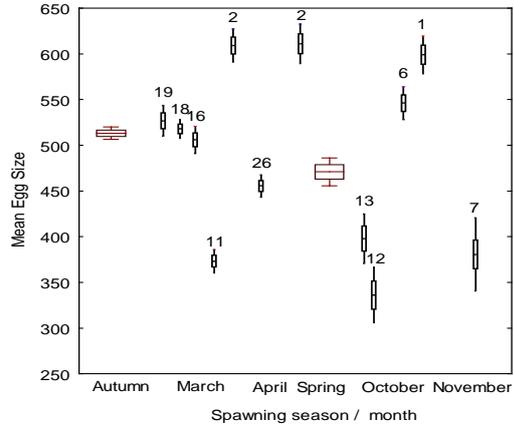
In addition to the variation among species, there was also considerable variation in fecundity and egg sizes among years and spawning seasons within most species. This variability confounded inferences about whether reproductive output for biannual spawners was higher during a particular season. Given a higher proportion of species and colonies spawning during autumn and that gametogenic cycles leading up to the autumn spawning occur during the summer months, then any variation among seasons was expected to be evident as higher reproductive output in autumn (Figure 7.6). However, both fecundity and egg size were lower in autumn than spring in *A. hyacinthus*, *A. microclados* and *A. spicifera*. In *A. tenuis*, fecundity and egg size were very similar between seasons. *A. florida* had greater fecundity and larger mean egg size in autumn than spring and *A. gemmifera* had greater fecundity but smaller egg size in autumn.

Fecundity

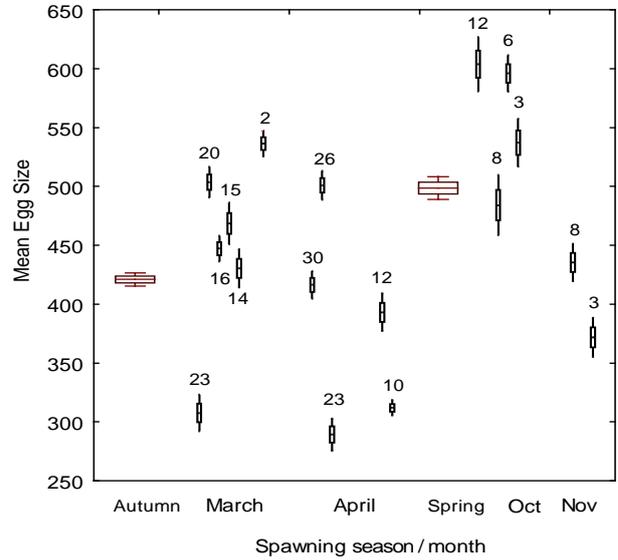
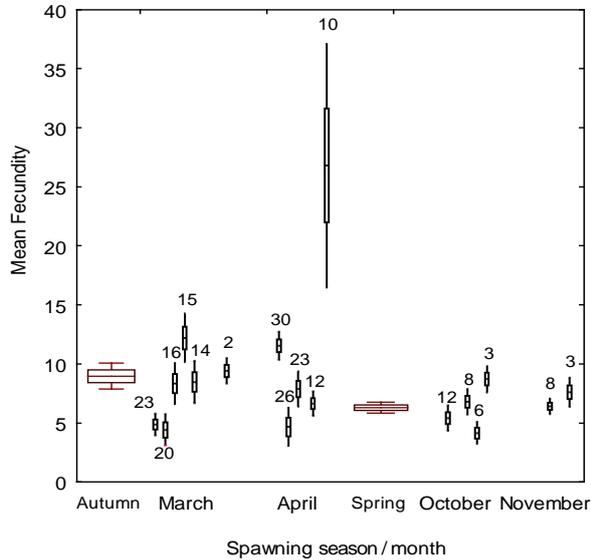
a) *Acropora florida* (N=15)



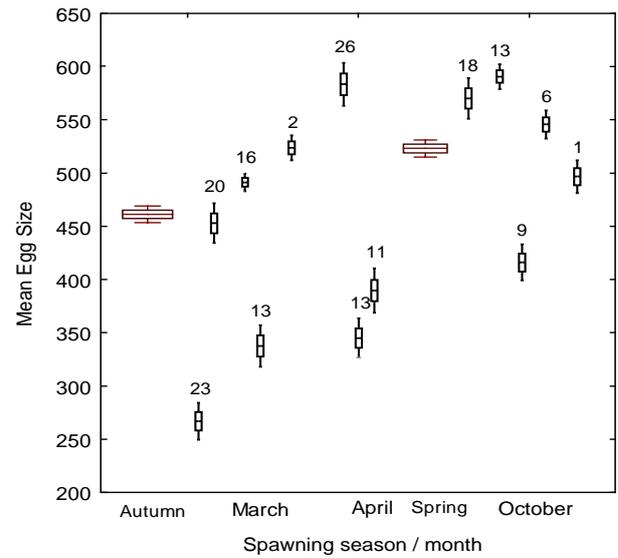
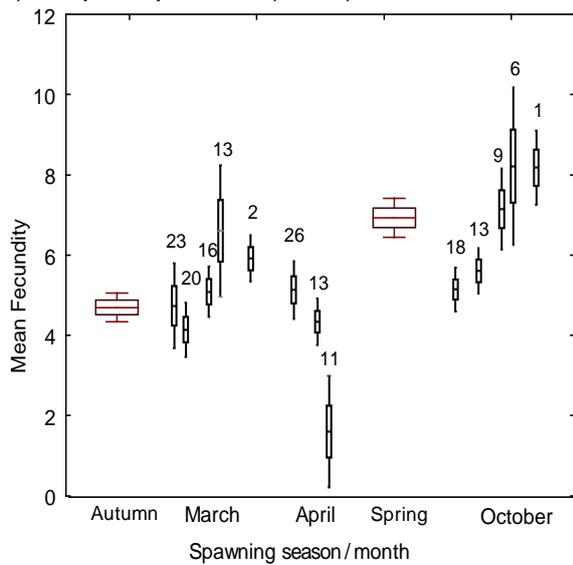
Egg size



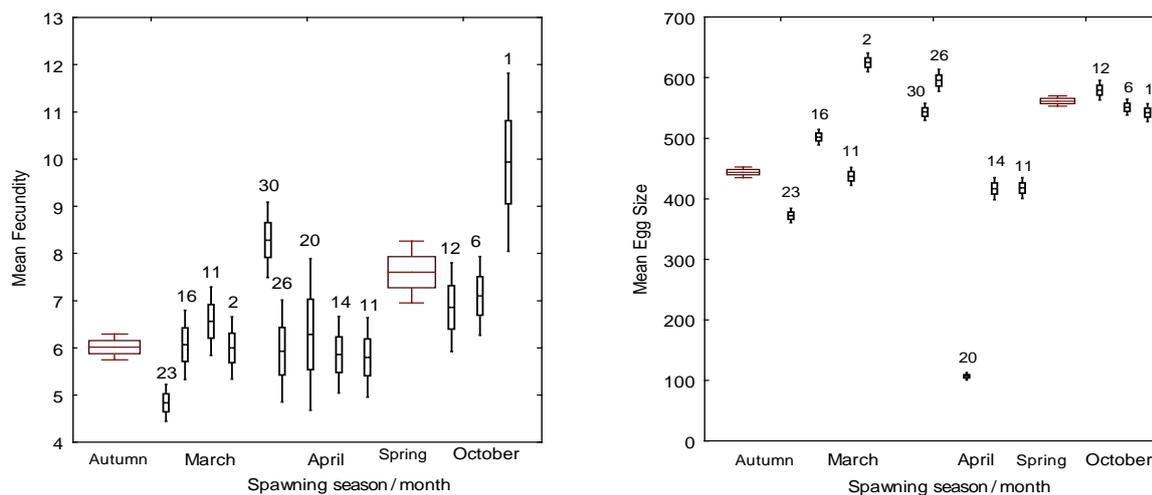
b) *Acropora gemmifera* (N=27)



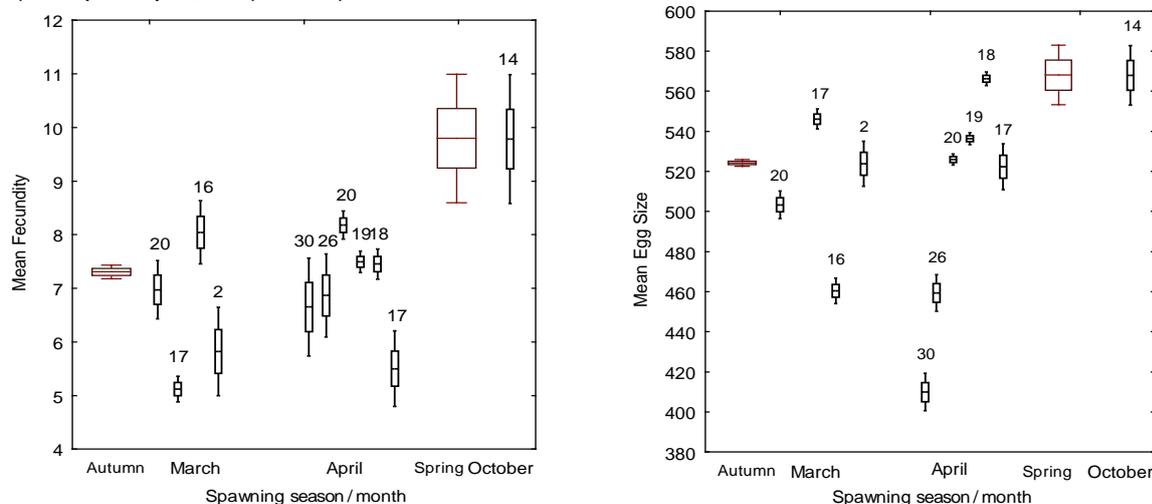
c) *Acropora hyacinthus* (N=30)



d) *Acropora microclados* (N=19)



e) *Acropora spicifera* (N=100)



f) *Acropora tenuis* (N=33)

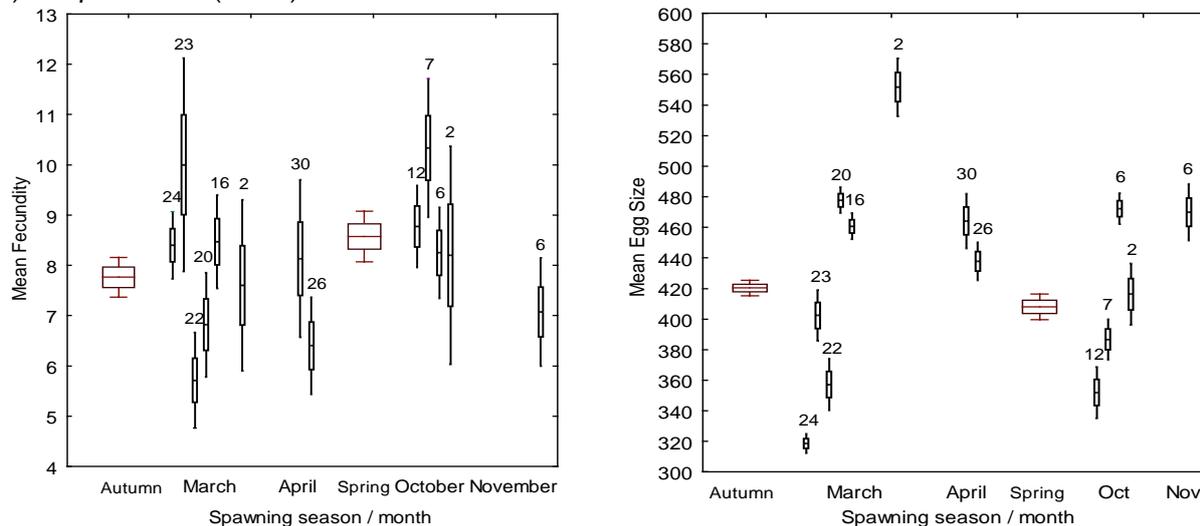


Figure 7.6. Mean fecundity and mature egg size in species of spawning corals. Average fecundity is given for autumn and spring (wide boxes), and for each month of spawning within each season. Numbers above the whiskers are the days remaining till the predicted spawning date at the time of sampling. Boxes represent 1 SE, and whiskers are 95% CI.

7.5 Discussion

The results of this study confirm that mass-spawning occurs twice a year at Scott Reef, during neap tides after full moon in autumn and spring. Most species and colonies participate in the autumn spawning, but there are at least 35 species now recorded to participate in the secondary spawning in spring. Indeed, a relatively high proportion of many of these species participate in the spring spawning, making it a true mass spawning event. However, there is evidence for only 5 of these species (*Acropora austera*, *A. millepora*, *A. vaughani*, *Diploastrea heliopora* and *Lobophyllia hemprichii*) participating solely in the spring spawning, while all the remainder also spawn in autumn. At least 20 species are confirmed spawn biannually, with confirmation of an additional 10 species requiring further replication.

Biannual spawning by multiple species within communities has been reported on other reefs off north-west Australia and around the world. Biannual spawning by corals on north-west Australian reefs, during spring and autumn, occurs at Barrow Island, the Dampier Archipelago and the Rowley Shoals (Rosser and Gilmour 2008; Gilmour et al. 2009). Although there is only limited sampling over this latitudinal gradient, current evidence suggests a breakdown in participation in the spring spawning with increasing latitude; there is minimal participation at Barrow Island and no evidence of participation at Ningaloo Reef (Rosser 2005), the Houtman Abrolhos Islands (Babcock et al. 1994) or Rottneest Island (Crane 1999). Biannual spawning has been documented on several other reefs around the world, but the timing on north-west Australian reefs is most similar to that on reefs off Singapore (Oliver et al. 1988; Guest et al. 2005; Mangubhai and Harrison 2008). Spawning seasonality highlights the need for further investigation of whether biannual spawning is happening elsewhere in WA (further north, e.g. Ashmore / Hibernia, and further south, e.g. Abrolhos / Rottneest).

Patterns of biannual spawning by populations of the same species are either a consequence of individual colonies spawning at different times of the year, or some individuals spawning twice a year. At Scott Reef, evidence suggests that almost all colonies reproduce in either autumn or spring, with a single gametogenic cycle. Individual colonies of some species appeared to be exceptions to this general pattern, with evidence of spawning in two or more successive seasons. This suggests that the potential for two gametogenic cycles within one year does exist. For many species, the spawning at different times by individual colonies may be a mechanism to enhance genetic diversity (Fukami et al. 2003). In some instances, species and/or morphs spawn in different months, either in consecutive months or different seasons (Penland et al. 2004; Wolstenholme 2004; Guest et al. 2005; Mangubhai and Harrison 2006). Where there are consistent differences in the times of spawning among colonies over years, these are evident in patterns of genetic variation and/or morphological features (Dai et al. 2000; Wolstenholme 2004). A degree of genetic isolation among colonies spawning in different seasons was confirmed for *A. tenuis* (Howells and Underwood unpubl. data), and may exist also for the other biannual spawners. The scale of genetic isolation among these populations needs to be confirmed in further sampling, but the limited existing evidence suggests it is consistent with the beginning of sympatric speciation. Restricted sampling in the Dampier Archipelago (north-west Australia) indicated that colonies of the same species and location consistently spawned at different times over consecutive years (Rosser and Gilmour 2008). Similarly, in a sympatric population of *Mycedium elephantotus* that spawned during two distinct periods on Taiwanese reefs, individual colonies had only one annual gametogenic cycle (Dai et al. 2000). Conversely, on other reefs around the world, individual colonies have been found to spawn twice a year (Stobart et al. 1992; Guest et al. 2005; Mangubhai and Harrison 2006; Mangubhai and Harrison 2008). Optimal conditions may well be required for colonies to spawn twice a year and it may happen only during some years (Harrison and Wallace 1990).

Fecundity and egg size varied substantially between species, and there was evidence of smaller eggs in species outside the genus *Acropora*. While fecundity of species was similar to that recorded in other regions, egg sizes at Scott Reef appear slightly smaller (Harrison and Wallace 1990, Wallace 1999, Mangubhai 2007). Establishing the average fecundity and mature egg size in coral species at the

time of spawning is important to inform predictions of exact spawning times. It is also important to understand the between-season variability in these parameters in biannual spawners. Within species that spawned biannually, there was some evidence of variability in fecundity and egg size, but this was not consistent among species. There was no obvious trend in fecundity or egg size, or correlation between the two life-history traits, as has been documented previously (Mangubhai 2007).

The massive *Porites* was a notable exception to the pattern of spring and autumn spawning. *Porites* colonies were dioecious and apparently spawned gametes during multiple months within the year, as well as the main months of spawning or at other times. Massive *Porites* colonies have been found to spawn during mass spawning events and at other times of the year around Australia (Kojis and Quinn 1982; Harriott 1983; Willis 1985; Babcock et al. 1986). Importantly, a small sample of massive *Porites* spp. at the Dampier Archipelago (north-west Australia) indicated that colonies spawned between November and January, months before the primary mass spawning in autumn (Baird et al. 2011).

Brooding corals were also found to reproduce outside the main annual spawning events, as cumulative reproductive output for brooding corals at other times of the year is probably higher than during the primary month of spawning. Brooding corals on other reefs around the world tend to have multiple cycles of gametogenesis, spawning and planulae release throughout the year (e.g. Fadlallah and Pearse 1982; Harrison and Wallace 1990; Richmond and Hunter 1990; Tanner 1996). In previous studies, there has been a tendency for mature gametes to occur more frequently around new and full lunar moons (Stoddart and Black 1985, Glynn et al 1991). This was especially evident for both eggs and testes in *Pocillopora damicornis* and *P. elegans* where mature gametes were found to be significantly clustered around the full moon. In the weeks preceding the full moon, different egg stages did not necessarily persist for a similar time-span; Stoddart and Black (1985) suggested that Stage IV eggs in *P. damicornis* may only be present for a few days. In *P. elegans*, Stage IV gametes disappeared within 3 days after the full moon, contributing to the indication that primary spawning probably occurred a few nights after the full moon, with some spawning activity also occurring on the new moon (Glynn et al 1991). Individual *P. damicornis* colonies were found to have up to 3 cycles of maturing gametes and planulae per season, with Stage I testes appearing when Stage IV was at its peak (Stoddart and Black 1985). The production of planulae also appeared to peak around the full moon (Stoddart and Black 1985). In *P. damicornis*, *Seriatopora hystrix* and *Favia fragum* the release of planulae was recorded between days 2 and 11 after the full moon (Szmant-Froehlich et al. 1985, Permata et al. 2000, Fan et al. 2002), although other studies recorded planula release in the week preceding the full moon (Tanner 1996). In contrast, *Stylophora pistillata* appeared to release planulae throughout the month (Tanner 1996), with a peak in planulation around 21 and 22 days after the full moon (Fan et al. 2002). It was more difficult to ascertain the periodicity of Stage I and II eggs; at least one species appeared to have these stages present throughout the lunar cycle (Szmant-Froehlich et al. 1985).

Mass spawning by corals over one or two months within a season at Scott Reef or other reefs in north-west Australia has implications for management decisions about whether human activities likely to create disturbance should be halted during these periods. Indeed, a means by which to assess the relative significance of spawning and the significance of reproductive output' during different months of the year is required to make some quantitative assessment about the possible consequences of impacting larval production and recruitment during one or more months. Further research at Scott Reef will provide insights into which environmental variables (e.g. moon phases, water temperature, solar insolation) are best correlated to the times of spawning (Oliver et al. 1988; Babcock et al. 1994; Penland et al. 2004), from which more accurate predictions can be made about the significance of reproductive output during the months within the autumn and spring spawning periods.

7.6 References

- 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, Willis B, Simpson CJ (1994) Mass spawning of corals on a high latitude coral reef. *Coral Reefs* 13:161-169
- Baird AH, Guest JR, Willis BL (2009) Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution, and Systematics* 40:551-571
- Baird AH, Blakeway DR, Hurley TJ, Stoddart JA (2011) Seasonality of coral reproduction in the Dampier Archipelago, northern Western Australia. *Marine Biology* 158:275-285.
- Carroll A, Harrison P, Adjeroud M (2006) Sexual reproduction of *Acropora* reef corals at Moorea, French Polynesia. *Coral Reefs* 25:93-97
- Crane KR (1999) Reproductive biology of scleractinian corals at Rottneest Island, Western Australia. Honours Thesis thesis, Murdoch University, p 160
- Dai CF, Fan TY, Yu JK (2000) Reproductive isolation and genetic differentiation of a scleractinian coral *Mycidium elephantotus*. *Marine Ecology Progress Series* 201:179-187
- Fadlallah YH, Pearse JS (1982) Sexual reproduction in solitary corals: Overlapping oogenic and brooding cycles, and benthic planulas in *Balanophyllia elegans*. *Marine Biology* 71:223-231
- Fan T-Y, Li J-J, Le S-X, Fang L-S (2002) Lunar periodicity of larval release by Pocilloporid corals in Southern Taiwan. *Zoological Studies* 41:288-294
- Fukami H, Omori M, Shimoike K, Hayashibara T, Hatta M (2003) Ecological and genetic aspects of reproductive isolation by different spawning times in *Acropora* corals. *Marine Biology* 142:679-684
- Gilmour J, Smith LD, Brinkman RMM (2009) Biannual spawning, rapid larval development and evidence of self-seeding for scleractinian corals at an isolated system of reefs. *Marine Biology* 156:1297-1309
- Glynn PW, Gassman NJ, Eakin CM, Cortes J, Smith DB, Guzman HM (1991) Reef coral reproduction in the eastern Pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador). *Marine Biology* 109:355-368
- Guest JR (2004) Reproductive patterns of Scleractinian corals on Singapore's reefs National University of Singapore,
- Guest JR, Baird AH, Goh BPL, Chou LM (2005) Reproductive synchrony in an equatorial assemblage of scleractinian corals. *Coral Reefs* 24:112-116
- Harriott VJ (1983) Reproductive ecology of four scleractinian species at Lizard Island, Great Barrier Reef. *Coral Reefs* 2:9-18
- Harrison P, Babcock RC, Bull GD, Oliver J, Wallace CC, Willis B (1984) Mass spawning in tropical reef corals. *Science* 223:1186-1189
- Harrison P, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) Chapter 7: Coral Reefs. Elsevier, Amsterdam, pp 133-179
- Kojis BL, Quinn NJ (1982) Reproductive ecology of two Faviid corals (colenterata: Scleractinia). *Marine Ecology Progress Series* 8:251-255
- Mangubhai S (2007) Reproduction and Recruitment of Scleractinian Corals on Equatorial Reefs in Mombasa, Kenya. PhD thesis, Southern Cross University, 283 pp.
- Mangubhai S, Harrison P (2006) Seasonal patterns of coral reproduction on equatorial reefs in Mombasa, Kenya.
- Mangubhai S, Harrison PL (2008) Asynchronous coral spawning patterns on equatorial reefs in Kenya. *Marine Ecology Progress Series* 360:85-96
- Oliver JK, Babcock BC, Harrison PL, Willis BL (1988) Geographic extent of mass coral spawning: clues to ultimate causal factors. *Sixth International Coral Reef Symposium*:803-810.

- Penland L, Kloulechad J, Idip D, van Woosik R (2004) Coral spawning in the western Pacific Ocean is related to solar insolation: evidence of multiple spawning events in Palau. *Coral Reefs* 23:133-140
- Permata WD, Kinzie III RA, Hidaka M (2000) Histological studies on the origin of planulae of the coral *Pocillopora damicornis*. *Marine Ecology Progress Series* 200:191-200
- Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. *Marine Ecology Progress Series* 60:185-203
- Rosser NL (2005) Reproductive seasonality and biannual spawning of *Acropora* on two north-west Australian reefs. Bachelor of Science with Honours thesis, Murdoch University, p 125
- Rosser NL, Gilmour JP (2008) New insights into patterns of coral spawning on Western Australian reefs. *Coral Reefs* 27:1-5
- Simpson CJ (1991) Mass spawning of scleractinian corals on Western Australian reefs and comparisons with the Great Barrier Reef. *Journal of the Royal Society of Western Australia* 74:85-91
- Stobart B, Babcock BC, Willis BL (1992) Biannual spawning of three species of scleractinian coral from the Great Barrier Reef. *Seventh International Coral Reef Symposium*:494-499.
- Stoddart JA, Black R (1985) Cycles of gametogenesis and planulation in the coral *Pocillopora damicornis*. *Marine Ecology Progress Series* 23:153-164
- Szmant-Froelich A, Reutter M, Riggs L (1985) Sexual reproduction of *Favia fragum* (Esper): Lunar patterns of gametogenesis, embryogenesis and planulation in Puerto Rico. *Bulletin of Marine Science* 37:880-892
- Tanner JE (1996) Seasonality and lunar periodicity in the reproduction of Pocilloporid corals. *Coral Reefs* 15:59-66
- Underwood JN, Smith LD, van Oppen MJH, Gilmour JP (2009) Ecologically relevant dispersal of a brooding and a broadcast spawning coral at isolated reefs: implications for managing community resilience. *Ecological Applications* 19:18-29
- Vargas-Angel B, Colley SB, Hoke MS, Thomas JD (2006) The reproductive seasonality and gametogenic cycle of *Acropora cervicornis* off Broward County, Florida, USA. *Coral Reefs* 25:110-122
- Veron JEN, Marsh LM (1988) Hermatypic corals of Western Australia: records and annotated species lists. *Records of the Western Australian Museum, Perth Suppl* 29
- Wallace CC (1988) Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. *Marine Biology* 88:217-233
- Wallace CC (1999) *Staghorn corals of the world : a revision of the coral genus Acropora*. CSIRO Publishing, Collingwood.
- Willis BL (1985) Phenotypic plasticity versus phenotypic stability in the reef corals *Turbinaria mesenterina* and *Pavona cactus*. *5th International Coral Reef Congress* 4:107-112.
- Wolstenholme JK (2004) Temporal reproductive isolation and gametic compatibility are evolutionary mechanisms in the *Acropora humilis* species group (Cnidaria; Scleractinia). *Marine Biology* 144:567-582

Appendix 7.1

Table A.7.1. Summary of number of colonies sampled *in situ* and in the laboratory for each species at Scott Reef and the Rowley Shoals. Note: not all the sampled colonies could be inferred to spawn.

Family	Species	Scott Reef				Rowley Shoals			
		Total	In situ only	Lab only	Both	Total	In situ only	Lab only	Both
<i>Acropora</i>	<i>A. abrolhosensis</i>	23	22		1				
	<i>A. aculeus</i>	8	5	2	1				
	<i>A. acuminata</i>	29	25	4					
	<i>A. anthocercis</i>	4	3	1		1		1	
	<i>A. austera</i>					1			1
	<i>A. carduus</i>	35	25		10				
	<i>A. cerealis</i>	93	84	3	6				
	<i>A. clathrata</i>	15	14		1	3		1	2
	<i>A. cytherea</i>	111	79	9	23	4	1	3	
	<i>A. desalwii</i>	1	1						
	<i>A. digitifera</i>	159	140	1	18	1			1
	<i>A. donei</i>	1		1					
	<i>A. echinata</i>	3	2	1					
	<i>A. florida</i>	202	130	13	59	8	5	1	2
	<i>A. gemmifera</i>	166	115	13	38	5		4	1
	<i>A. grandis</i>	9	8	1					
	<i>A. granulosa</i>	26	25		1				
	<i>A. horrida</i>	2	2						
	<i>A. humilis</i>	212	151	15	46	10	2	4	4
	<i>A. hyacinthus</i>	134	78	15	41				
	<i>A. indonesia</i>	9	9						
	<i>A. intermedia</i>	76	41	12	23				
	<i>A. latistella</i>	38	33	5		2		2	
	<i>A. listeri</i>	1	1						
	<i>A. loisietteae</i>	1	1						
	<i>A. loripes</i>	8	8						
	<i>A. lutkeni</i>	33	32		1	19	1	10	8
	<i>A. microclados</i>	107	65	9	33	10		7	3
	<i>A. microphthalma</i>	132	90	21	21	1		1	
	<i>A. millepora</i>	169	132	4	33	2		1	1
	<i>A. mille/hya</i>	12	10		2				
	<i>A. monticulosa</i>	43	36	4	3	22	17	1	4
	<i>A. munted</i>	4	4						
	<i>A. muricata</i>	109	73	12	24				
	<i>A. nasuta</i>	119	89	9	21	3		3	
	<i>A. polystoma</i>	134	102	8	24	2		1	1
	<i>A. robusta</i>	1	1			2		2	
	<i>A. samoensis</i>	55	40	4	11				
	<i>A. samo/gemm</i>	41	21	1	18	1		1	
	<i>A. spicifera</i>	469	279	17	173	10		6	4
	<i>A. subglabra</i>	42	34		8				
	<i>A. subulata</i>	11	8	2	1	3		1	2
	<i>A. tenuis</i>	327	260	11	56	30	3	10	17
	<i>A. valenciennesi</i>	18	17	1		1		1	

Family	Species	Scott Reef				Rowley Shoals			
		Total	In situ only	Lab only	Both	Total	In situ only	Lab only	Both
	<i>A. valida</i>	59	52	3	4	3		3	
	<i>A. vaughani</i>	4	3	1		1		1	
Diploastrea	<i>D. heliopora</i>	12	10	2		8	4		4
Echinopora	<i>E. lamellosa</i>	25	2	23					
Favia	<i>F. danae</i>	2	2						
	<i>F. matthaii</i>	4	4						
	<i>F. pallida</i>	10	7	2	1	3		3	
	<i>F. stelligera</i>	37	4	28	5	3		3	
Favites	<i>F. abdita</i>	4	4			1		1	
	<i>F. russelli</i>	1	1						
Galaxea	<i>G. astreata</i>	3	3						
	<i>G. fascicularis</i>	26	4	22					
Goniastrea	<i>G. aspera</i>	1	1						
	<i>G. edwardsi</i>	31	11	20					
	<i>G. favulus</i>	3	3						
	<i>G. pectinata</i>	1	1						
	<i>G. retiformis</i>	9	4	5		2		2	
Isopora	<i>I. brueggemanni</i>	21	21						
	<i>I. palifera</i>	11	11			1		1	
Lobophyllia	<i>L. hemprichii</i>					3		1	2
Merulina	<i>M. ampliata</i>	2	2						
Montipora	<i>Montipora encrusting spp.</i>	31	4	23	4	4		4	
Mycedium	<i>M. mancaoi</i>	3	3						
Pavona	<i>P. venosa</i>	4		4					
Pectinia	<i>P. lactuca</i>	1	1						
Platygyra	<i>P. daedalea</i>	2	2						
	<i>P. ryukyuensis</i>	2	2						
Pocillopora	<i>P. meandrina</i>	1		1					
	<i>P. verrucosa</i>					1		1	
Porites	<i>Porites massive sp.</i>	1	1						
Seriatopora	<i>S. hystrix</i>	2	1	1					
Symphyllia	<i>S. recta</i>	1	1						

8. Recruitment and connectivity of corals

8.1 Summary

A strong stock-recruitment relationship was found for broadcast spawning and brooding scleractinian corals at Scott Reef, an isolated West Australian reef system. Coral cover and larval supply of scleractinian corals following the autumn mass spawning event was quantified at Scott Reef for ten years between 1996 and 2010. In 1998, a catastrophic bleaching event caused a decrease in coral cover of between 74 to 89% across the entire reef system. Following the bleaching, larval supply of corals (measured by recruitment tiles) was also drastically reduced across the reef, with observed recruitment rates over the following four years only 3% of that seen in pre-bleaching years. Recruitment rates remained very low for 8 years and were not seen to reach pre-bleaching levels until 2008, almost ten years after the bleaching event, lagging behind the recovery of the adult population. For spawning corals, the stock-recruitment relationship was strong at the scale of the whole reef, with recruitment rates severely depressed across the reef until coral cover reached approximately 80% of its pre-bleaching levels. For brooding corals of the genus *Isopora*, it appeared that recruitment was strongly dependant on the presence of brood stock at the location scale (< 5 km), with *Isopora* communities failing to recover at locations where 100% of colonies were lost following the 1998 bleaching. In contrast, locations with some surviving brood-stock following the bleaching received hundreds of recruits in the following years and now have higher numbers of adult colonies than before the bleaching.

In years of good recruitment (pre-bleaching and post-recovery), larval supply from broadcast spawning corals was spatially variable at the scale of locations within the reef (<5km). Locations SL1 and SS2 received 73% of total observed recruitment between them, SL4 and SS1 received only 8% of total recruitment), a pattern decoupled from adult abundance at these localities. This pattern may indicate source and sink areas within the reef system, influenced by local hydrodynamic conditions. The variation in larval supply at the spatial scale of locations affected the dynamics of the local coral communities, with a strong correlation between local larval supply (as measured on recruitment tiles) and number of 1st year recruits (1-2cm colonies) visible on transects the following year.

The tight correlation between adult stocks and larval supply at the reef scale for both broadcast spawning and brooding corals is a major result of the study and very relevant to the understanding of coral reef resilience for the system. Our results suggest that isolated reefs will rely on local adult brood-stock for the maintenance and recovery of their coral communities from disturbance at least at ecological timescales. If severe disturbances act over a scale greater than routine larval dispersal, the potential for replenishment and recovery of reefs may be greatly reduced. Therefore to understand the potential for reef resilience in the face of increasing disturbance, it is imperative to better understand the scale and nature of stock recruitment relationships for reefs with varying degrees of connectivity.

8.2 Introduction

The existence of a dispersive larval phase in the life cycle of scleractinian corals enables genetic mixing and the maintenance of a wide geographic range of species over evolutionary time scales. It also plays a key role in the resilience of coral communities, by providing new individuals to reef areas affected by a disturbance. The degree to which a reef can rely on the supply of recruits from elsewhere depends on its connectedness to other reefs. Highly connected reefs such as many within the Great Barrier Reef (GBR), may receive a sufficient supply of coral larvae from unaffected reefs to facilitate recovery following a severe disturbance. Many of the world's reefs however are physically isolated (by distance or ocean currents) from other reefs and are unlikely to receive sufficient larvae

from elsewhere to maintain their coral communities. Recent studies of larval distribution (reviewed by Swearer et al. 2002; Levin 2006; Cowen and Sponaugle 2009) are finding increasing evidence of short-distance dispersal of coral larvae and self seeding (Ayre and Hughes 2000; Whitaker 2004; Nishikawa and Sakai 2005). Population genetic studies have found significant genetic variation between coral populations, indicating restricted gene flow between, and in some cases within reefs (Ayre and Hughes 2004; Baums et al. 2005; Miller and Ayre 2008; Underwood et al. 2009b). A genetic study by Ayre and Hughes (2004) on four brooding species and one broadcast spawning *Acropora* species, found evidence that even the highly connected reefs of the GBR were mostly self seeded at ecological timescales, and that levels of gene flow between populations separated by a few 100 km of open water may be generally very low.

One of the major implications of these findings is that for many reefs, the recruitment essential for population maintenance and recovery is dependent on the brood-stock of local adults. Therefore, if disturbances to the adult community act over a scale larger than that of routine larval dispersal, the potential for recovery may be severely diminished. With disturbances to coral reefs such as bleaching expected to increase in scale and severity (Hoegh-Guldberg 1999; Knowlton 2001) it is imperative to increase our understanding of larval dispersal and stock-recruitment relationships on reefs (Hastings and Botsford 2006; van Oppen and Gates 2006; Pineda et al. 2007) and to determine the effect of large scale disturbances on the demographic processes that underpin reef resilience, larval production and recruitment.

Scott Reef is a large and relatively isolated reef system off the coast of Western Australia. The nearest reef system is more than 240 km away, and the velocity and complexity of surface currents in the region suggest larval transport times of at least 30 days between these reefs (Cresswell et al. 1993). Given that competency periods for coral larvae are generally less than 30 days (Ayre and Hughes 2000; Miller and Mundy 2003; Nishikawa et al. 2003), it is likely that Scott Reef relies largely on self seeding for the maintenance and recovery of its coral populations (Gilmour 2007; Underwood et al. 2007; Underwood et al. 2009b).

Here, we investigate the effects of a large-scale bleaching event on the coral cover and recruitment rates at Scott Reef, by assessing the scale and nature of the stock-recruitment relationship across the reef system. The spatial and temporal patterns of recruitment within the reef over ten years are compared with local adult abundances for both broadcast spawning and brooding corals. Further, we explicitly test for a “genetic stock-recruitment relationship” by measuring the genetic relatedness among recruits and potential brood stock at each location.

8.3 Methods

We 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 Reefs, which are located 270 km off the north-western Australian coastline (Figure 8.1). The reef system is extensive, spanning 60 km (north-south), and has 520 km² 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, means it is relatively unaffected by anthropogenic stressors (e.g. pollution, run-off) common on other coral reefs.

8.3.1 Changes in coral cover

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 locations), South Scott (4 locations) and Seringapatam (1 location) reefs. At each location there were three sites, approximately 500 m apart (Figure 8.1). 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, 2003, 2004, 2008 and 2010. 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 40 regular intervals along each transect and identifying the benthic category under each of five fixed points, giving a total of 200 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. 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) lagoon 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 lagoon 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.

8.3.2 Changes in rates of recruitment

The rate of coral recruitment was quantified during ten autumn mass spawning events between 1996 and 2010 (years 1996 to 1999, 2002, 2003, 2006, 2008, 2009 and 2010) at the Scott Reef reef-slope monitoring locations. At each of five locations at North and South Scott Reef, 6 terracotta recruitment tiles (110mm x 110mm x 10mm) were deployed at each of 3 sites separated by 50m on the reef slope (18 tiles location⁻¹ year⁻¹). The 6 tiles were spaced haphazardly, approximately 1 m apart, and attached to the reef (see Mundy 2000) 2 weeks (\pm 4 days) prior to the predicted mass coral spawning in autumn and collected 8 weeks later (\pm 5 days). After collection, the recruitment tiles were bleached and the coral recruits identified to one of four taxonomic groups (Family Acroporidae, Pocilloporidae, Poritidae or other) according to (Babcock et al. 2003), using a dissecting microscope. In 2010, the autumn mass spawning was split between two spawning events. At location SL1, one set of tiles was laid in time to capture both events, and another replicate set was laid to capture the second event only. At the rest of the locations only the second event was captured. In order to compare the 2010 spawning effort to previous years, the recruit counts at locations where only one event was captured were standardised according to the ratio at SL1 between the second spawning event, and the two events combined.

8.3.3 Analysis

Variation in spatial and temporal patterns of recruitment were analysed using a repeated measures hierarchical variance partitioning. This is a modified version of GLM (Mac Nally 2000) with a Poisson fitted function. Hierarchical partitioning calculates goodness of fit measures and, using the partition function, applies the hierarchical partitioning algorithm of Chevan and Sutherland (1991). For each dependent variable (number of recruits, coral cover) the percentage contribution of available independent effects (year, location, site, tile and adult cover) can be calculated. A permutation test

was used to calculate the significance (at a confidence interval of greater than 95% each) of independent effect, the significance of z-scores greater than 1.65, equivalent to the 95% confidence interval, are indicated by an asterisk in the table (Table 8.2). The stock-recruitment relationship was explored using generalized additive models (GAMs) (McCullagh and Nelder 1989), that examined the relationship between percent coral cover (*Acropora*) and number of recruits on recruitment tiles. GAMs were applied as there was a non-linear relationship between cover and recruitment, in which this model fits a smoothing curve through the data.

To explore the stock-recruitment relationship of spawning corals between locations, several models were developed, including linear regression, GAMS, and generalized mixed-effects models. Various measures of goodness of fit were applied to identify the 'best' model, these measures included R², Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and the (restricted) log-likelihood test. For all measures the GAMS were the best model, hence this model was selected. All models were analysed using the R (R Development Core Team 2007) function *gam*. Estimated trends and observed means for each measure were plotted against survey month and year to provide a visual presentation of the temporal patterns, also included in each plot was the lower and upper confidence from the model.

8.3.4 Genetic sampling, genotyping and analysis

To provide an independent test of the degree of self-recruitment, we measured the genetic relatedness between recruits and their brood stock at several locations at Scott Reef. In March 2009, branching tips of 30-32 small (< 8 cm) colonies of the brooding coral *Seriatopora hystrix* were collected from 3 locations (SL1, SL2 and SSI). Collection and genotyping procedure followed (Underwood et al. 2007). Genotypes from these 2009 colonies were then combined and compared with genotypes of colonies collected in 2003. The small size of 2009 colonies meant that they would have recruited since the 2003 sampling, and therefore allowed us to test for genetic affinities through time. We conducted a Principal Coordinates Analysis (PCoA) to visualise the genetic relationships among the 2003 and 2009 samples for both species based on pairwise Nei's unbiased genetic distance D_A (Nei 1978). This measure is appropriate for unequal and small sample sizes.

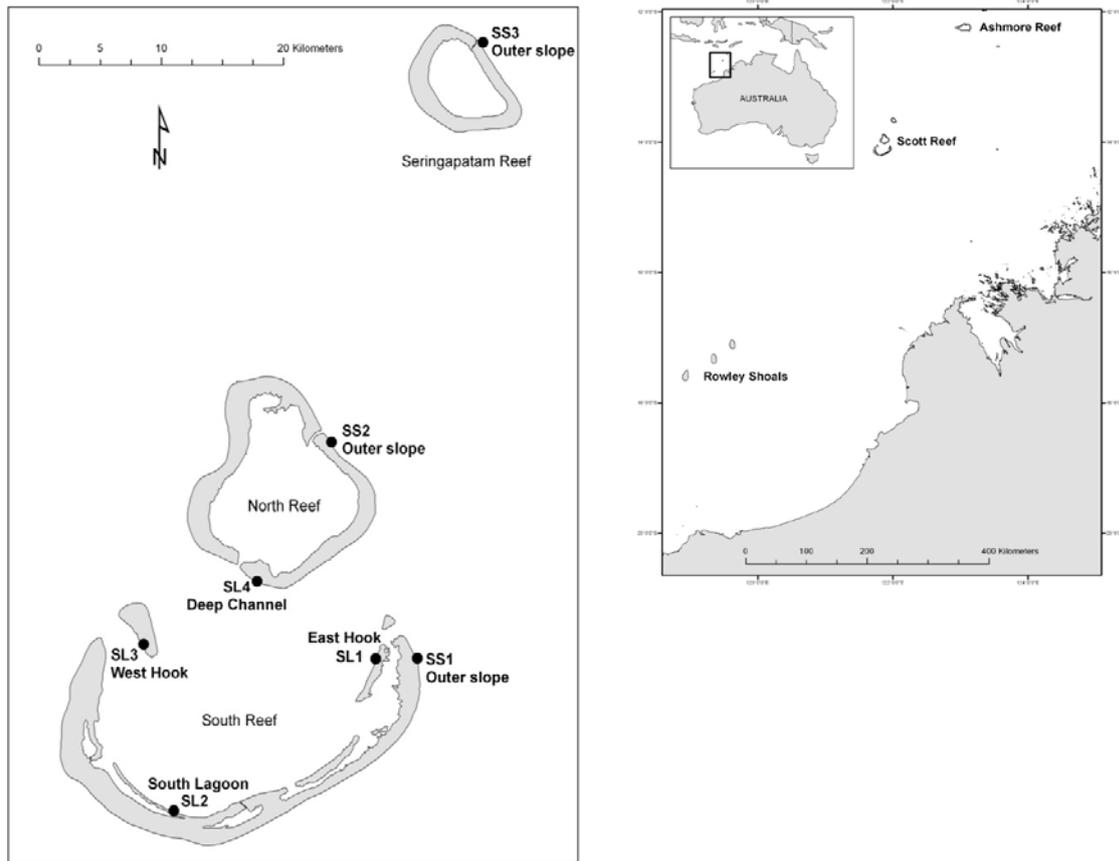


Figure 8.1 Position of Scott Reef off north-western Australia and its study locations. Locations are on the outer- (SS1, SS2, SS3) and inner-slope, with further distinction among inner-slope locations according to their proximity to East Hook (SL1), the Southern Lagoon (SL2), the West Hook (SL3) and the Deep Channel (SL4).

8.4 Results

In 1998, the coral communities across the Scott Reef system suffered catastrophic mortalities following elevated seawater temperatures. During March and May 1998, sea-surface temperatures exceeded 34°C and ranged between 30 and 32°C at 16 m depth, whereas during the previous three years temperatures at 16 m had rarely exceeded 31°C. As a result, all hard corals we observed to a depth of 20 m had expelled their zooxanthellae and bleached. Within a year of the bleaching, coral cover had decreased dramatically across the entire Scott Reef system; relative decreases in cover ranged from 74 to 89% at all of the five habitats that were surveyed (shallow lagoon, reef crest, lower reef crest, upper reef slope, reef slope). The shallow lagoon corals suffered the highest rates of mortality, with coral cover dropping from 77% prior to the bleaching to less than 9% following it. However, even corals within the reef habitat that suffered the lowest mortality, the reef slope still exhibited rates of mortality greater than 70%.

Following the loss of coral cover, the observed recruitment rate at Scott Reef decreased by 97% over all locations, with mean recruits $\text{tile}^{-1} \text{ year}^{-1}$ falling from 39.1 (± 12.6 SE) in the pre-bleaching years, to 1.3 (± 0.2 SE) over the following four years (Figure 8.2). In some years, notably 1999 and 2002, there was almost complete recruitment failure at Scott Reef, with only 0.25 (± 0.1 SE) coral recruits $\text{tile}^{-1} \text{ yr}^{-1}$ averaged across all monitoring locations. That is in the two sampling years, 1999 and 2002, we counted a total of only 45 recruits on our experimental recruitment tiles compared to a total of 8167 recruitments in the pre-bleaching years of 1996 and 1997. Recruitment levels remained low for eight years following the bleaching, with average recruit numbers still at only 15% of pre-bleaching levels in 2006. In 2008, 2009 and 2010, recruit numbers were similar to or higher

than those seen in 1996 and 1997 at the reef slope locations, with recruits tile⁻¹ year⁻¹ at 70.42 (± 14.9 SE), 60.05 (± 6.3 SE), and 44.02 (± 5.5 SE) respectively (Figure 8.2). The recovery of recruitment rates lagged behind initial recovery of adult cover, until a dramatic increase was seen in 2008 when coral cover reached approximately 80% of its pre-bleaching levels, suggesting a non-linear relationship between coral cover and larval supply. The broadcast spawning Acroporidae was the dominant recruit type, making up 88-94% of total recruits. Both the broadcast spawning and brooding coral groups showed a similar reduction in adult numbers in 1998 and eventual recovery. Brooder recruits were seen to return to pre-bleaching levels in 2006, earlier than the Acroporidae (Figure 8.3).

At the whole reef scale, Scott Reef exhibited a strong stock-recruitment relationship, the nature of which differed between spawning and brooding corals.

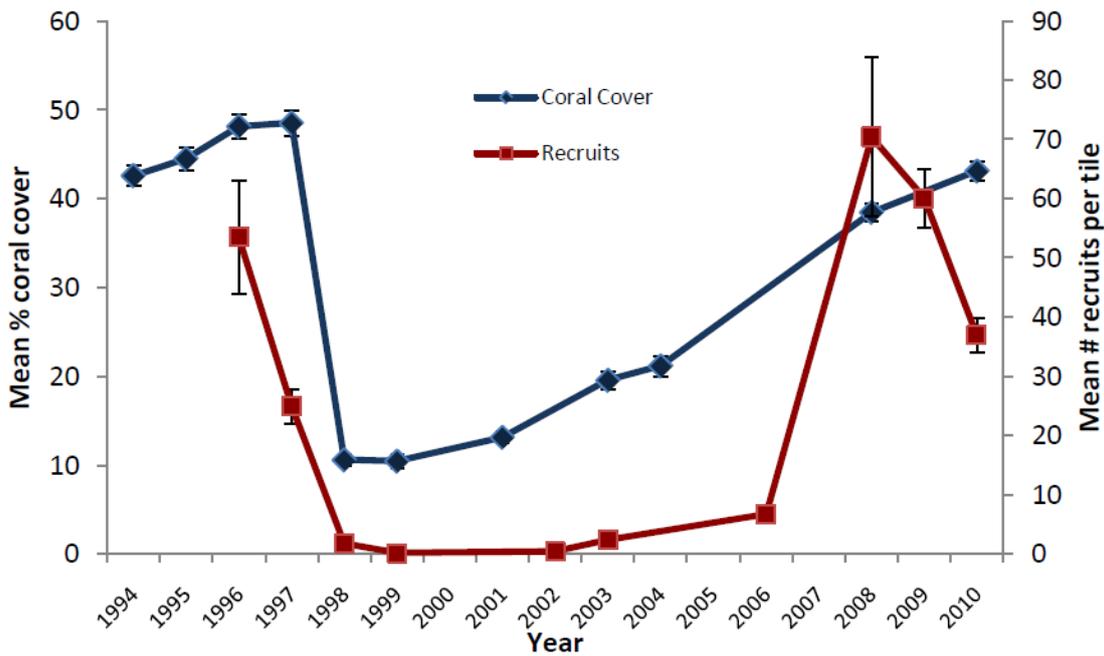


Figure 8.2: Mean % cover of Scleractinian corals (\pm S.E.) across all locations at Scott Reef (blue line), with mean number of recruits per tile (\pm S.E.) across all locations at Scott Reef (red line).

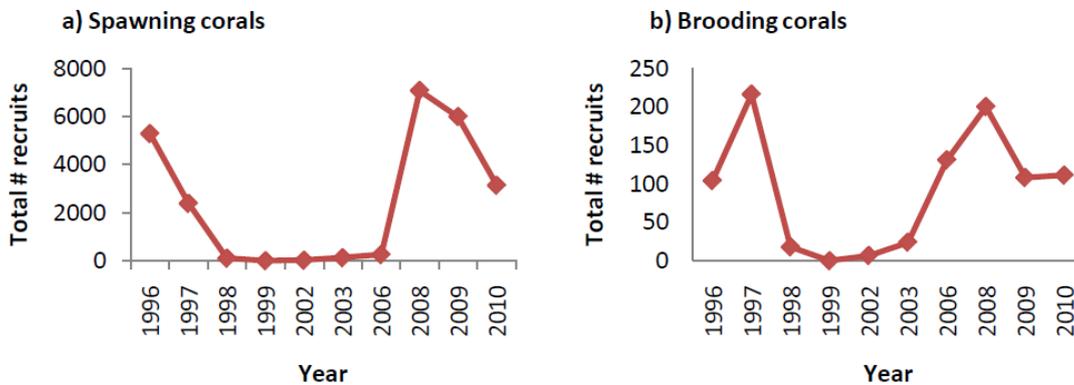


Figure 8.3: a) Total recruit numbers for spawning corals (Acroporidae, excluding *Isopora*) across all locations. b) Total recruit numbers for brooding scleractinian corals (Pocilloporidae and *Isopora*) across all locations.

8.4.1 Broadcast spawning corals

Recruitment of the broadcast spawning *Acropora* was closely correlated ($r^2 = 0.9$) to cover of *Acropora* corals at the whole reef scale, when cover and recruitment was averaged across all locations, (Figure 8.4) indicating that at the reef scale, recruitment of spawning corals was very dependent on the amount of adult brood-stock. However, this relationship broke down at the location scale (Figure 8.5). Some locations (e.g. SL2 and SS1) had high cover of *Acropora* cover but low recruitment, while other locations (e.g. SL1) had only moderate cover of *Acropora* cover but very high recruitment (Figure 8.6).

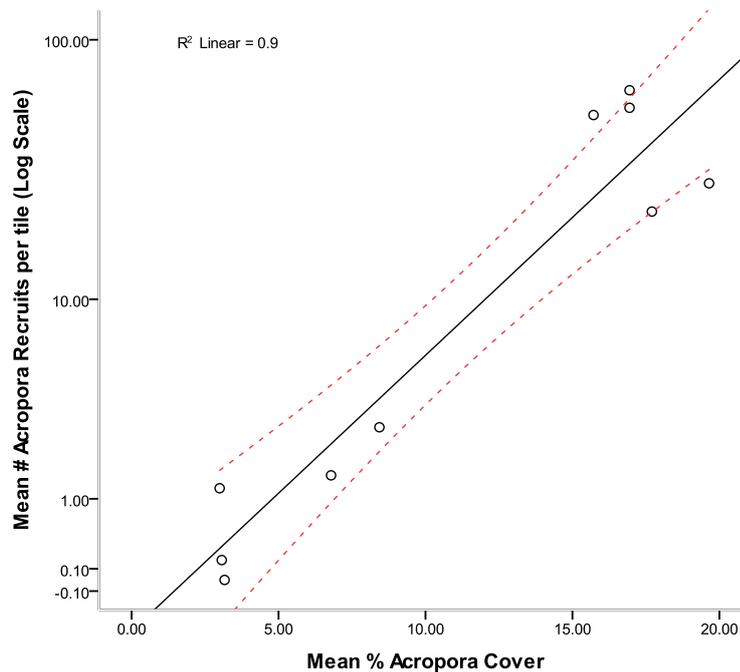


Figure 8.4: Correlation between mean percent cover of *Acropora* and mean numbers of *Acropora* recruits on recruitment tiles averaged across all Scott Reef locations.

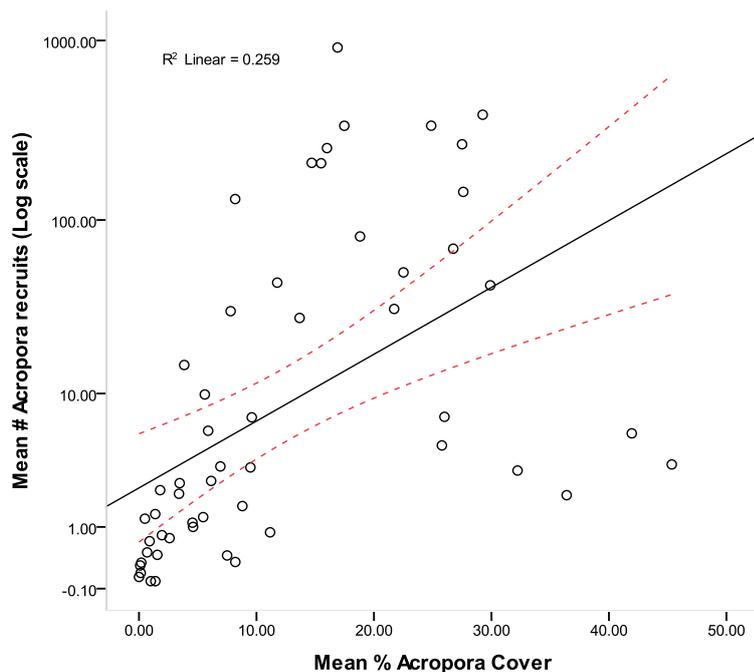


Figure 8.5: Correlation between mean number of *Acropora* recruits from spawning corals and mean % *Acropora* cover at each location per year.

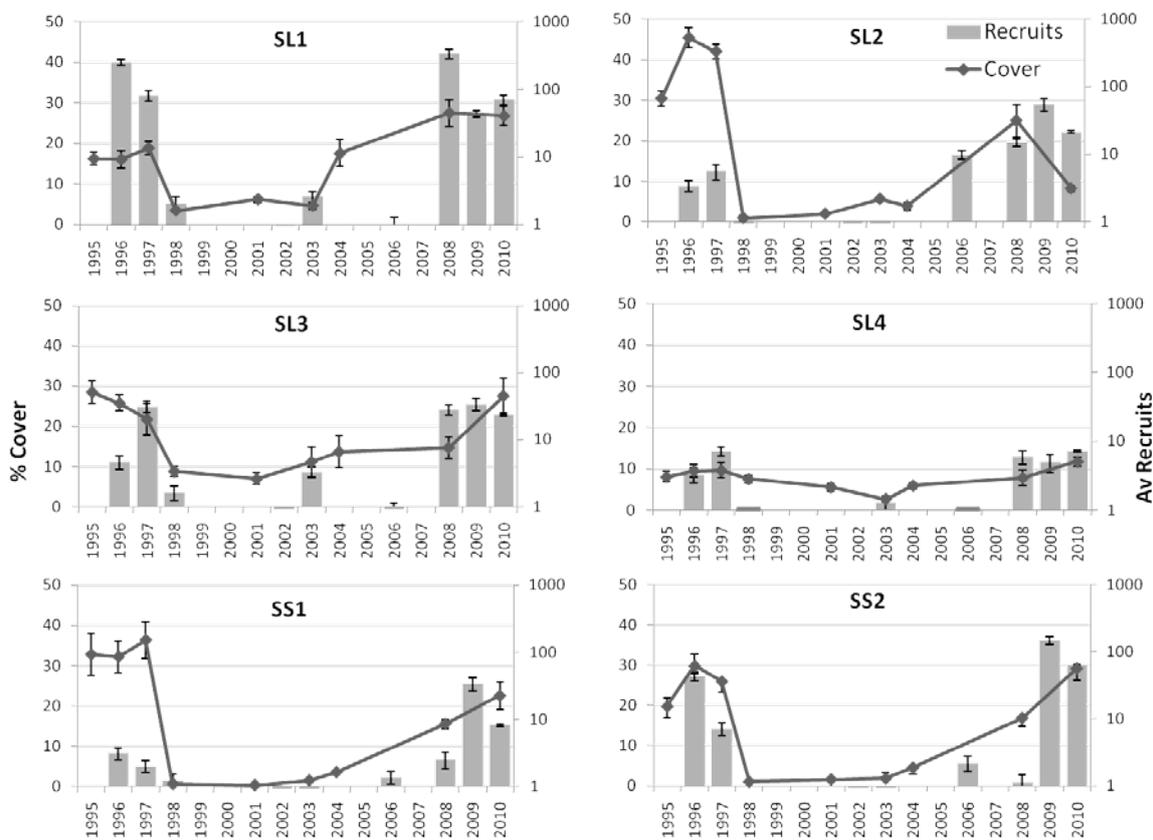


Figure 8.6: Mean % cover of *Acropora* (\pm S.E.) (lines) at Site 1 at each location with mean number of *Acropora* recruits per recruitment tile (\pm S.E.) (bars) at each location on the secondary axis (Log10 scale).

8.4.2 Spatial and temporal variation in recruitment

Recruitment of spawning corals at Scott Reef was found to be significantly variable both temporally and spatially. The main temporal variation occurred among pre-bleaching, post-bleaching and recovery periods (1996-1997, 1998-2006, and 2008-2010 respectively). Recruitment at all locations dropped significantly following the 1998 bleaching and then returned to pre-bleaching levels in 2008-2010 (Table 8.1).

Larval supply was highly variable among locations at Scott Reef, with some locations consistently receiving much higher numbers of recruits than others. Variance partitioning analysis found that the majority of variance in recruits of spawning corals was explained by location (scale <5km), with less than 5% explained by site or tile within location (Table 8.2). In years of good recruitment, SL1 and SS2 between them account for between 59 - 92% of the total recruits captured on the tiles each year (early post-bleaching years are excluded as total numbers were too low) (Figure 8.7). SL1 in particular saw massive spikes in recruit numbers in 1996, 1997 and 2008, with mean recruits tile⁻¹ 255.5 (25.2 SE), 82.77 (14.17 SE) and 354.33 (51.46 SE) respectively, up to tenfold higher than the other locations in those years. Other locations such as SS1 and SL4 were seen to consistently receive a low proportion of the recruits, together receiving between 4-12% of total recruit numbers each year. This pattern is decoupled from adult abundance and may indicate source and sink areas for coral larvae within the reef.

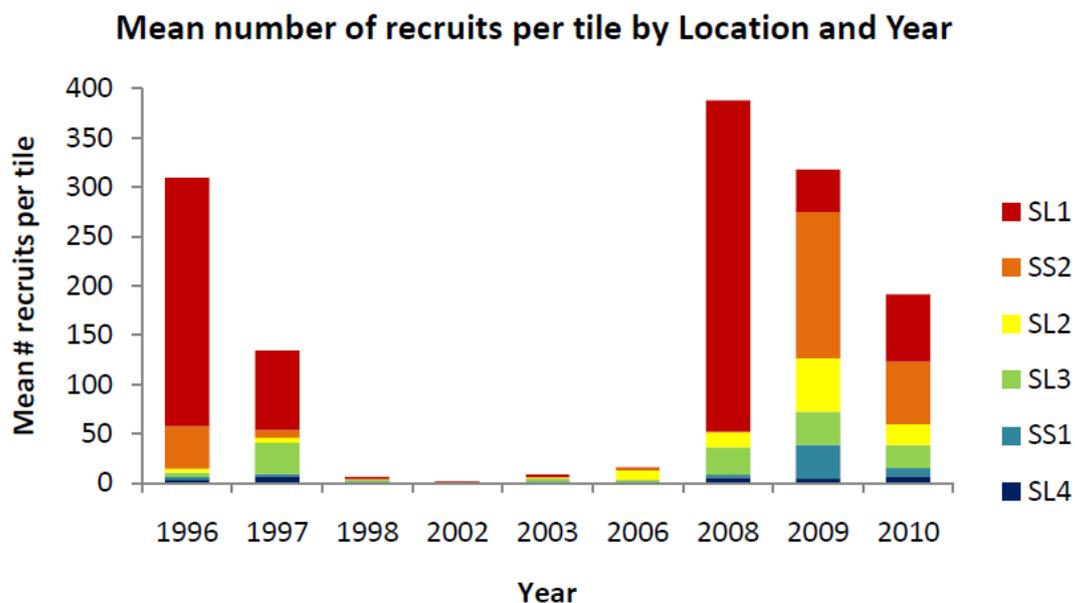


Figure 8.7: Stacked bar graph of the mean number of recruits per recruitment tile at each location for each surveyed year. Indicating the high proportion of recruits seen at SL1 and SS2 compared with other locations.

Table 8.1: Results of GAM for temporal trends in coral recruitment within each reef.

	edf	Ref.df	F	p-value
Year : SL1	8.719	8.832	78.98	<0.0001
Year : SL2	8.471	8.794	37.09	<0.0001
Year : SL3	8.662	8.826	34.36	<0.0001
Year : SL4	8.553	8.81	21.12	<0.0001
Year : SS1	9.631	9.823	32.85	<0.0001
Year : SS2	7.81	7.836	63.07	<0.0001

Table 8.2: Permutation test for hierarchical partitioning of *Acropora* recruits by year, location, site and tile.

	Obs	Z.score	sig95
Year	0.10	69.61	*
Location	0.09	24.55	*
Site	0.00	0.25	
Tile	0.00	1.06	

An exploration of the stock-recruitment relationship at the location scale for *Acropora* using GAMs shows that there was a significant relationship at this scale, however the relationship was skewed by SL2 with its high cover of *Acropora* but fairly low recruitment and SL1 with moderate cover of *Acropora* but very high recruitment (Figure 8.8). When it is assumed that SL2 is a source and SL1 a sink for recruits, and that recruits are shared from SL2 to SL1, the model fit is improved (Table 8.3).

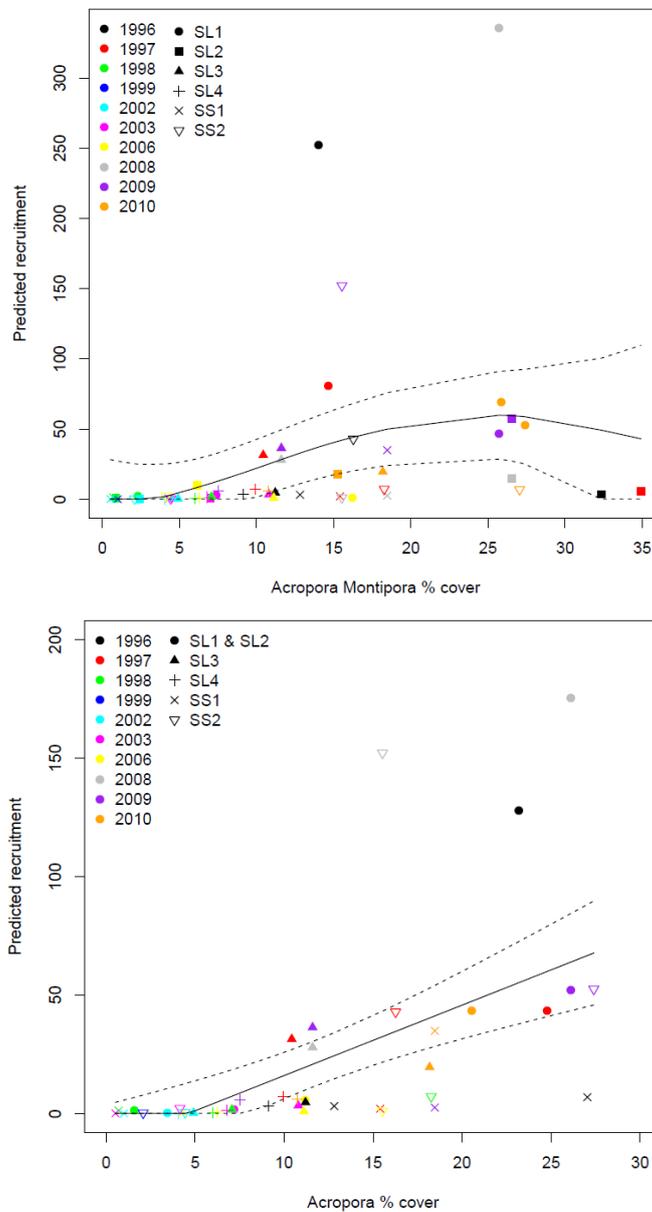


Figure 8.8: GAM fitted to *Acropora* cover vs *Acropora* recruitment. a) shows all locations separately and is skewed by SL1 and SL2. b) shows an improved relationship by assuming recruits are shared from SL2 to SL1.

Table 8.3: Summary of GAM to examine the relationship between *Acropora* coral cover and recruitment.

	Estimated df	Reference df	F	P	R ²
<i>Acropora</i>	3.707	4.551	2.671	0.037	16.9
<i>Acropora</i> – SL1 & SL2 recruits shared	1.105	1.202	21.73	<0.00001	37.8

8.4.3 Brooding Corals:

At the whole-reef scale there was only a very weak correlation between recruits of the brooding coral *Isopora* and local adult brood stock (Figure 8.9). Unlike the pattern seen for broadcast spawning corals, this relationship was strengthened when investigated at the scale of locations (Figure 8.10). *Isopora* recruitment at each location appears to be strongly dependant on the presence or absence of adult broodstock at that location. Following the bleaching, *Isopora* did not recover at locations where 100% of adults were lost from the transects. In contrast, locations in which some *Isopora* survived the bleaching (SL3 and SL4) received hundreds of recruits over the following years and now have higher numbers of *Isopora* colonies than before the bleaching (Figure 8.10).

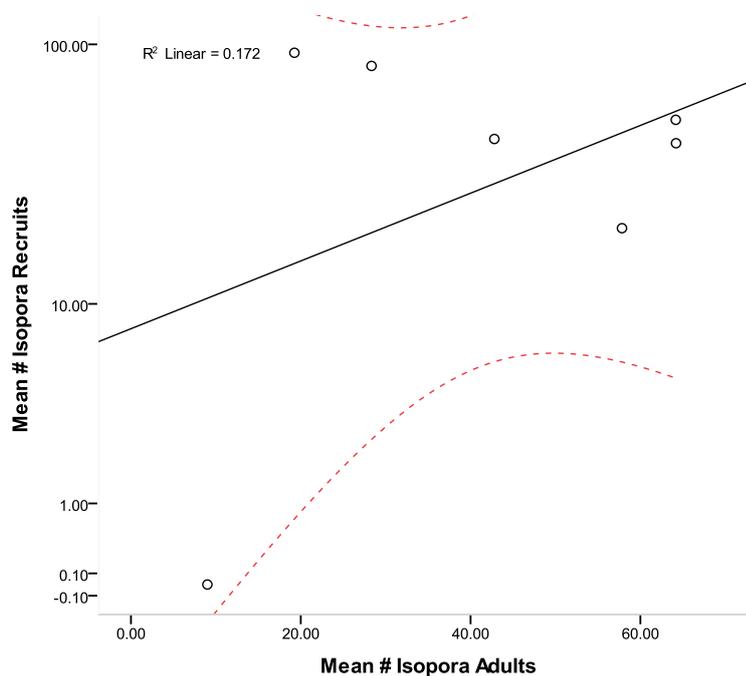


Figure 8.9: Correlation between *Isopora* recruits and adults at the whole reef scale.

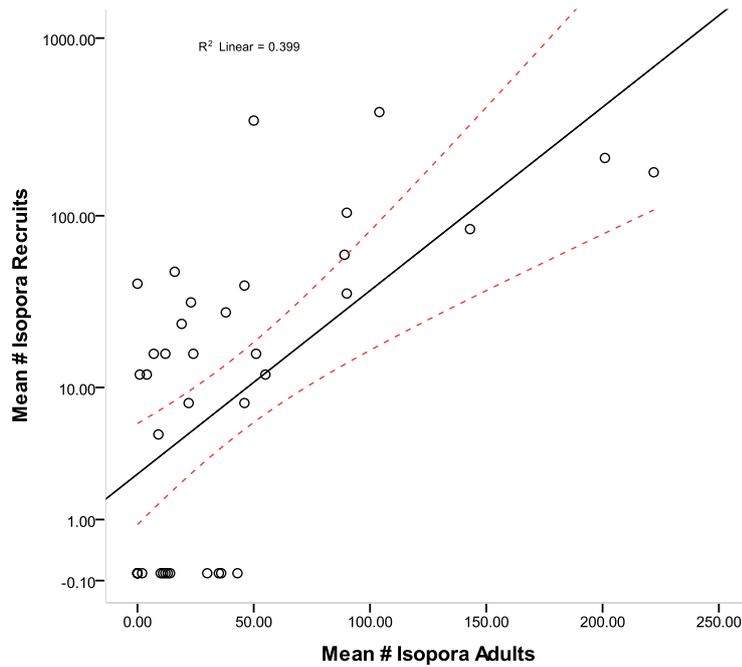


Figure 8.10: Correlation between *Isopora* recruits and adults at each location and year.

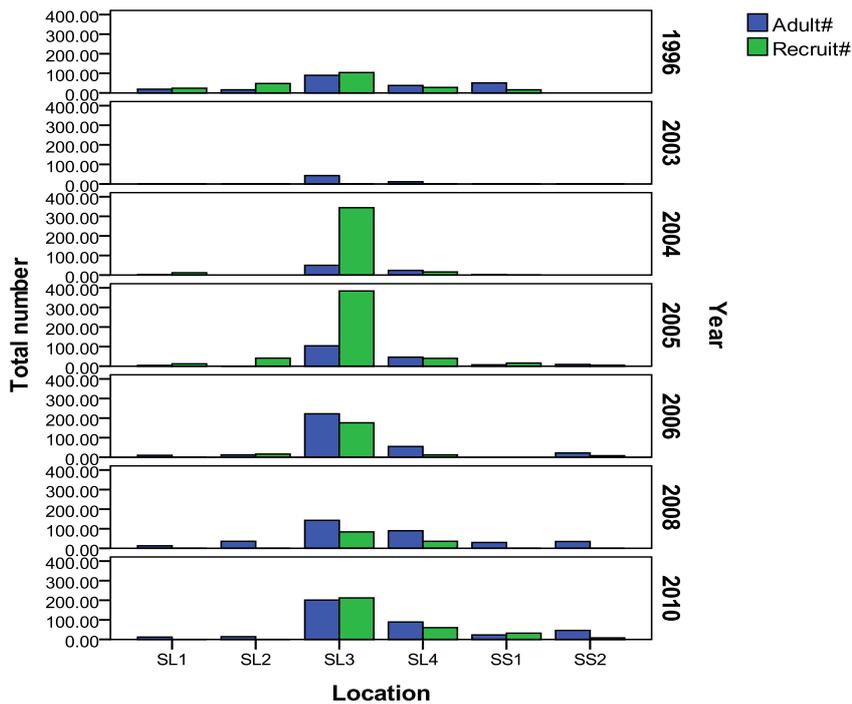


Figure 8.11: *Isopora* recruits (<2cm colonies) with adults (>15cm colonies). Note that in 1996 *Isopora* cover was highest at SS2, however size frequency data was not measured at SS2 in 1996.

8.4.5 Genetic stock-recruitment:

The genetic analysis of the brooding coral *Seriatopora hystrix* shows strong genetic affinities between the 2009 recruit samples and samples collected in 2003 located at the same site. The PCoA plot illustrated that recruit samples (SL1-R, SL2-R and SS1-R) cluster tightly with their associated 2003

population (SL1, SL2 and SS1) in (Figure 8.12). This pattern contrasted markedly to a strong spatial separation among locations, particularly among those located within the sheltered lagoon of the south Scott Reef (SL1, SL2 and SL5), and those located on the outside slopes of north Scott Reef (SL4, SS1) and Seringapatam (SS3) that are exposed to the open ocean. These results indicate a strong genetic stock-recruitment relationship in which the majority of recruits are clearly derived from the brood stock at each particular location for this brooding coral.

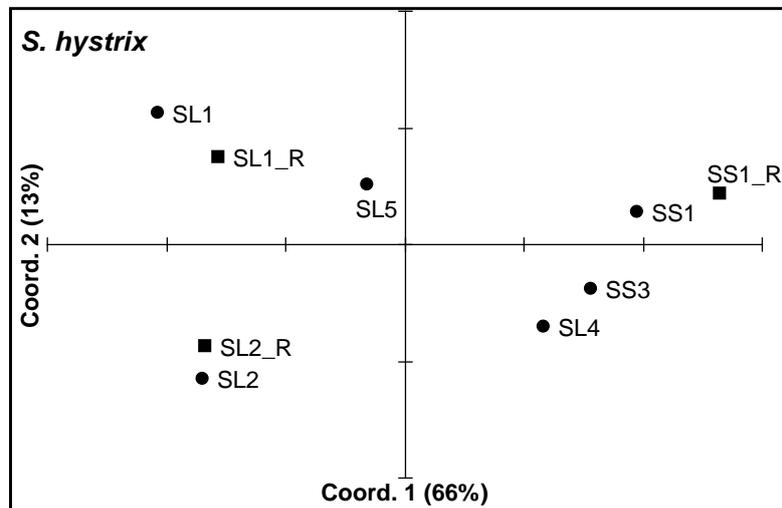


Figure 8.12: Principal coordinate analysis (PCoA) depicting the genetic relationships among 2003 samples (circles) and 2009 recruit samples (squares) of the brooding coral *Seriatopora hystrix*. The multidimensional ordination is based on a pairwise distance matrix of Nei's unbiased genetic distance (D_s). The percentage variation explained by each axis given in brackets.

8.4.4 Importance of larval supply:

Locations that received high recruitment on the tiles (indicating high larval supply) were seen to have correspondingly high numbers of 1-2cm recruits on transects in the following year ($r^2 = 0.792$) (Figure 8.13). In addition, at SL1, the location that received the highest number of recruits, cover of *Acropora* returned to pre-bleaching levels before any other location (2004) and has now increased to higher than pre-bleaching cover, possibly due to high recruitment facilitating recovery, and the fast-growing *Acropora* taking advantage of free space following disturbance. At SL4, both cover and recruits have remained low throughout the study, while at SS1, where low numbers of recruits were received, *Acropora* cover is still not at pre-bleaching levels (Figure 8.6).

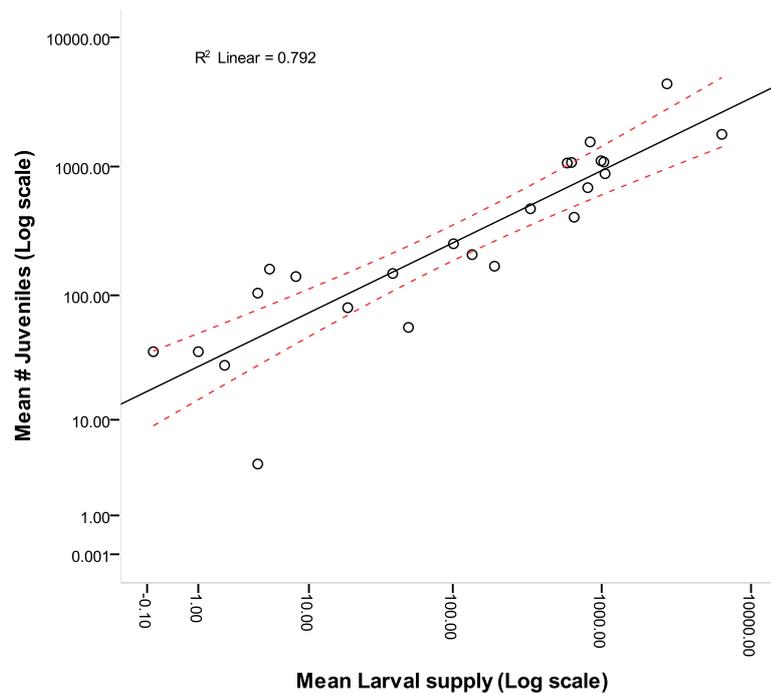


Figure 8.13: Acroporidae recruitment seen per location on our recruitment tiles correlates closely with the number of 1-2cm recruits seen per location on the transects in the following year.

8.5 Discussion

8.5.1 Disturbance and recovery of the Scott Reef system

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 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%, likely as a result of both the extent and severity of the disturbance to the adult brood stock, and the isolation (> 240 km) of the system from unaffected reefs in the region. 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. 1993). Given that competency periods for coral larvae are often less than 30 days (Ayre and Hughes 2000; Miller and Mundy 2003; Nishikawa et al. 2003), and that larval mortality is high for many species during the first few weeks (Graham et al. 2008; Nozawa and Okubo 2011) it is not surprising that larval supply from unaffected reefs was insufficient to replenish the Scott Reef system.

Due to the location of Scott Reef, it is relatively free of anthropogenic pressures such as reduced water quality and overfishing of herbivores. The benthic organisms that can exclude and out-compete scleractinian corals such as macroalgae, sponges and soft corals did not proliferate on available substrata following the bleaching (Smith et al. 2008). This environment has allowed high survival and growth of coral in the absence of disturbance, and may have assisted the eventual recovery of Scott Reef despite low recruitment levels.

8.5.2 Recruitment rates at Scott Reef compared with other regions

The overall recruitment rates at Scott Reef during years of good adult coral cover (excluding 1998-2003) are relatively high in comparison to rates recorded at reefs around the world. The average number of recruits per tile at Scott Reef (averaged over all locations for pre-bleaching and recovered years) was 49.23 (\pm 4.03 SE) recruits per tile, equivalent to 1721.3 recruits per m² over a period of one month following the annual mass spawning event. These rates are similar to that seen on the Great Barrier Reef (GBR), where recruitment rates are some of the highest recorded (Harrison et al. 1990; Glassom et al. 2006). Hughes et al. (2000) reports an average recruit rate of 24.8 (\pm 1.1 SE) recruits per tile (867.1 m⁻²) in year 1, and 86.9 (\pm 4.2) recruits per tile in year 2 (3038.5 m⁻²) on tiles left out for two months post mass spawning on 33 GBR reefs. Recruitment rates on other reefs around the world are reported to be generally much lower (See Glassom et al. 2004; Abelson et al. 2005), for example 76 corals m⁻² 6 months⁻¹ at St Johns, Caribbean (Green and Edmunds 2011), 35 recruits m⁻² 5 months⁻¹ Eilat, Red Sea (Abelson et al. 2005), 37 recruits m⁻² per 2 months in Bermuda (Smith 1992).

8.5.3 Stock recruitment relationship

Recruitment of spawning corals at Scott Reef is highly dependent on the amount of adult brood-stock on the reef. However, the relationship between coral cover and recruitment at the location scale is more complicated. For spawning corals, it is unlikely that populations at the location scale (<10 km) are completely self seeded. The patterns of recruitment we observed over the 10 years of this study are best explained when oceanographic patterns during the time of spawning are taken into account. Broad and fine scale oceanographic patterns play a major role in determining larval distribution and gene flow within and between reefs (Gilg and Hilbish 2003; Mitarai et al. 2009; Weersing and Toonen 2009; White et al. 2010). Although we do not have a conclusive particle mapping model of Scott Reef during spawning conditions, we know that the autumn mass spawning event occurs during neap tides and low wind, which is seen to minimise surface currents and facilitate fertilisation success, larval retention and local recruitment (van Woesik 2009). Around the autumn mass spawning, there is generally a current moving from west to east through Scott Reef, with faster water movement past SL3 and SL4 between North and South Scott, and slow easterly water movement past SL2 at the bottom of South Scott Reef towards the East Hook lagoon and SL1. We hypothesise that much of the coral larvae produced at SL3, SL4 and SL2 may move eastward before becoming competent to settle, and that the reef around Location SL1 may acquire a proportion of this larvae. This results in SL1 being a sink for spawning coral recruits, with very high larval supply despite having only a moderate amount of adult brood-stock. The reef near SL2 at the bottom of South Scott, with high *Acropora* cover, is likely to be an important upstream source of *Acropora* recruits to other areas of the reef. The effect of hydrodynamic regimes on larval supply and the existence of 'recruitment hotspots' on reefs is explored by Eagle (2006).

The recovery of larval supply levels of the broadcast spawning *Acropora* lagged behind the increase in adult cover, and the relationship between the two appears non-linear. The dramatic increase in recruitment in 2008 may indicate a disproportionate increase in reproductive success and larval survival, with increased adult numbers. This is similar to the disproportionate increase in larval supply with fecundity of brood stock, found by Hughes et al (2000). The fertilisation success of a number of coral species has been found to decrease with decreasing conspecific sperm concentration or adult density (Oliver and Babcock 1992; Babcock et al. 1994; Omori et al. 2001; Miller and Mundy 2005), with fertilisation rates of some broadcast spawning marine taxa found to decrease exponentially with increasing distance from nearest male (Denny and Shibata 1989). 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 continues to decrease, then the potential exists for their resilience to decrease more rapidly than would otherwise be predicted.

For the brooding corals, the stock-recruitment relationship appeared to be strongest at the location scale. Brooding coral larvae are ready to settle quickly (Richmond 1987; Carlon and Olson 1993), and while capable of surviving long periods in the water column, are often found to recruit close to natal populations (Best and Resing 1987; Carlon and Olson 1993) and show genetic population structure at smaller scales than broadcast spawning species (Nishikawa et al. 2003; Miller and Ayre 2008; Underwood et al. 2009a). Numerous studies have found consistency in spatial patterns of recruitment for brooding corals (Pocilloporids, mostly *pistilata*), in relation to highest densities of adults (Harriott 1999; Glassom et al. 2004). The number of brooding corals (*Pocillopora* and *Isopora*) seen on the tiles was small compared to that of broadcast spawning *Acropora* (1-3%), however these species are known to spread their reproductive effort over numerous months of the year (Harrison et al. 1990; Richmond and Hunter 1990; Tanner 1996; Fan et al. 2006). These results from the demographic data were strongly supported by the genetic analysis of the brooding coral *Seriatopora hystrix*; a strong genetic stock-recruitment relationship was detected in which recruits collected in 2009 were closely related to their putative parents (collected in 2003) at each location contrasted to large genetic differences among locations across space. This conclusion is consistent with an earlier genetic study showing that most brooded larvae recruit within 100 m of their natal reef area (Underwood et al. 2007).

8.5.4 Evidence of the importance of larval supply as a demographic process

The variation in larval supply at the location scale was seen to affect the dynamics of the local coral communities, with a strong correlation between local larval supply (as measured on recruitment tiles) and 1st year recruits (1-2cm colonies) visible the following year in the size frequency transects at location scales, indicating that early post-settlement mortality did not obscure larval supply patterns. Additionally, *Acropora* cover at the location which generally received the highest numbers of *Acropora* recruits -SL1, was the first to recover to pre-bleaching *Acropora* cover levels (in 2004) despite high mortality in 1998, and now has a higher *Acropora* cover than seen before the disturbance (see coral cover Chapter 4). Of the two locations with low recruitment - SL4 and SS1, cover and recruitment of *Acropora* has remained low at SL4, and at SS1 *Acropora* cover has still not reached pre-bleaching levels in 2010.

8.5.5 Implications

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 disturbance 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 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 decades (Wilkinson 2002). Disturbances occurring over entire regions are predicted to become more severe and frequent e.g. 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 that 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.

8.6 References

- Abelson A, Olinky R, Gaines S (2005) Coral recruitment to the reefs of Eilat, Red Sea: temporal and spatial variation, and possible effects of anthropogenic disturbances. *Marine Pollution Bulletin* 50: 576-582
- 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 of reef-building corals. *Ecology Letters* 7: 273-278
- Babcock RC, Baird AH, Pirovaragorn S, Thomson DP, Willis BL (2003) Identification of scleractinian coral recruits from Indo-Pacific reefs. *Zoological Studies* 42: 211-226
- Babcock RC, Mundy CN, Whitehead D (1994) Sperm Diffusion-Models and in-Situ Confirmation of Long-Distance Fertilization in the Free-Spawning Asteroid *Acanthaster Planci*. *Biological Bulletin* 186: 17-28
- Baums IB, Miller MW, Hellberg ME (2005) Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. *Molecular Ecology* 14: 1377-1390
- Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* 429: 827-833
- Best BA, Resing JM (1987) Active settlement of coral planulae: the effects of flow and swimming behavior on local recruitment. *American Zoologist* 127: 103A
- 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 and Systematics* 27: 477-500
- Carlson DB, Olson RR (1993) Larval dispersal distance as an explanation for adult spatial pattern in two Caribbean reef corals. *Journal of Experimental Marine Biology and Ecology* 173: 247-263
- Chevan A, Sutherland M (1991) Hierarchical partitioning. *The American Statistician* 45: 90-96
- Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16 (Suppl): 101-113
- Cowen RK, Sponaugle S (2009) Larval Dispersal and Marine Population Connectivity. *Annual Review of Marine Science* 1: 443-466
- Cresswell G, Frische A, Peterson J, Quadfasel D (1993) Circulation in the Timor Sea. *Journal of Geophysical Research-Oceans* 98: 14379-14389
- Denny MW, Shibata MF (1989) Consequences of surf-zone turbulence for settlement and external fertilization. *The American Naturalist* 134: 859-889
- Eagle JV (2006) Recruitment hotspots around a coral reef: the roles of hydrodynamics and habitats. PhD thesis. Marine Biology, Townsville
- Fan TY, Lin KH, Kuo FW, Soong K, Liu LL, Fang LS (2006) Diel patterns of larval releases by five brooding scleractinian corals. *Marine Ecology Progress Series* 321: 133-142
- Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301: 958-960
- Gilg MR, Hilbish TJ (2003) The geography of marine larval dispersal: coupling genetics with fine-scale physical oceanography. *Ecology* 84: 2989-2998
- Gilmour J (2007) Biannual spawning, rapid larval development and evidence of self seeding for corals at an isolated system of reef Australian Coral Reef Society, Fremantle
- Glassom D, Celliers L, Schleyer MH (2006) Coral recruitment patterns at Sodwana Bay, South Africa. *Coral Reefs* 25: 485-492
- Glassom D, Zakai D, Chadwick-Furman NE (2004) Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. *Marine Biology* 144: 641-651
- Graham EM, Baird AH, Connolly SR (2008) Survival dynamics of scleractinian coral larvae and implications for dispersal. *Coral Reefs* 27: 529-539
- Green DH, Edmunds PJ (2011) Spatio-temporal variability of coral recruitment on shallow reefs in St. John, US Virgin Islands. *Journal of Experimental Marine Biology and Ecology* 397: 220-229
- Harriott VJ (1999) Coral recruitment at a high latitude Pacific site: A comparison with Atlantic reefs. *Bulletin of Marine Science* 65: 881-891

- Harrison P, Wallace C, Dubinsky Z (1990) Reproduction, dispersal, and recruitment of scleractinian corals Ecosystems of the World: Coral Reefs. Elsevier Publishers New York
- Hastings A, Botsford LW (2006) Persistence of spatial populations depends on returning home. Proceedings of the National Academy of Sciences of the United States of America 103: 6067–6072
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50: 83-866
- 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, Moltschaniwskyi NA, Pratchett MS, Tanner JE (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity and larval recruits. Ecology 81: 2241-2249
- Knowlton N (2001) The future of coral reefs. Proceedings of the National Academy of Sciences 98: 5419-5425
- Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. Integrative and Comparative Biology 46: 282-297
- Mac Nally R (2000) Regression and model-building in conservation biology, biogeography and ecology: The distinction between and reconciliation of 'predictive' and 'explanatory' models. Biodiversity and Conservation 9: 655-671
- McCullagh P, Nelder JA (1989) Generalized linear models (Monographs on statistics and applied probability 37). Chapman Hall, London
- Miller K, Mundy C (2003) Rapid settlement in broadcast spawning corals: implications for larval dispersal. Coral Reefs 22: 99-106
- Miller KJ, Ayre DJ (2008) Protection of genetic diversity and maintenance of connectivity among reef corals within marine protected areas. Conservation Biology 22: 1245-1254
- Miller KJ, Mundy CN (2005) In situ fertilisation success in the scleractinian coral *Goniastrea favulus*. Coral Reefs 24: 313-317
- Mitarai S, Siegel DA, Watson JR, Dong C, McWilliams JC (2009) Quantifying connectivity in the coastal ocean with application to the Southern California Bight. J. Geophys. Res 114: 1–21
- Mundy CN (2000) An appraisal of methods used in coral recruitment studies. Coral Reefs 19: 124-131
- Nei M (1978) Estimation of average heterozygosity and genetic distance from a small number of individuals.. Genetics 89: 583-590
- Ninio R, S. Delean, K. Osborne, 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, Katoh M, Sakai K (2003) Larval settlement rates and gene flow of broadcast-spawning (*Acropora tenuis*) and planula-brooding (*Stylophora pistillata*) corals. Marine Ecology Progress Series 256: 87-97
- Nishikawa A, Sakai K (2005) Genetic connectivity of the scleractinian coral *Goniastrea aspera* around the Okinawa Islands. Coral Reefs 24: 318-323
- Nozawa Y, Okubo N (2011) Survival Dynamics of Reef Coral Larvae With Special Consideration of Larval Size and the Genus *Acropora*. Biological Bulletin 220: 15-22
- Nystrom M, Folke C (2001) Spatial Resilience of Coral Reefs. Ecosystems 4: 406-417
- Oliver J, Babcock RC (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 and Oceanography 46: 704-706
- Pineda J, Hare JA, Sponaugle S (2007) Larval Transport and Dispersal in the Coastal Ocean and Consequences for Population Connectivity. Oceanography 20: 22-39
- Richmond RH (1987) Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. Marine Biology 93: 527-533
- Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. Marine Ecology Progress Series 60: 185-203

- Sheppard CRC (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature* 425: 294-297
- Smith LD, Gilmour JP, Heyward AJ (2008) Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. *Coral Reefs* 27: 197-205
- Smith SR (1992) Patterns of Coral Recruitment and Post-settlement Mortality on Bermuda's Reefs: Comparisons to Caribbean and Pacific Reefs. *American Zoologist* 32: 663-673
- Swearer SE, Shima JS, Hellberg ME, Thorrold SR, Jones GP, Robertson DR, Morgan SG, Selkoe KA, Ruiz GM, Warner RR (2002) Evidence of self-recruitment in demersal marine populations. *Bulletin of Marine Science* 70: 251-271
- Tanner JE (1996) Seasonality and lunar periodicity in the reproduction of *Pocilloporid* corals. *Coral Reefs* 15: 59-66
- 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 (2009a) Ecologically relevant dispersal of a brooding and a broadcast spawning coral at isolated reefs: implications for managing community resilience. *Ecological Applications* 19: 18-29
- Underwood JN, Smith LD, van Oppen MJH, Gilmour JP (2009b) Ecologically relevant dispersal of corals on isolated reefs: implications for managing resilience. *Ecological Applications* 19: 18-29
- van Oppen MJH, Gates RD (2006) Conservation genetics and the resilience of reef-building corals. *Molecular Ecology* 15: 3863-3883
- van Woesik R (2009) Calm before the spawn: global coral spawning patterns are explained by regional wind fields. *Royal Society of London Proceedings* 277: 715-722
- Veron JEN (1986) Reef Building Corals. In: Berry PF (ed) Faunal surveys of the Rowley Shoals, Scott Reef and Seringapatam Reef North-western Australia. . Records of the Western Australian Museum, Perth, pp 27
- Weersing K, Toonen RJ (2009) Population genetics, larval dispersal, and connectivity in marine systems. *Marine Ecology-Progress Series* 393: 1-12
- Whitaker K (2004) Non-random mating and population genetic subdivision of two broadcasting corals at Ningaloo Reef, Western Australia. *Marine Biology* 144: 593-603
- White C, Selkoe KA, Watson J, Siegel DA, Zacherl DC, Toonen RJ (2010) Ocean currents help explain population genetic structure. *Proceedings of the Royal Society B: Biological Sciences* 277: 1685-1694
- Wilkinson CR (2002) Status of Coral Reefs of the World. Australian Institute of Marine Science, Townsville, Queensland

9 Water Temperature and sedimentation regimes

9.1 Introduction

Mass bleaching has been the most severe and widespread disturbance to coral communities at Scott Reef since the start of monitoring in 1994. In 1998, extreme sea-water temperatures caused mass-mortality of hard and soft corals and the impacts were so severe that they also caused major changes to the fish communities across Scott Reef. The effects of the mass-bleaching in 1998 are still evident today.

High water temperatures outside the tolerance range of corals interfere with coral reproduction and feeding, reduce zooxanthellae numbers and reduce zooxanthellae photosynthesis (Coles and Brown 2003). Elevated sedimentation rates have also been identified as a cause of decline in coral cover and diversity on coral reefs around the world (Bellwood et al. 2004). Increased sedimentation rates can result in the smothering of corals, abrasion of coral tissue, reduced sexual recruitment and growth, lower coral growth rates and excess energy expenditure (Rogers 1990a; Crabbe and Smith 2005). In some settings, however, certain coral species have been shown to tolerate high sediment loadings (Woolfe and Larcombe 1998) and others use sediments as a source of food, thus benefitting coral health (Rosenfeld et al. 1999; Anthony 2000). As it is often difficult to separate causes of reef decline (Dubinsky and Stambler 1996), long-term research monitoring is important to understand and separate the most significant impacts in particular regions. Monitoring of water temperature across different regions of the reef is necessary in order to identify and understand the cause of any future coral mortality, as occurred in the recent 2010 coral bleaching event reported in Gilmour et al. (2010). This component of the study thus provides water temperature and sedimentation data that have been collected at the main long-term monitoring locations at Scott Reef to inform interpretation of patterns of change of coral reef communities at Scott Reef.

9.2 Materials and methods

9.2.1 Study area and sampling regime

This component of the study is focused on capturing the temporal and spatial dynamics of water temperature and sedimentation on the shallow reef slope at Scott Reef. Water temperature is monitored at each of the six main study locations (SL1 SL2, SL3, SL4, SS1, SS2). A single Odyssey temperature logger has recorded water temperature at 6 to 9m depth and with the additional deployment of Sensus loggers in March 2010, water depth as a proxy for tidal range is now also monitored. Sedimentation rates were estimated by deploying five replicate sediment traps at each of the six locations at Scott Reef from March 2007-October 2010. Prior to May 2008, a gravimetric filtration method had been used to determining sedimentation rates at Scott Reef, however, this was discontinued as blockage of the membrane filter became a problem for samples that contained high total sediment volumes as a result of deployment periods of > 1 month. After this time, the sediment contained within each trap was firstly wet sieved through a 500 µm sieve to remove unwanted biological organisms (crustaceans, echinoderms and fishes). The retained sediment was placed in a plastic vial, labelled, stored frozen and transported to the Particle Analysis Service Laboratory of CSIRO where samples were processed to determine particle size distributions (PSD) and the total dry weight of sediment. Due to missing temperature loggers and/or sediment traps, the datasets for each method may differ in their continuity at the monitoring locations.

9.2.3 Sediment weight, particle size and composition

The particle size distributions were determined using a Malvern Mastersizer-X laser particle-sizer to measure particles in the 0.2 μm to 500 μm size range. This method of analysis utilises the diffraction properties of laser light when passed through a medium containing suspended particles, and provides a normalised measure of the relative mass of particles in many size fractions of the sample (Syvitski 1991). The percentage contributions of nine size fractions were derived for each sample by the summation of the following output classes from the laser particle sizer and were based on the Wentworth grain size scale: clay (< 3.9 μm), very fine silt (3.9-7.8 μm), fine silt (7.8-15.6 μm), medium silt (15.6-31 μm), coarse silt (31-63 μm), very fine sand (63-125 μm), fine sand (125-250 μm), medium sand (250-500 μm) and coarse sand (> 500 μm). In some plots, these fractions were reduced to six classes, i.e. clay, very fine silt, fine silt, fine sand, medium sand and coarse sand. The total dry weight of each replicate sediment sample was then determined by drying replicate samples in pre-weighed porcelain crucibles at 100°C and then reweighing the sample and subtracting the prior weight from the final weight. The sedimentation rate, expressed as $\text{mg cm}^{-2} \text{d}^{-1}$, was calculated for each replicate sample from the equation:

$$\text{Sedimentation rate (cm}^{-2} \text{d}^{-1}) = (\text{Dry Weight (DW) of sample} / \text{Area of trap entrance}) / \text{Duration (d)}$$

Calculation of sedimentation rate in this manner allows for cross-study comparisons. A restricted number of samples (one from each location in October 2008) were also studied with a scanning electron microscope (SEM) to determine the mineral composition of various particles within the samples. Samples were analysed for total carbon (TC) content by heating at 1400°C in an oxygen-enriched atmosphere so that the carbon in the sediment was converted to CO_2 gas. This was carried through drying and particulate removal stages to an IR cell for measurement against standards. A subsample was treated with a 50% Nitric acid solution that reacted with the inorganic carbon (TIC) content only to produce CO_2 gas. This was removed by heating and drying and the residue organic carbon (TOC) was then analysed as for the total carbon and the inorganic carbon content of the sample was calculated by difference.

9.2.4 Data analysis

Three-way Analysis of Variance (ANOVA) was used to determine whether sedimentation rates and average sediment size differed significantly among locations (5 df), seasons (2 df) and years (1 df). Data from the four monitoring locations with the most complete temporal sequence were selected for these analyses. Prior to subjecting the sedimentation rates to ANOVA data were Log_{10} transformed to conform with assumptions of the analysis. Data derived from sediment trap deployments from March 2007 to March 2008 were not included in this analysis due to the year-long duration of sampling. All other deployments lasted no more than approximately 3 months. Analyses were carried out in PASW v 18.0 statistical software.

9.3 Results and Discussion

9.3.1 Water temperature

Water temperatures in shallow (ca 9 m) waters at Scott Reef between 2007 and 2010 followed a seasonal cycle of high temperatures in early summer (December/January) followed by a secondary peak in autumn (April/May) with lowest temperatures being recorded in late winter in August and September (Figure 9.1). Although not as severe as the bleaching event in 1998, mass-bleaching also occurred at Scott Reef between March and May 2010 (Gilmour et al 2010 Report SRRP-RP-RT-045). The bleaching event coincided with the 2009-2010 El Niño-Southern Oscillation (ENSO) warming

conditions and sustained sea surface temperatures above 31°C (Figure. 9.2). The NOAA Bleaching Watch issued for Scott Reef on 18 February 2010 was upgraded to a Bleaching Warning on 22 March 2010, and to a Bleaching Alert Level 1 (≥ 4 Degree Heating Weeks) on 12 April 2010. This is the first bleaching alert for Scott Reef since NOAA began this alert program in 2000. The ecological impact that this extended period of high water temperatures has had on the benthic communities is discussed in Chapters 2 and 4.

Water temperatures at Scott Reef climbed to over 31°C between March 25 and April 12 2010 and reached 32°C at SSI on the exposed eastern edge of north Scott where coral bleaching was moderate to severe (Figure 9.1; 9.3). Temperatures at most locations showed two peaks during this period with each occurring during either side of the March spring tide, *i.e.* when water movement was lower. The higher water temperatures at Scott Reef during this period coincided with a period of low wind “doldrum” conditions which have been shown elsewhere to facilitate rising water temperatures associated with coral bleaching events (Miller et al. 2009). Water temperature at the most southern location on the inner side of south Scott lagoon (SL2) where water circulation is low, tended to not vary more than 1°C in a 24h period, whereas temperatures at locations with high tidal influence and short distances to deeper oceanic water (SL3 and SL4) exhibited wide ranges $> 1^\circ\text{C}$ in a 24 h period (Figure 9.3). This latter pattern provides an example of the cooling influence of water originating from the deep channel separating North and South Scott Reef (Brinkman et al. SRRP Final Report Project 3.1 2010). Such cool water intrusions are primarily semi-diurnal in timing, driven by the strong semi-diurnal periodicity in the prevailing internal wave and tide regime in the channel, combined with horizontal shear due to the strong tidal currents that can entrain water from below the sill depth up into the lagoon (Brinkman et al. SRRP Final Report Project 3.1 2010). Average daily water temperatures following the bleaching period at Scott Reef in early 2010 declined through to *ca* 27°C in August and then increased through October.

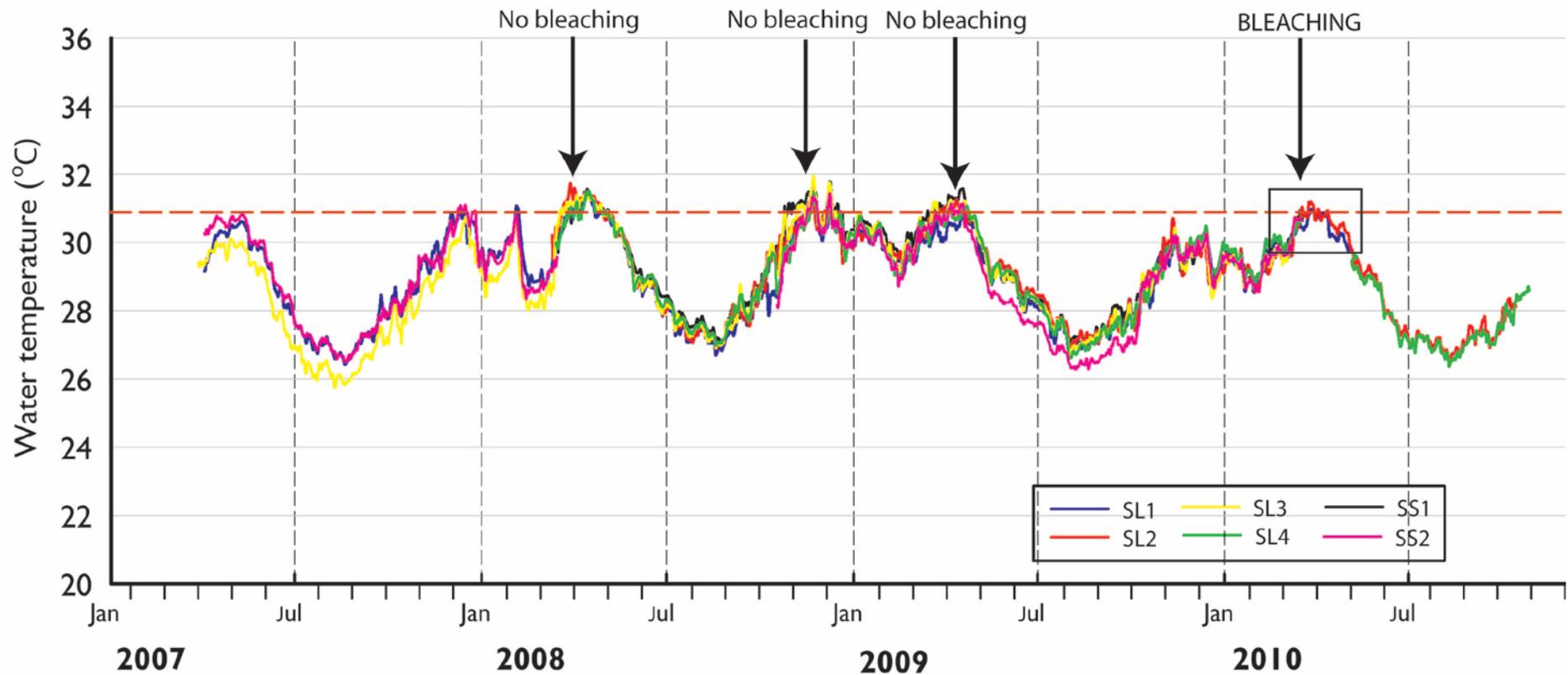


Figure 9.1. Average daily water temperatures recorded at six locations at Scott Reef between April 2007 and October 2010. The NOAA bleaching threshold represents a calculated value that is 1°C above the maximum mean monthly sea surface temperature at Scott Reef. Temperature loggers deployed at Scott Reef record temperature at 6 to 9m below the surface. Note, in October 2010 loggers were only present at two locations, i.e. SL2 and SL4



Figure 9.2 El Niño-Southern Oscillation (ENSO) monitoring graph issued by the Australian Bureau of Meteorology (BOM, 2011) the peak in the Nino 3.4 SST index in December 2009 and the period of bleaching at Scott Reef between March and May 2010. Monthly values $> +0.8$ indicate typical El Niño conditions.

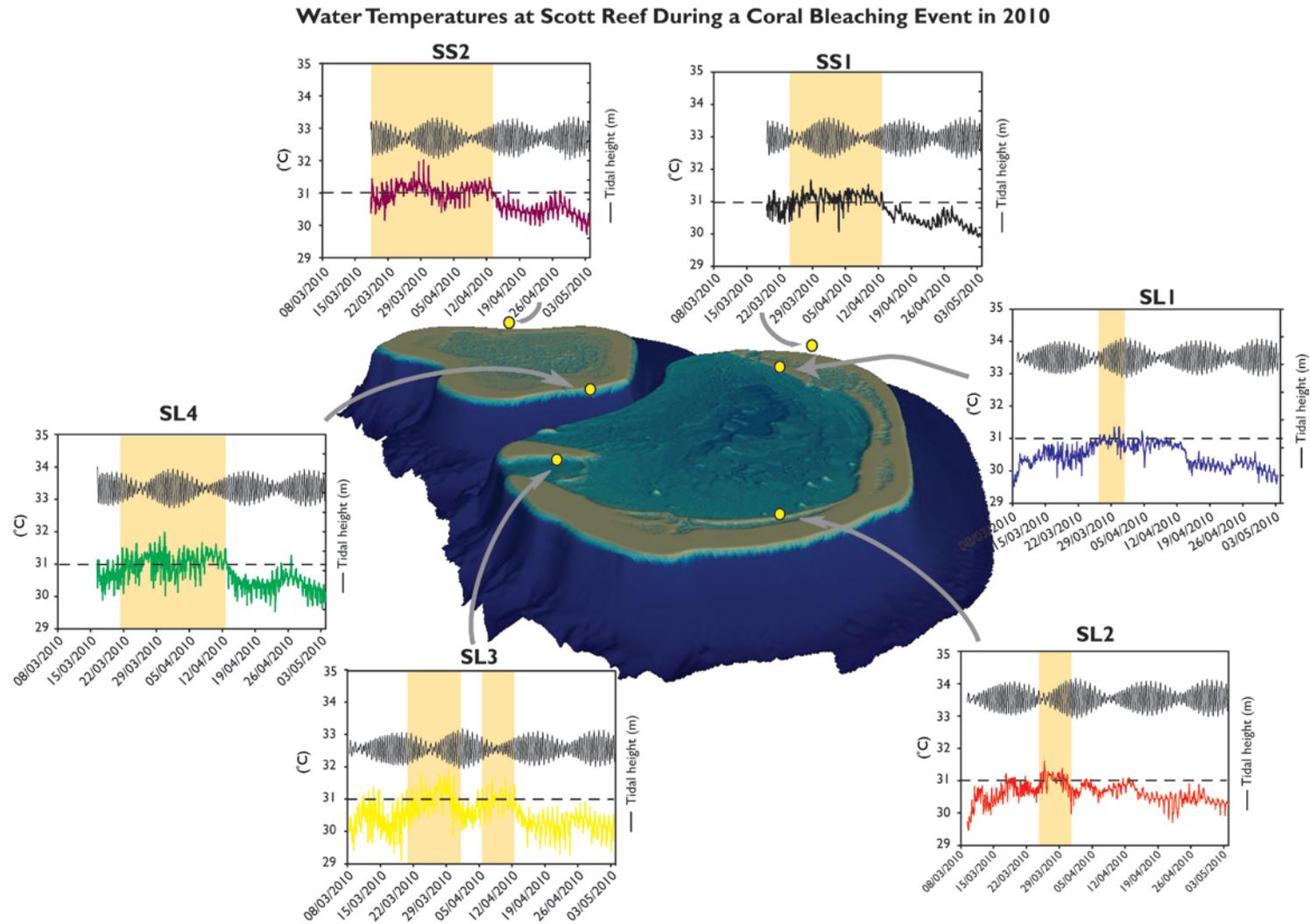


Figure 9.3 Water temperatures during the 2010 coral bleaching event at Scott Reef varied with distance to the deep-channel between north and south Reef and with distance oceanic influence. Inner lagoon locations (SL1 and SL2) recorded temperatures at or just below 31°C whereas other locations closer to deeper-water (SL3, SL4) showed more extreme ranges both above and below 31°C.

9.3.2 Sedimentation regime

9.3.2.1 Sedimentation rate

Sedimentation rates in shallow (6 to 9 m) water depths at Scott Reef differed significantly among seasons and locations (both $P < 0.001$) but not among years and all interactions were significant (Table 9.1). In terms of main effects the mean squares were similar for location and season, however the highest mean square was recorded for the interaction between year and season (0.82). Mean sedimentation rates tended to be lower than $2 \text{ mg cm}^{-2} \text{ d}^{-1}$ at all locations, particularly at SL1 and SL2 (Figure 9.5). However, sediment rates greater than this were recorded at certain locations when exposed to seasonal onshore winds. For example, rates at SL3 and SL4 were greater during the summer periods when these locations are exposed to frequent westerly winds, whereas the highest rates at SS1 and SS2 were recorded during the autumn through spring period when easterly winds are mainly onshore at the eastern outer reef edge. During periods of onshore winds, wave energy increases and thus the amount of suspended material transported to reef edges increases. In contrast, lagoon water is persistently low in suspended matter. A separate study in the deeper central lagoon of Scott Reef (Brinkman et al. SRRP Final Report Project 3.1 2010) recorded very low total suspended sediment concentrations that were often close to the limits of detection, *i.e.* $< 1 \text{ mg L}^{-1}$. Furthermore, mean sedimentation fluxes determined from in-situ sediment traps within the deeper sections of the lagoon were also low (site deployment means – $0.2\text{-}0.5 \text{ mg DW cm}^{-2} \text{ day}^{-1}$).

9.3.2.2 Particle size distribution

Three-way ANOVA, using data only for SL1, SL2, SL3 and SL4, showed that mean sediment grain-size differed significantly among years, seasons and locations (all $P < 0.001$) and there were significant interactions between these factors (Table 9.1) although the greatest mean square was for the interaction between year and season (42.11), those for the main effects were greater than for all other interactions. Mean grain size was consistently smallest (ca $50 \mu\text{m}$) at the most protected location where water circulation is least (SL2) and was over $200 \mu\text{m}$ at SL3 and SS2 during the seasons when these locations were exposed to onshore winds, *i.e.* summer in the case of SL3 and winter in the case of SS1 and SS2 (Figure 9.6).

Small sediment grain size (clay and silt) characterised ($> 80\%$) sediments at the most protected lagoon location (SL2) in all seasons, is presumably due to the lower water circulation regime at this location which is related to a small influence of tides and a greater protection from winds (Figure 9.7). In contrast, at locations that were more exposed to seasonal winds, larger grain sizes contributed $> 60\%$ to sediments such as during the summer period at SL3 when westerly winds dominated and in winter on the east side of the reef when easterly winds were onshore.

Table 9.1. Mean squares (MS) and their significance levels (*P*) for ANOVAs of the sedimentation rate and sediment size in summer, autumn and spring at four locations at Scott Reef between 2008 and 2010. df, degrees of freedom.

	df	Sedimentation rate		Sediment size	
		MS	<i>P</i>	MS	<i>P</i>
Year	1	0.01	0.81	12.30	<0.001
Season	2	0.47	<0.001	17.51	<0.001
Location	3	0.52	<0.001	19.19	<0.001
Year × season	2	0.82	<0.001	42.11	<0.001
Year × location	3	0.15	<0.01	2.82	<0.05
Season × location	6	0.48	<0.001	2.09	0.06
Year × season × location	6	0.15	<0.001	5.24	<0.001
Residual	91	0.29		0.02	

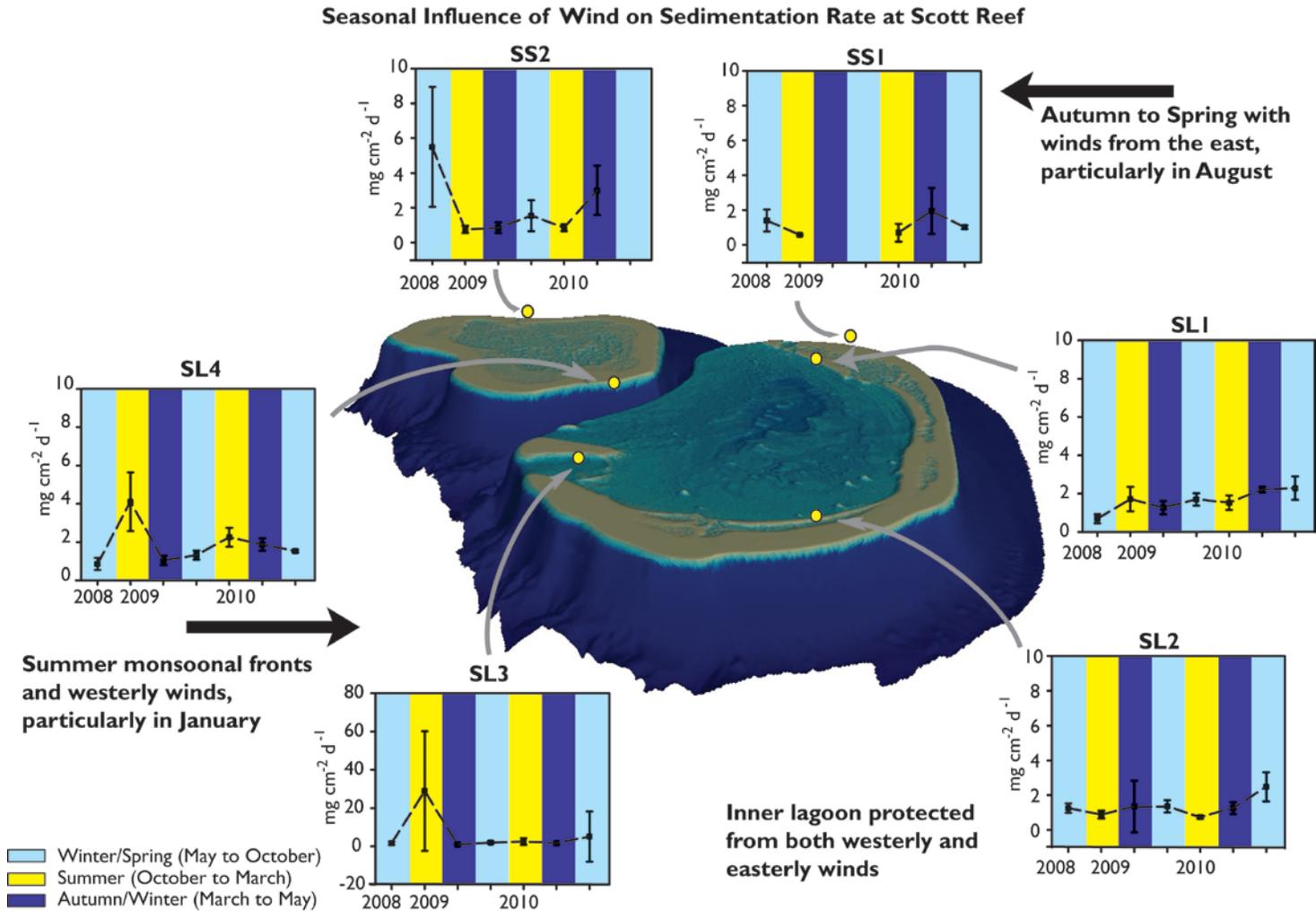


Figure 9.4 Variation in mean sedimentation rates across regions at Scott Reef that differ in their tidal water movement and wind and wave exposure. Locations within the protected inner reef where exposure and tidal circulation are least such as SL2 have low rates throughout the year whereas more exposed locations have higher rates, particularly in the seasons when they are exposed to the prevailing winds, e.g. summer on the western side of the reef (SL3 and SL4) and autumn through spring on the eastern side of the reef (SS1 and SS2).

Seasonal Influence of Wind and Waves on Sediment Size at Scott Reef

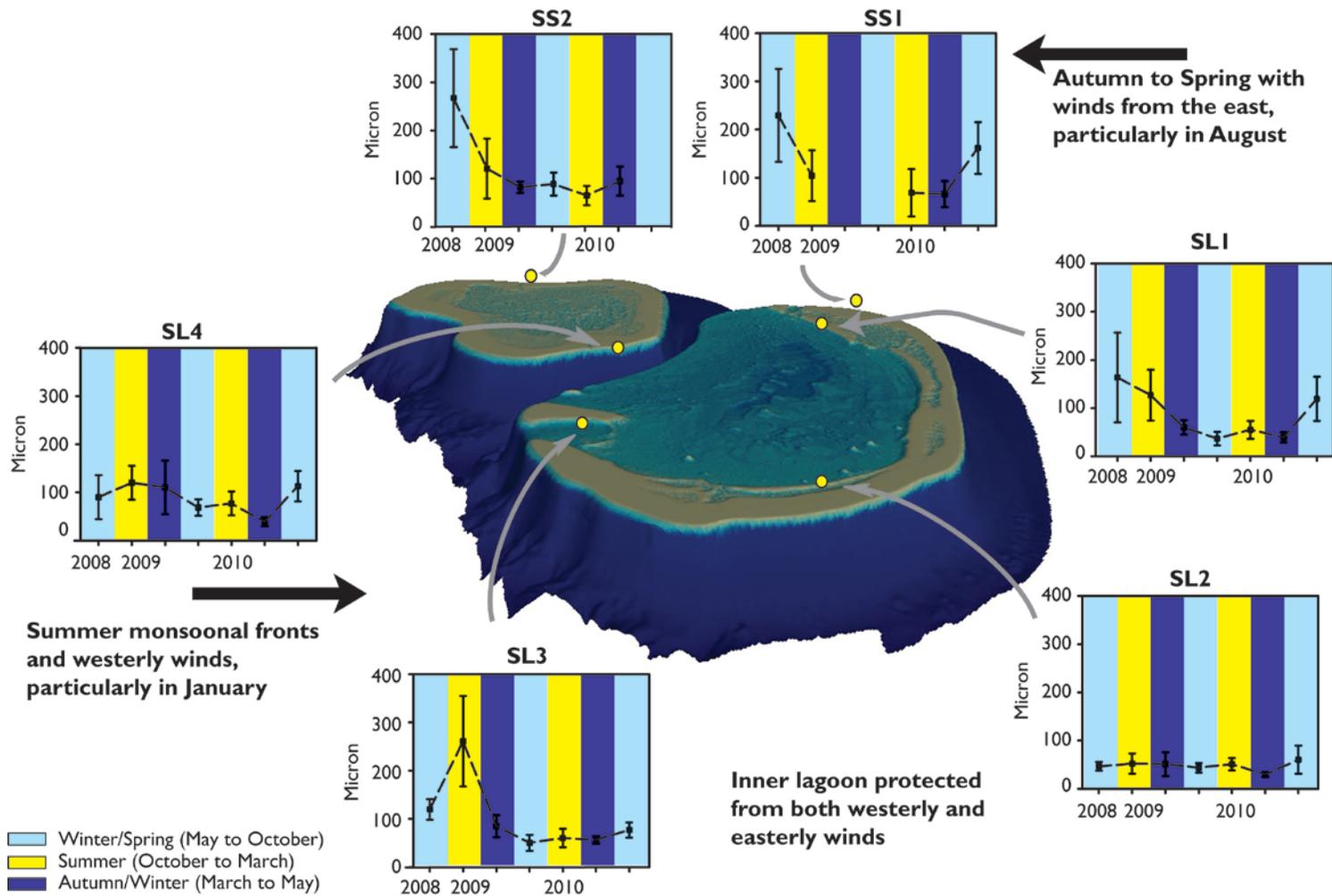


Figure 9.5 Variation in mean sediment size across regions at Scott Reef that differ in their tidal water movement and wind and wave exposure. Locations within the protected inner reef where exposure and tidal circulation are least such as SL2 have low medium size throughout the year whereas more exposed locations have larger mean sizes, particularly in the seasons when they are exposed to the prevailing winds, e.g. summer on the western side of the reef (SL3 and SL4) and autumn through spring on the eastern side of the reef (SS1 and SS2).

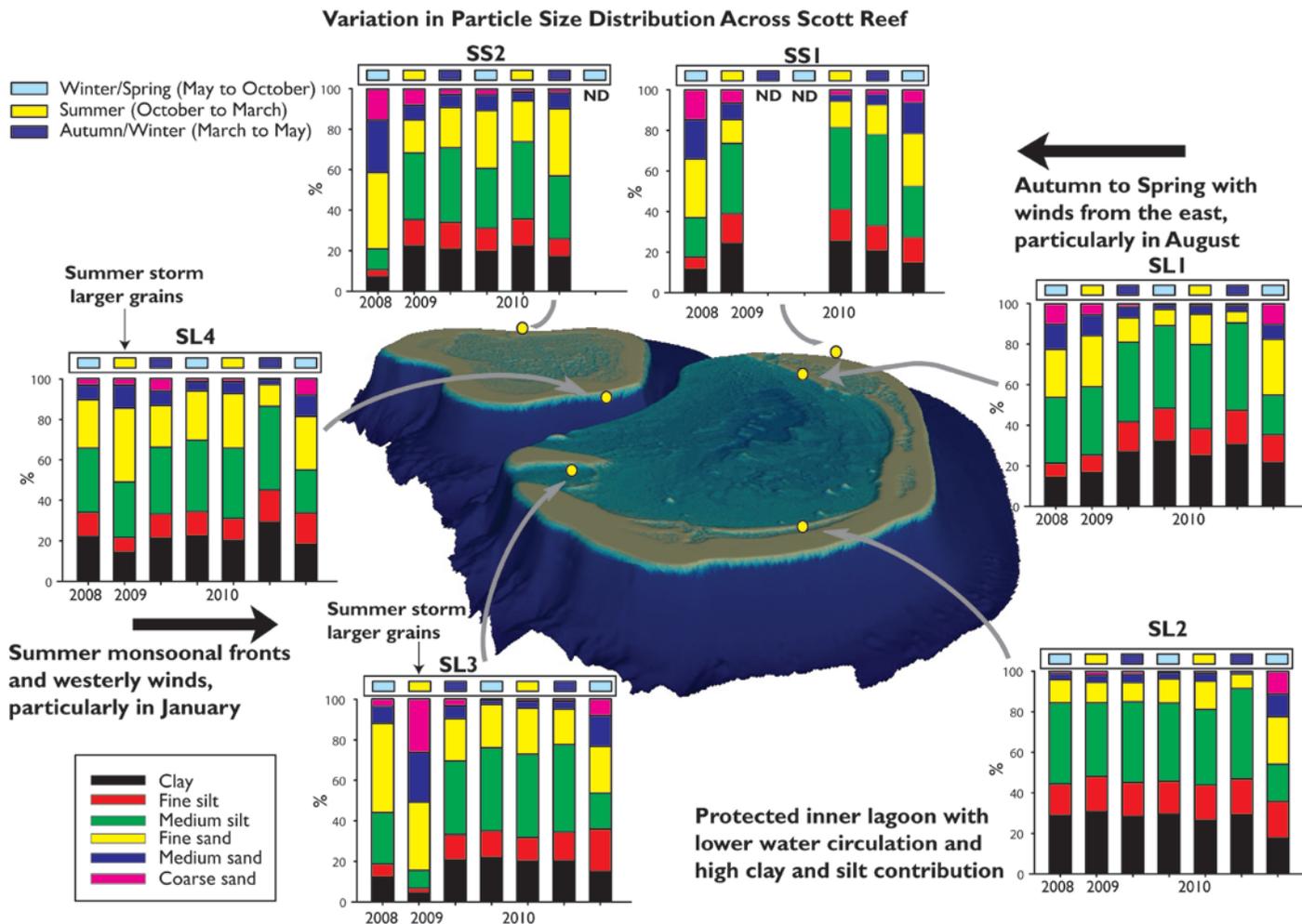


Figure 9.6. Variation in particle size distribution across regions at Scott Reef that differ in their tidal water movement and wind and wave exposure. Locations within the protected inner reef where exposure and tidal circulation are least such as SL2 have high clay and silt contributions throughout the year whereas more exposed locations have higher concentrations of sand sized particles, particularly in the seasons when they are exposed to the prevailing winds, e.g. summer on the western side of the reef (SL3 and SL4) and autumn through spring on the eastern side of the reef (SS1 and SS2).

9.3.3 Comparisons with other regions

Mean sedimentation rates at Scott Reef between May 2008 and October 2010 are at the lower extent of the range (< 1 to 10 mg cm⁻² d⁻¹) observed for reefs not subjected to stresses from human activities (Rogers 1990b). These are consistent with mean sedimentation rates of clear water sites in north-western Australia (Simpson 1988; Babcock and Smith 2000), New Guinea (Kojis and Quinn 1984) and locations in Jamaica and the U.S. Virgin Islands (Dodge et al. 1974). Although sedimentation rates were higher during summer, this was largely driven by higher levels at two locations, (SL3 and SL4). The overall increase in sedimentation rate at Scott Reef during summer is presumably driven by the increase in wind and wave activity associated with storms passing through the region, as is the case with inshore locations on the GBR (Wolanski et al. 2005) and in coastal waters of Hawaii (Bothner et al. 2006) and Mexico (Fernandez and Perez 2008). For example, rates during the dry season in Mexico were 6.8 to 73.5 mg cm⁻² d⁻¹ whereas during the wet season they reached 147.6 cm⁻² d⁻¹ (Fernandez and Perez 2008). The height of wind-induced waves is thought to largely control patterns of suspended sediment on the GBR and thus largely influences the conditions for these coral communities (Larcombe et al. 1995).

9.3.4 Significance of variation in particle size

The contribution of smaller silt and clay-sized particles was greatest at SL2, which has the greatest protection from wave energy and the lowest water circulation. This combination of small sediments, protected aspect and low circulation may also influence the composition of the coral community at this location, which has relatively high abundances of foliose corals (see Chapter 4). Such corals are characterised by their fragile laminar morphology and a relatively poor ability to shed larger size classes of sediment (Hubbard and Pocock 1972).

The total contribution of carbon to the sediment samples at all locations at Scott Reef was small (ca 12%) and was almost entirely composed of inorganic carbon with only a slight contribution of organic carbon (Table 9.2). SEM analyses demonstrated that the sediment was mostly calcium based.

Table 9.2 Percentage contributions of total carbon (TC), total inorganic carbon (TIC) and total organic carbon (TOC) in a single sediment trap sample from each of the six locations at Scott Reef in October 2008.

Location	TC (%)	TIC (%)	TOC (%)
SS1	11.7	11.1	0.55
SS2	11.8	11.3	0.47
SL1	11.4	10.6	0.76
SL2	12.0	10.9	1.10
SL3	11.8	11.3	0.54
SL4	11.6	10.6	1.02

9.4 References

- Anthony KRN (2000) Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). *Coral Reefs* 19: 59-67
- Babcock R, Smith LS (2000) Effects of sedimentation on coral settlement and survivorship. 9th International Coral Reef Symposium, Bali, Indonesia, pp 245-248
- Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* 429: 827-833
- BOM, (2011) Australian Bureau of Meteorology ENSO monitoring graph accessed online at <http://www.bom.gov.au/climate/enso/indices.shtml> on 20/4/2011.
- Bothner MH, Reynolds RL, Casso MA, Storlazzi CD, Field ME (2006) Quantity, composition, and source of sediment collected in sediment traps along the fringing coral reef off Molokai, Hawaii. *Marine Pollution Bulletin* 52: 1034-1047
- Brinkman, R., M. AD, et al. (2010). Scott Reef Research Project 3.1: 2010 Final Report Australian Institute of Marine Science for Woodside Energy Ltd. **Rev 0**.
- Coles SL, Brown BE (2003) Coral bleaching - Capacity for acclimatization and adaptation. *Advances in Marine Biology* 46: 183-223
- Crabbe MJC, Smith DJ (2005) Sediment impacts on growth rates of *Acropora* and *Porites* corals from fringing reefs of Sulawesi, Indonesia. *Coral Reefs (Online First)* 24: 437-441
- Dodge R, Aller R, Thomson J (1974) Coral growth related to resuspension of bottom sediments. *Nature* 247: 574-577
- Dubinsky Z, Stambler N (1996) Marine pollution and coral reefs. *Global Change Biology* 2: 511-526
- Fernandez MRG, Perez RAL (2008) Sedimentation on reef communities at Bahias de Huatulco, Oaxaca, Mexico. *Revista De Biología Tropical* 56: 1179-1187
- Gilmour JP, Travers MJ, Underwood JN, Markey KL, Gates EN, Fitzgerald KL, Case M, Ninio R, Meekan MG, O'Leary R, Radford B, Ceccarelli D, Hoey AS (2010) Long-term monitoring of coral and fish communities at Scott Reef. AIMS Document No. SRRP-RP-RT-045. SRRP Project I: 2010 Annual Report for Woodside as operator of the Browse LNG Development. Australian Institute of Marine Science, Perth, Western Australia
- Hubbard J, Pocock Y (1972) Sediment rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. *Geologische Rundschau* 61: 598-626
- Kojis BL, Quinn NJ (1984) Seasonal and depth variation in fecundity of *Acropora palifera* at two reefs in Papua New Guinea. *Coral Reefs* 3: 165-172
- Larcombe P, Ridd PV, Prytz A, Wilson B (1995) Factors controlling suspended sediment on inner-shelf coral reefs, Townsville, Australia. *Coral Reefs* 14: 163-171
- Miller J, Muller E, Rogers C, Waara R, Atkinson A, Whelan KRT, Patterson M, Witcher B (2009) Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. *Coral Reefs* 28: 925-937
- Rogers CS (1990a) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology-Progress Series* 62: 185-202
- Rogers CS (1990b) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology-Progress Series* 62: 185-202
- Rosenfeld M, Bresler V, Abelson A (1999) Sediment as a possible source of food for corals. *Ecology Letters* 2: 345-348
- Simpson CJ (1988) Ecology of scleractinian corals in the Dampier Archipelago, Western Australia. Environmental Protection Agency, Technical Series No 23
- Syvitski JPM (1991) Principles, methods and application of particle size analysis. Cambridge University Press, Cambridge, U.K.
- Wolanski E, Fabricius K, Spagnol S, Brinkman R (2005) Fine sediment budget on an inner-shelf coral-fringed island, Great Barrier Reef of Australia. *Estuarine Coastal and Shelf Science* 65: 153-158
- Woolfe KJ, Larcombe P (1998) Terrigenous sedimentation and coral reef growth: a conceptual framework. *Marine Geology* 155: 331-345