Appendix F21

Gilmour et al. 2009b

Long-term Monitoring of Shallow-water Coral and Fish Communities at Scott Reef, Annual Report 2008

BROWSE FLNG DEVELOPMENT
Draft Environmental Impact Statement

EPBC 2013/7079
November 2014

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

Gilmour JP, Travers MJ, Underwood JN, McKinney DW, Meekan MG, Gates EN, Fitzgerald KL, O'Leary R

PRODUCED FOR
WOODSIDE ENERGY LIMITED
as agent for the
BROWSE JOINT VENTURE PARTNERS

Australian Government | Australian Institute of Marine Science

PERTH 2009
Report No. SRRP-RP-RT-032

Australian Institute of Marine Science

PMB No 3 Townsville MC Qld 4810

UWA Oceans Institute (M096) 35 Stirling Hwy Crawley WA 6009

PO Box 41775 Casuarina NT 0811

This report should be cited as:
Gilmour JP, Travers MJ, Underwood JN, McKinney DW, Meekan MG, Gates EN, Fitzgerald KL O'Leary R(2009) Long-term monitoring of shallow-water coral and fish communities at Scott Reef. AIMS SRRP Annual Report September 2009- Project 1. AIMS Document No SRRP-RP-RT-032. Project 1 Report to the Browse Joint Venture Partners. Australian Institute of Marine Science, Townsville. 228pp.

Revision History
Draft Rev A 30 September 2009
Draft Ref B 15 January 2010
Final Rev 0 24 February 2010

ACKNOWLEDGEMENTS
The authors wish to acknowledge Kylie Cook, Kim Brooks, Janelle Eagle, Andrew Heyward, Jamie Oliver, and the Master and crew of the RV Solander for their contributions to this project.

DISCLAIMER

While reasonable efforts have been made to ensure that the contents of this document are factually correct, AIMS does not make any representation or give any warranty regarding the accuracy, completeness, currency or suitability for any particular purpose of the information or statements contained in this document. To the extent permitted by law AIMS shall not be liable for any loss, damage, cost or expense that may be occasioned directly or indirectly through the use of or reliance on the contents of this document.

Contents

List of Figures

List of Tables

1. Introduction

1.1. Background and Scope of work

The Australian Institute of Marine Science (AIMS) entered into a contract (No. 4600001754) with Woodside Energy Limited (WEL), as agent for the Browse Joint Venture Partners (JVP), 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 within the SRRP is divided among three projects, and each project is required to submit a report during September and February each year, as part of their contractual requirements. This September Report for 2009 summarises the results to date for Project 1: Understanding the shallow-water coral and fish communities. The research within Project 1 falls into 4 sub-projects: 1.1 Long term monitoring of coral and fish communities; 1.2 Coral demography and population models; 1.3 Genetic connectivity of coral and fish populations; 1.4 Reproduction and recruitment of corals.

1.1.1. Structure of this report

Following the Introduction, this report consists of 2 subsequent chapters.

Chapter 2 is largely the contribution of Project 1 research to the joint publication of the annual Scott Reef Status Report. Chapter 2 follows the agreed format of the Status Report, providing an overview of the condition of the coral and fish communities, their recovery from the mass-coral bleaching in 1998 and cyclone disturbances in 2004 and 2006, and their exposure to other disturbances in the last year.

Chapter 3 provides more detailed information about each of the sub-projects, including an Introduction that places the work in a global and/or historic perspective, Materials and Methods that describe in detail how the research was conducted and the data analysed, Results with the most recent findings presented in greater detail than in previous chapters, and a Discussion that highlights the significance of the results and the extent to which they may differ from similar studies.

2. Status of Scott Reef

2.1. About this report

This report has been prepared to provide a comprehensive overview of all research conducted at Scott Reef and to communicate the current understanding of the reef ecosystem.

This report aims to:

- Highlight the current status and health of the biological communities at Scott Reef and describe any natural or anthropogenic impacts to its flora and fauna (Chapters 2.2, 2.3);
- Describe the current state of knowledge of Scott Reef based on historical and ongoing research (Chapter 2.4.1, 2.4.2);
- Update the outcomes of research at Scott Reef (Chapter 2.4.3).

2.1.1. Structure of this chapter

This chapter largely represents the contribution of Project 1 research to the joint publication of the annual Scott Reef Status Report. It follows the agreed format of the Status Report and gives an overview of the condition of the coral and fish communities, their recovery from the mass-coral bleaching and cyclone disturbances, and their exposure to other disturbances since September 2008. An update of the research highlights within each of the sub-projects then follows.

2.2. Scott Reef Overview

Scott Reef is one of three oceanic reef systems that occur along the edge of the continental shelf off north-west Australia in the Timor Sea (Fig. 2.2.1). The reefs that comprise the Scott Reef system (South Reef, North Reef and Seringapatam) are isolated from the coast and are located 270 km north-west of the mainland, 250 km to the south west of Ashmore Reef and 400 km to the northeast of Rowley Shoals. Due to this isolation, there is a lack of nutrient and sediment inputs from either natural or anthropogenic sources and water quality is high. Scott Reef lies in the path of the Indonesian Throughflow, which funnels warm, nutrient poor water from the western Pacific Ocean into the eastern Indian Ocean. In the area of Scott Reef, a weak north-eastward drift of surface waters occurs between September and January and a stronger south-westward drift from March to August [1, 2]. Local currents are primarily influenced by interaction with the semi-diurnal tides and the physical shape of the reef, which means that water movements are limited by the geomorphology within the South Reef lagoon [3]. Water temperatures follow a seasonal cycle of lows (min of 25°C) between June and October and highs (max of 31°C) from December to March [4]. However, a small decrease in water temperature occurs in January due to increased cloud cover and wind. The low

turbidity at Scott Reef means that light penetrates to great depths relative to coastal systems and corals are able to survive and grow in depths of up to 70 m in the South Reef lagoon [3, 5].

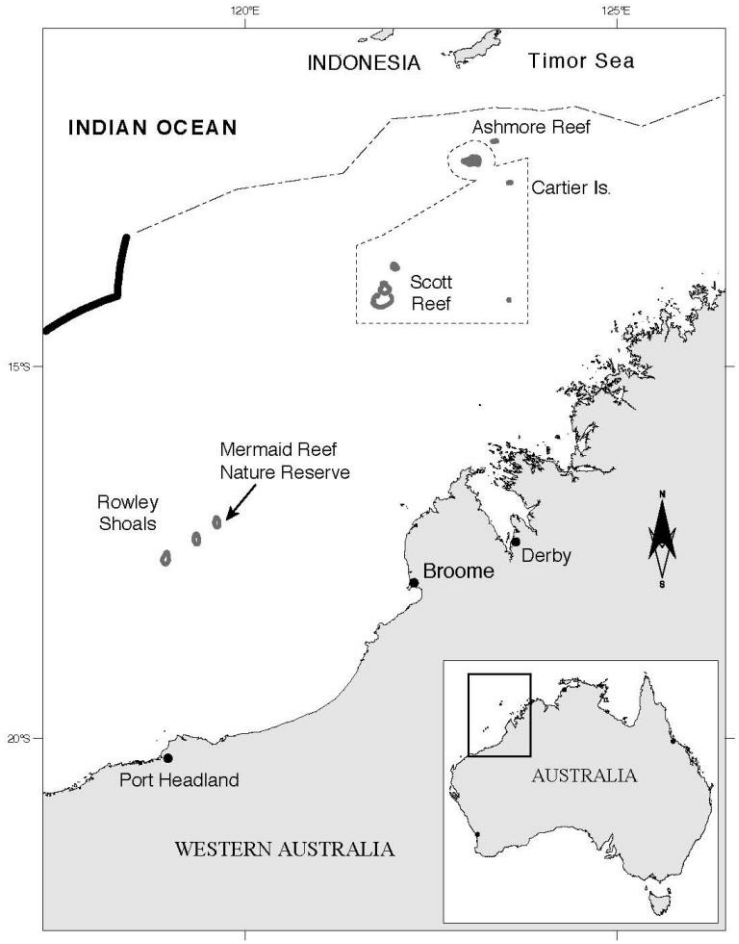


Fig. 2.2.1 Coral atolls off north-west Australia; Rowley Shoals, Scott and Seringapatam Reefs and Ashmore and Cartier Reefs. The dashed line shows the boundary of the Memorandum of Understanding (MoU) box around Ashmore and Scott Reefs.

Coral reefs are one of the most biodiverse of all ecosystems. Scott Reef is close to the centre of biodiversity for coral reef systems and hosts at least 720 species of fishes, 300 corals (including 58 genera of 14 different families), 118 crustaceans, 372 molluscs and 117 echinoderms. These occupy over 460 km^2 of reef habitat between the surface and depths of 70 m. In addition to the benthic species, many whales and dolphins are associated with Scott Reef, and the Sandy Islet on East Hook is used by a small number of migrating sea-birds and nesting turtles. Although the biological assemblages at Scott Reef are similar to the other offshore reefs in the region and are a subset of Indo-Pacific reefs, recent work indicates that a number of unnamed endemic invertebrates exist at this locality [6]. In particular, communities in the unique deepwater lagoon of South Reef (35-70m) add significantly to the biodiversity value of the reef system.

Scott Reef has been a valuable resource for Indonesian fishers for more than 300 years. In 1974, a Memorandum of Understanding (MoU) was signed between the Australian and Indonesian Governments that permitted Indonesians to fish using traditional vessels and equipment in the offshore areas surrounding Scott Reef (Fig. 1). Fishing by Indonesians now involves the collection of a range of animals, including sea cucumbers, trochus, reef fish and sharks. Fishing effort can be high at Scott Reef during peak season between July and October, with more than 70 vessels observed in reef waters in Oct 2007 [7, 8]. As a result, all target species are now over-exploited [6, 8, 9, 10].

Research at Scott Reef began with a photographic survey in the 1930's [11], and sporadic taxonomic collections were made in the 1970s and 1980s, culminating in an extensive collection of benthic organisms by the Western Australian Museum in 1984 [12]. There has since been a significant increase in research effort as a result of a proposal to commercialise hydrocarbon resources within the Browse Basin. In 1993, AIMS undertook a comprehensive survey of coral and fish communities at Scott and Seringapatam Reefs. The following year, with funding from the Commonwealth Government, AIMS established a long-term monitoring program to assess spatial and temporal changes within the shallow water fish and benthic communities [13].

2.3. Status of Scott Reef - 2009

This section provides a summary of any significant disturbances to biological communities at Scott Reef in 2009 and an assessment of the condition of coral and fish communities.

2.3.1. Disturbances in 2009

There were no major disturbances at Scott Reef during 2009. The few cyclones that formed in the region during 2008/9 season had little or no influence on the biological communities of the reef. Although a sustained period of higher-than-average water temperatures resulted in NOAA Coral Reef Watch issuing a 'bleaching watch' for coral communities at Scott Reef in November 2008, no bleaching was observed during trips prior to or after the summer of 2008/9.

Cyclones are the most common acute disturbance to affect communities at Scott Reef. Coral reefs have evolved with cyclones over evolutionary time scales and periodic cyclones can maintain species diversity [14]. Although they can have severe impacts, the effects of cyclones are usually spatially limited [15, 16] and sheltered locations can supply larvae to recolonise communities exposed to the cyclone's path. Since long-term monitoring at Scott Reef commenced in 1994, several cyclones have caused damage to communities. In 2004, category 5 Cyclone Fay tracked directly across Scott Reef causing extensive physical damage to communities on the eastern side the reef, dislodging coral outcrops and pushing them up onto the reef flat [17, 18]. In 2007, Cyclone George tracked close to Scott Reef and caused minor localised damage, primarily to the exposed, shallow (<5m depth) coral communities. Between

2005 and 2007, three further cyclones came close to Scott Reef (Raymond in 2005, Clare in 2006 and Glenda in 2006), but these were relatively minor systems and did not have significant impacts. Although severe and widespread damage by cyclones occurs only rarely at present, the severity and frequency of storms and cyclones is predicted to increase due to climate change [19] and this could have implications for the resilience of coral and fish communities at Scott Reef in the future.

Mass coral bleaching is the most severe and widespread disturbance that has occurred at Scott Reef since the start of the monitoring program. In 1998, extreme sea-water temperatures caused widespread mortality of hard and soft corals. There were dramatic reductions in coral cover in all habitats and communities took several years to recover [20]. The impacts were so severe that they caused major changes to the fish communities across Scott Reef [21] and the effects of the bleaching event are still evident more than a decade later.

The isolation of Scott Reef and its distance from the coastline means it does not experience many of the chronic disturbances degrading the world's coral reefs (see Box 1). However, the reef communities are subject to increasing fishing pressure. At least 70 traditional fishing boats visited Scott Reef in 2009 and fished a range of animals, including sea cucumbers, trochus, reef fish and sharks. Many of these stocks are heavily over-exploited [10, 22] and the wider implications for the biological communities at Scott Reef are not known.

BOX 1. DISTURBANCES TO CORAL REEFS: THE SLIPPERY SLOPE TO SLIME?

In the past, most coral reefs have been resilient to natural disturbances [23, 24]. However, today the frequency, severity and types of disturbances are increasing and the rates of reef recovery are slowing [25, 26]. Evidence of human impacts on coral reefs have been accumulating for some time [27]. Two decades ago there was increasing concern about the effects of agriculture and urbanisation on levels of sedimentation and eutrophication on nearshore coral reefs. The widespread death of corals and proliferation of algae in Kanehoe Bay, Hawaii, in the 1970s [28] illustrated the sensitivity of coral reefs to changes in water quality. Massive outbreaks of populations of the coral eating crown-of-thorn starfish from the Great Barrier Reef to Okinawa have also been tentatively linked to elevated nutrient levels and removal of predatory reef fishes [29, 30]. At the same time, there was increasing concern about the effects of overfishing, particularly of herbivorous fish. Coupled with the mass-mortality of sea urchins due to disease, overfishing caused some coral reefs throughout the Caribbean to become dominated by algae, rather than hard corals [31, 32]. These conditions persist today, providing a dramatic example of how disturbances can have synergistic and long-lasting consequences for coral reef ecosystems.

Although they have caused extensive mortality to corals, these disturbances have acted over relatively limited spatial scales, so local management initiatives can often remove the cause. However, in the 1980s and 1990s coral bleaching events provided the first evidence of severe human impacts to coral reefs occurring at regional and global scales [33]. This phenomenon involves the expulsion of the symbiotic algae that live within the coral tissue during abnormally high sea-water temperatures, and often results in the death of the coral. In 1998, wide-spread bleaching was caused by the combination of extremely calm conditions during an El Niño event and high seawater temperatures in the tropics, attributed partly to increasing atmospheric carbon concentrations and the warming of the earth's climate. The 1998 bleaching event destroyed16% of the world's coral reefs [34]. Further extreme water temperatures in 2004 caused bleaching and mortality of many corals on the Great Barrier Reef, and again in 2005 in the Caribbean [34]. At the same time, there were increases in the prevalence of coral disease on reefs around the world [35], prompting speculation that this was due to the combination of degraded water quality and increasing sea-water temperatures.

Threats to coral reef ecosystems include degraded water quality and overfishing, outbreaks of predators such as crown-of-thorns starfish and elevated water temperatures that cause coral bleaching

The global impacts of climate change on coral reefs are not restricted to mass coral bleaching and disease, with ocean acidification emerging as another major cause for concern. Increases in atmospheric carbon due to the burning of fossil fuels have been absorbed into the oceans, creating carbonic acid and causing them to acidify [36]. The predicted impacts of ocean acidification are particularly insidious: further increases in acidity may affect the ability of a huge range of organisms to produce the external structures and skeletons critical for their survival, including foraminifera, corals, urchins, crustaceans and molluscs [37, 38, 39].

In recent decades there has been a dramatic increase in the number and scale of disturbances to corals reefs, which is causing their loss around the world. In 2008, it was estimated that 19% of the world's coral reefs have been effectively lost, a further 15% are seriously threatened within the next 10–20 years; 20% are under threat in 20 to 40 years [34]. These losses have dramatic repercussion for the goods (e.g. food) and services (e.g. tourism) of many countries [40]. This also affects Australia, which has among the best managed and healthiest reefs around the world and there is concern for the future health of the Great Barrier Reef if climate change remains unchecked [41]. Many of the world's coral reefs now appear to be on a 'slippery slope to slime' if the causes of their degradation are not slowed and reversed [42, 43]. Although it will not protect coral reefs from the impact of climate change, minimising local stressors will provide the best chance for resilience until atmospheric carbon is reduced to below levels that have already caused wide-spread destruction of this valuable ecosystem [44].

2.3.2. *Status of coral communities*

Monitoring of the coral and fish communities at Scott Reef has been underway since 1994. This monitoring program has focused on the reef slope habitat at 9 m water depths. Changes in the communities of this habitat have been recorded during most years at locations across North and South Reef, reflecting different disturbances and periods of recovery. During each survey, the percentage cover of several hundred groups of benthic organisms has been recorded, including hard and soft corals, algae and sponges. Abiotic categories such as sand and rubble were also recorded.

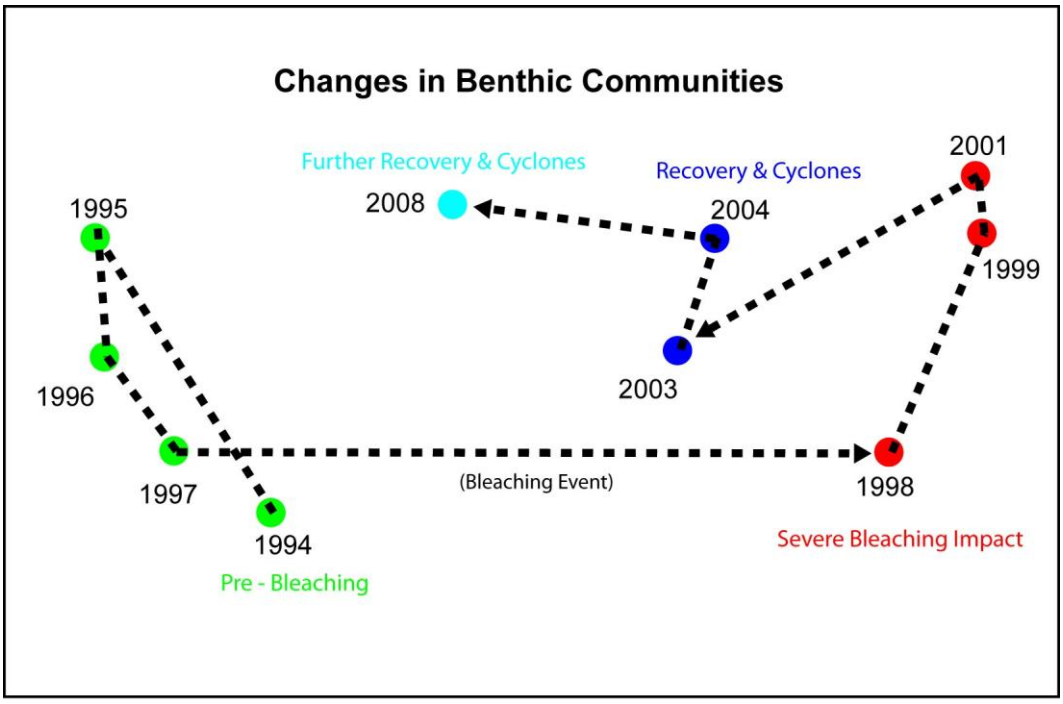


Fig. 2.3.2.1 Changes in the structure of benthic communities at Scott Reef from 1994-2008. The distances between the years reflect the degree of similarity in community structure. These measures are derived from the changes in percentage cover of benthic categories in the reef slope habitat over 15 years.

There have been major changes in the structure of the coral communities at Scott Reef during the monitoring program (Fig. 2.3.2.1). Prior to the bleaching communities were relatively similar, however the bleaching event caused a large shift to an entirely different benthic community. Most hard and soft corals were killed by the elevated water temperatures and in many places coralline and turfing algae replaced corals. Gradually, corals were able to recolonise the sites and there was a strong recovery towards the pre-bleaching structure in 2003. Cyclone Fay in 2004 slowed this recovery, but the impact of this and other cyclones was restricted to only a few locations. Recovery continued from 2004 to 2008 so that benthic assemblages began to resemble those prior to bleaching. Cover of hard corals now

approaches levels seen prior to bleaching and algal cover has declined, although recovery of soft corals has been relatively slow.

The 1998 bleaching event decreased the cover of hard corals from 46% to 11%, a relative loss of 76% (Fig. 2.3.2.2). Soft corals suffered a similar (77%) relative decline, from 9% to 2% of total cover. Conversely, there was an increase in the cover of turfing and coralline algae that grew on the skeletons of the dead corals. The cover of macroalgae remained low (< 1%) throughout this time. After a slow initial period of recovery following the bleaching (1999 - 2002), the cover of hard corals has increased more rapidly in recent years. Initial recovery was driven largely by the production of recruits by the few surviving corals at Scott Reef, but not by the supply of recruits from other reef systems. Consequently, the numbers of new recruits were initially small, but ongoing increases in coral cover and the number of adult corals have caused more rapid increases in recruitment with time. Cover of hard corals at reef slope sites is now 37%, which is close to that in the years prior to the bleaching, and there have been corresponding decreases in the cover of algae. However, the recovery of the soft coral communities has been far slower. The cover of soft corals is only half (48%) that prior to the bleaching, and whereas the recovery of hard corals has accelerated in recent years, the recovery of soft corals each year has remained static since the bleaching.

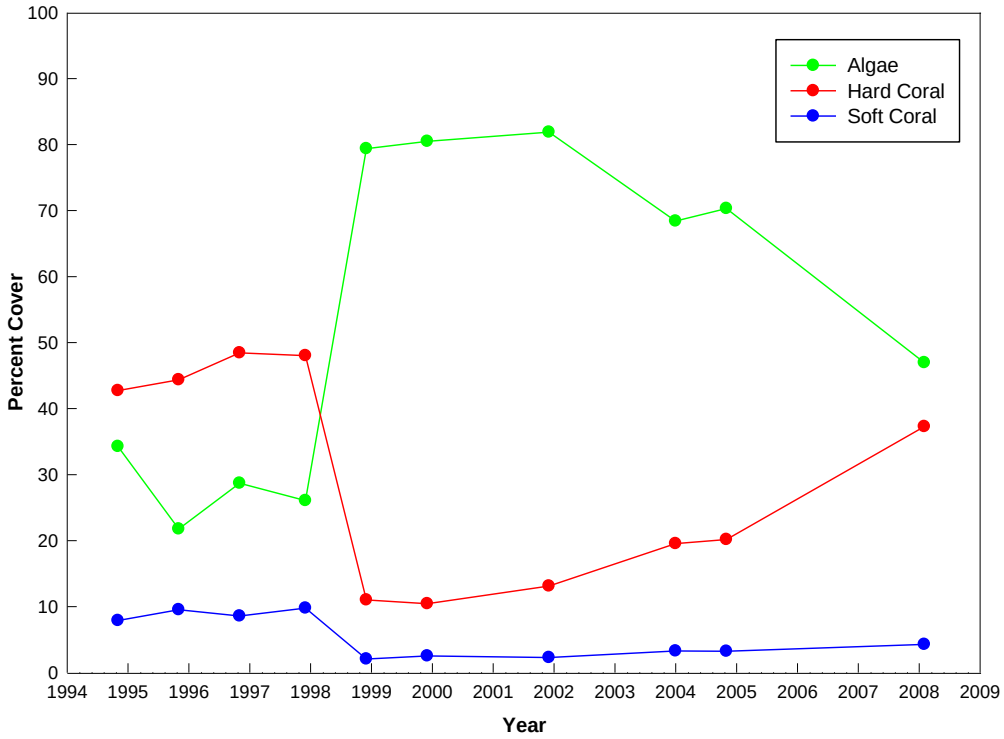


Fig. 2.3.2.2 Percent cover of hard coral, soft coral, and algae in the 9 m depth habitat between 1994 and 2008. The decrease in hard and soft coral cover in 1998 is the result of thermal-induced bleaching. The algae category consists of turfing and coralline algae, rather than macro-algae.

The long-term monitoring of coral and fish communities at Scott Reef has focused primarily on the reef slope habitat in 9 m of water, in-line with standard AIMS monitoring procedures on the Great Barrier Reef. However, there have been additional surveys at several other

shallow-water (<15 m) habitats to provide some context for changes observed in the reef slope communities. These additional habitats are: the reef crest in less than approximately 1 m of water; the lower reef crest in approximately 3 m of water, the upper reef slope in approximately 6 m and the reef slope in approximately 9 m. Coral communities on outcrops between 4 and 15 m depth in the North Reef lagoon were also surveyed (Fig. 2.3.2.3).

Similar to the reef slope, coral communities in all shallow-water habitats were severely impacted by the bleaching, causing relative decreases in cover of hard and soft corals of more than 75%, with the exception of upper reef slope (6 m) where relative declines were less severe (54%). Since this disturbance, the cover of hard corals has recovered so that in most habitats it is now similar to or greater than prior to the bleaching, with some notable exceptions. The relative cover of hard corals has returned to ≥80% of its pre-bleaching cover at the lower reef crest (3 m) and reef slope (9 m) habitats, and is higher than (150%) its pre-bleaching cover at the upper reef slope (6 m) habitat (Fig. 2.3.2.4). In these habitats, increases in coral cover were matched by corresponding decreases in algae, although algal cover remains higher than prior to the bleaching. In contrast, the recovery of hard corals was far slower in the reef flat and North Reef lagoon habitats.

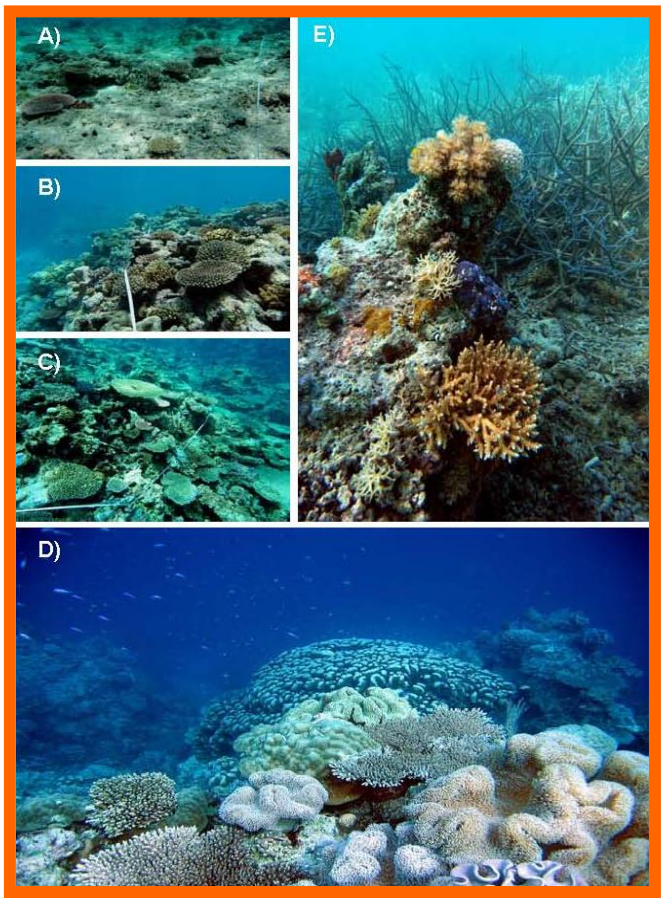


Fig. 2.3.2.3 Shallow-water habitats with coral communities at Scott Reef. A) reef flat, B) reef crest, C) upper reef slope, D) reef slope, and E) North Reef lagoon

The reef flat habitat had the lowest coral cover prior to bleaching and has since returned to only 37% of this previous level (Fig. 2.3.2.4). This slow recovery may be due to the exposure of this shallow water (1 m) habitat to repeated cyclone impacts since the bleaching. In contrast to the reef flat, coral cover in the North Reef lagoon habitat (5 to 14 m depth) was the highest (76%) of all habitats, and the relative decrease (89%) following the bleaching most severe. Unlike other habitats, the communities in the North Reef lagoon were dominated by a single group, the staghorn corals. Due to their growth form, these corals are very susceptible to the impacts of elevated water temperatures and cyclone disturbances and there has been little increase in their cover within this habitat since 1998, which remains at 12% of its pre-bleaching cover. The slow recovery of hard corals in the North Reef lagoon may be related to the severity of the bleaching at this habitat, with few survivors available to supply new recruits. Recovery is complicated by the sandy and unstable nature of the habitat, which provides limited hard surfaces on which new corals can settle.

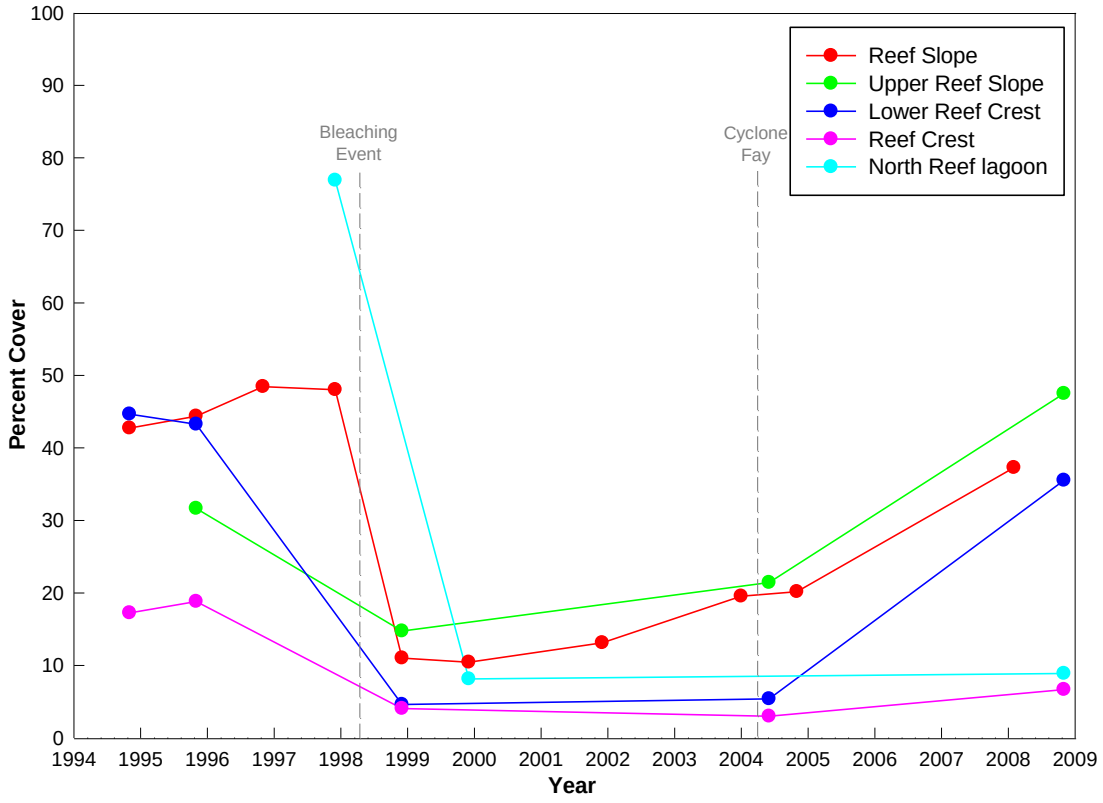


Fig. 2.3.2.4 Percent cover of hard coral in the reef crest (1 m water depth), lower reef crest (3 m), upper reef slope (6 m), reef slope (9 m), and North Reef lagoon habitats at Scott Reef between 1994 and 2008. Pre-bleaching cover at North Reef lagoon is derived from the mean cover of 20 sites ranging from 4 to 15 m depth.

Recovery of the soft coral communities after bleaching has been far slower than for the hard corals. Prior to bleaching, cover of soft corals was far less than that of hard corals; as low as 1% at the North Reef lagoon habitat and < 14% at all other habitats. However, the relative decreases in cover of soft corals following the bleaching were larger (> 75%) than hard corals. In 2008, the relative cover of soft corals was less than half that prior to the bleaching in the reef slope habitat, and <20% in all other habitats. This slow rate of recovery probably reflects the slow growth rates and the limited sexual reproduction of these taxa [45, 46]. These traits mean that recovery must occur through asexual reproduction of colonies that remained in habitats after bleaching, with little provision of new recruits from other habitats. Our results confirm that some soft corals may be particularly susceptible to increasing sea-water temperatures associated with climate change [47].

2.3.3. *Status of fish communities*

Similar to the coral communities, assemblages of fishes also underwent a cycle of change that was initiated by the bleaching event in 1998, but are yet to return to patterns of composition and abundance that resemble the pre-bleaching state (Fig. 2.3.3.1). While most corals were killed immediately by bleaching, changes in assemblages of fishes mostly took place 12 to 18 months after this event, with this lag related to the gradual erosion of the bleached coral skeletons that fishes previously relied on for food and/or shelter [21, 48]. Despite abundances of some fishes returning to pre-bleach levels (Fig. 2.3.3.4) and earlier indications that communities were starting to return toward pre-bleached structures [21], fish communities at Scott Reef are still undergoing changes 10 years after the bleaching event (Fig. 2.3.3.1).

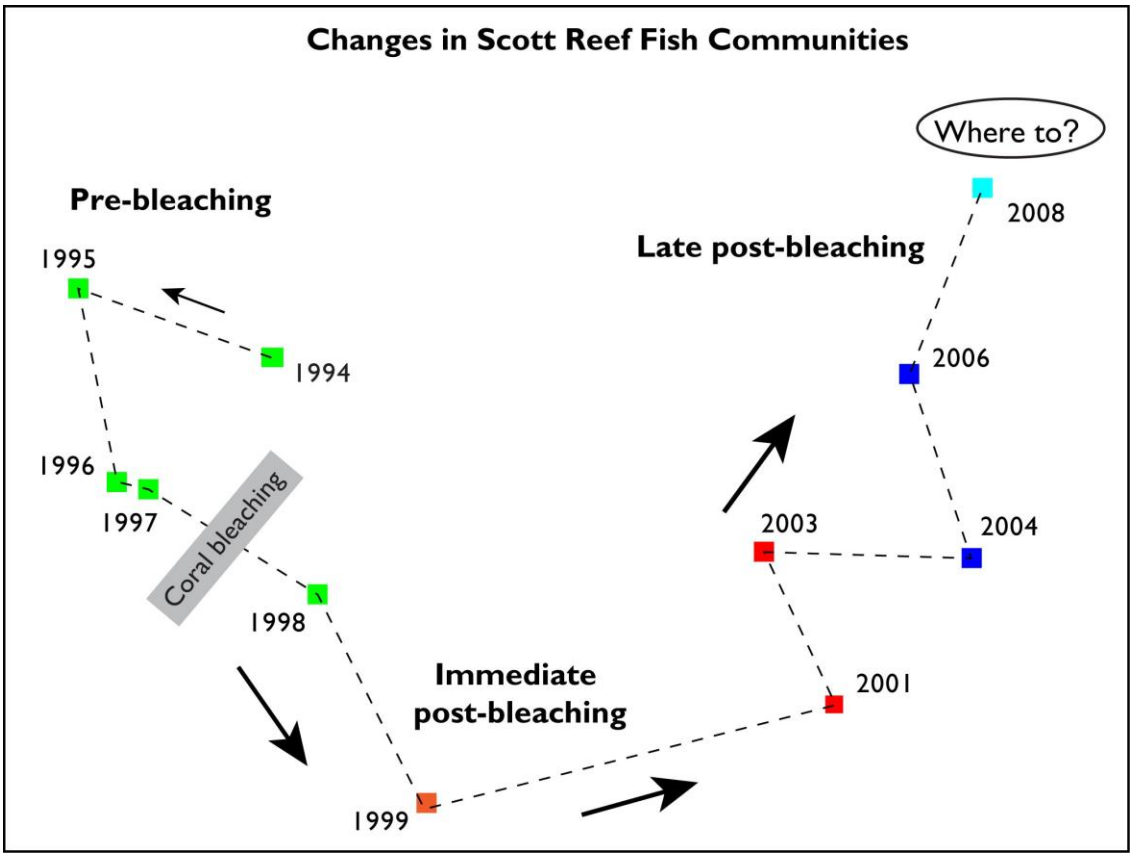


Fig. 2.3.3.1 Changes in the structure of the fish communities at Scott Reef from 1994-2008. The distances between the years reflect the degree of similarity in community structure.

The 1998 bleaching severely impacted species that used live coral for food, such as butterflyfishes [49], or those that relied on the structure of live coral for shelter, such as many plankton-feeding damselfishes [50] (Fig. 2.3.3.1 & 2). Conversely, herbivorous species increased in abundance following the overgrowth of dead coral by algae [51] (Fig. 2.3.3.2 & 3). Both plankton feeders and herbivorous fishes began to gradually return to pre-bleaching numbers approximately three years after the bleaching event. In contrast, numbers of coral feeding species have not recovered, although there is some suggestion that numbers have been gradually increasing over the last two years of monitoring.

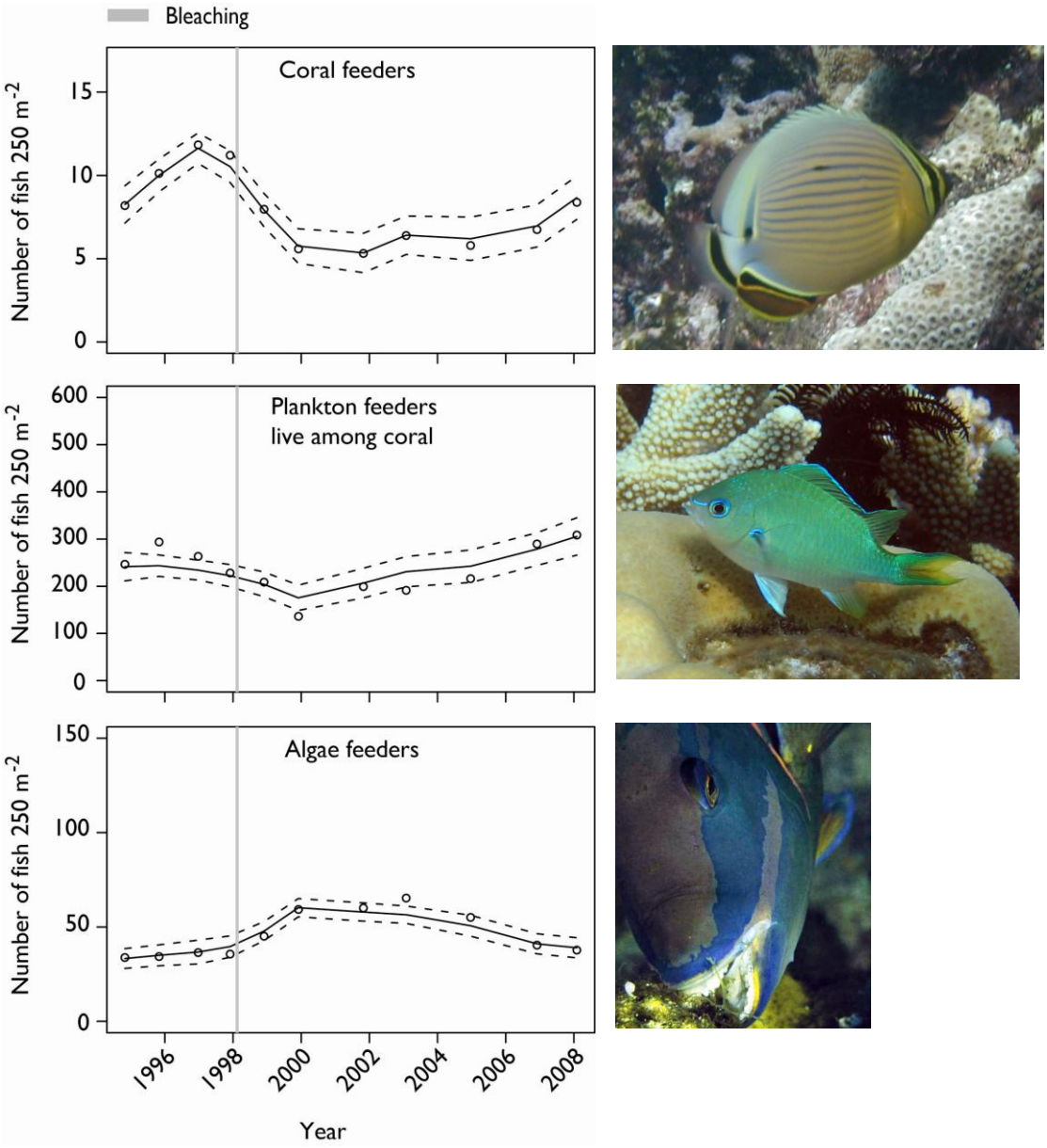


Fig. 2.3.3.2 Mean (± 95 C.I.) densities of coral, plankton and algae feeding fishes at Scott Reef between 1994 and 2008. Solid line represents mean densities and dashed line 95% Confidence Limits.

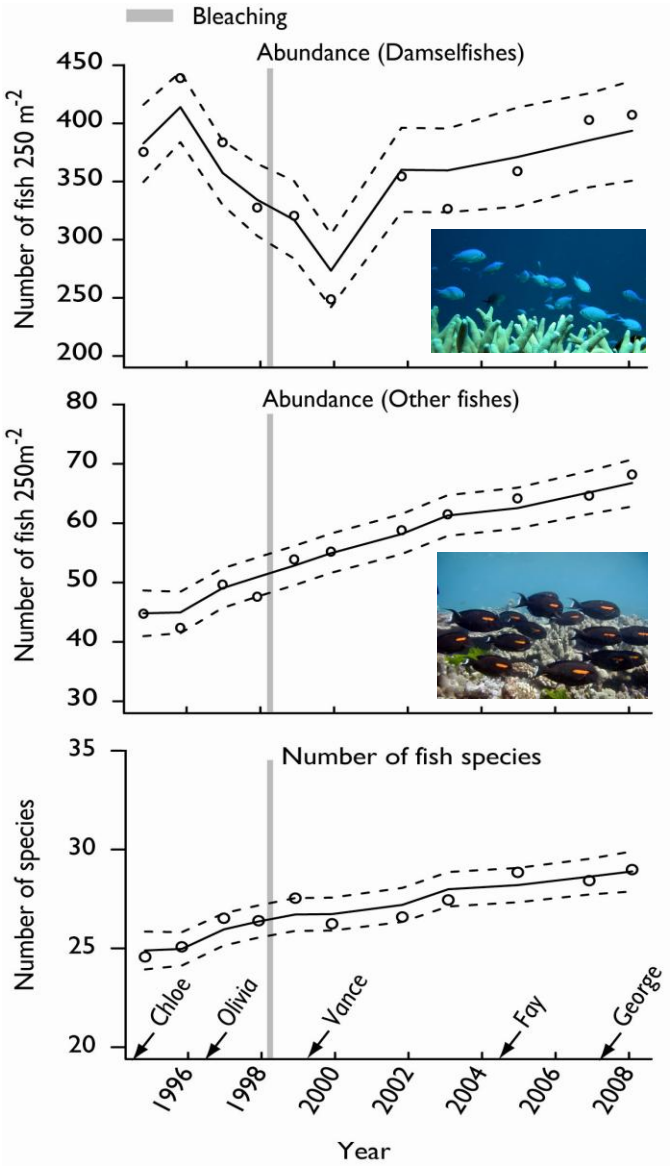


Fig. 2.3.3.3 Mean (± 95 C.I.) densities of damselfishes, other fishes and numbers of all species recorded at Scott Reef between 1994 and 2008. Names and timing of major cyclones that have affected Scott Reef during this period are shown. The circles represent the observed mean densities. Solid line represents mean densities and dashed line 95% Confidence Limits.

The variable effects of the bleaching event are also evident in trends in the abundance and diversity of some of the major families of reef fishes (Fig. 2.3.3.3). Numbers of damselfishes declined steeply after the bleaching, although there was considerable variation in abundances of this family prior to the disturbance. Abundances then sharply recovered following surveys in 2000, coincident with the return of branching corals to the reef slope habitat (Fig. 2.3.3.3). In contrast, total abundances of other fishes showed no effect of bleaching or cyclone disturbances and have increased in a roughly linear fashion throughout the study. Numbers of reef fishes, other than damselfishes are now one and a half times those recorded at the start of the study (Fig. 2.3.3.3). Similarly, the mean number of fish species has also increased throughout the study with the numbers now 20% greater than at the start of the study.

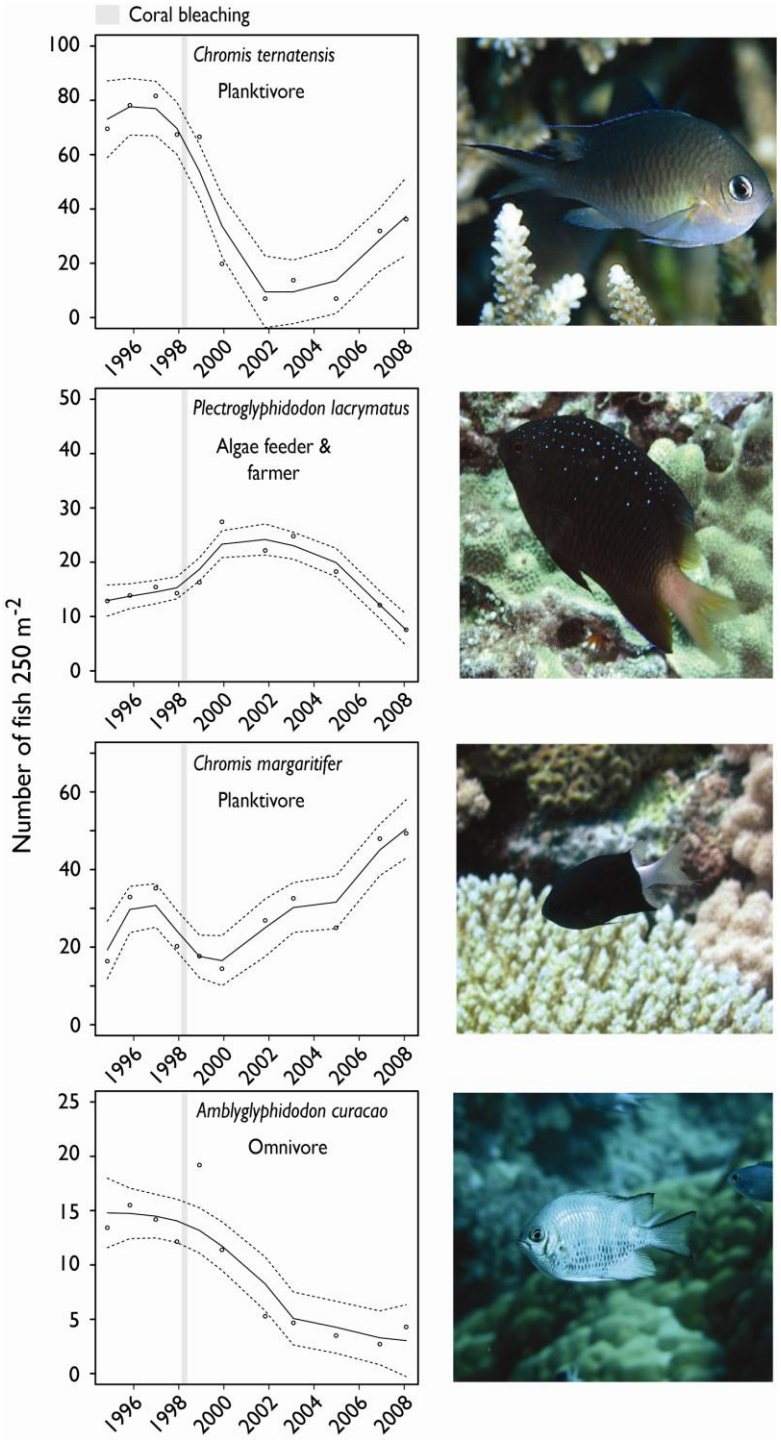


Fig. 2.3.3.4 Mean (± 95 C.I.) densities of species that characterize fish assemblages during periods of impact and recovery at Scott Reef between 1994 and 2008. Solid line represents mean densities and dashed line 95% Confidence Limits.

Some of the variability in fish communities can be explained by differing response of individual species to habitat modification induced by bleaching. (Fig. 2.3.3.4). For example, the ternate damsel (*Chromis ternatensis*) declined in numbers following the bleaching, then showed signs of recovery as the cover of their preferred habitat of branching coral increased [52, 53]. In contrast, numbers of the algal feeding jewel damselfish (*Plectroglyphidodon lacrymatus*), were highest when algal cover was at its peak, then decreased as algae became less dominant and corals recovered. Other fish species showed trends of continuous increase, such as the half and half puller (*Chromis margaritifer*), or decrease, such as the staghorn damsel (*Amblyglyphidodon curacao*), so that abundances of these species are now very different to those at the start of the monitoring program (Fig. 2.3.3.4). In the case of the latter species, the slow recovery of soft corals at Scott Reef [53] may have played a role in its continued decline [54].

2.4. Research Programs at Scott Reef

2.4.1. AIMS Scott Reef Research Program (SRRP)

The Australian Institute of Marine Science (AIMS) has been conducting research in Western Australian waters for more than 20 years. In 1993, AIMS conducted a comprehensive survey of the coral and fish communities at offshore reef systems in north-western Australian, including Scott and Seringapatam Reefs. The following year, AIMS established its permanent long-term monitoring sites at Scott Reef to assess natural variation in coral and fish communities. Since this time, AIMS has conducted regular expeditions to Scott Reef to study both its biological and physical environment, many of these expeditions have been co-funded by WEL and its Joint Venture Partners. This represents the longest monitoring program of its kind in Western Australia.

Using the outcomes of a workshop in 2007, which identified the research needs of managers to inform any potential LNG development at Scott Reef, AIMS designed a three year program that addressed key gaps in knowledge for science, management and industry. This research was structured around the following questions:

- What is the status of major (corals and fish) communities of Scott Reef?
- How do these communities relate to the environment?
- What are the natural dynamics of these communities and how will they respond to disturbances?
- How important are these communities in a regional context?

The AIMS Scott Reef Research Project (SRRP) commenced in 2008. The research focuses on the distribution and dynamics of benthic communities across Scott Reef in shallow and deep habitats. The key hydrodynamic and pelagic processes (e.g. water movements, temperature, turbidity, light, plankton) that shape communities are also being investigated. Long-term monitoring of shallow-water communities continues at locations established more than a decade ago, to provide insights into variation in coral and fish communities and their patterns of impact and recovery following natural disturbances. Additionally, key life-history traits of corals are being investigated in both shallow and deep water habitats to provide a better understanding of their patterns of distribution and abundance, relative to their physical environment. Genetic markers are being used to estimate the dependence of coral populations at Scott Reef on local reproduction, which will be a crucial component of risk and resilience mapping. A suite of life history traits and physiological measurements are being quantified for deeper-water corals to estimate their resilience to changes in physical conditions (e.g. light levels). The structure and dynamics of coral and fish communities at Scott Reef are compared with the nearest set of similar reefs (Rowley Shoals) to provide insights into the regional significance of the Scott Reef system within the greater region of north-western Australia.

The research being conducted as part of the Scott Reef Research Project (SRRP) is divided among three projects:

Project 1: Shallow water coral and fish communities
Project 2: Deeper-water coral communities
Project 3: Physical and biological oceanography

2.4.2. Project 1: shallow water coral and fish communities

Within the broader SRRP, Project 1 focuses on the shallow-water (< 15m depths) coral and fish communities at habitats across Scott Reef (Fig. 3.1.1). A wide range of data are collected within Project 1 to better understand how different disturbances affect biological communities and the processes by which they recover. These data and the associated studies are divided among four subprojects:

1.1 Long-term monitoring of shallow-water coral and fish communities
1.2 Birth, growth and survival of corals: coral demography
1.3 Genetic connectivity of coral and fish populations
1.4 Reproduction and recruitment of corals

Project 1.1 Long-term monitoring of coral and fish communities

The AIMS long-term monitoring program was established at Scott Reef in 1994 to quantify the natural variability of coral reef communities, particularly their responses to disturbances such as cyclones and coral bleaching. The program is the most comprehensive coral reef monitoring program in Western Australia with many surveys having been conducted over 15 years. Benthic and fish communities are surveyed by divers along fixed transects at multiple locations around Scott Reef. At each location, there are three sites that each contain five 50 m transects along the 9 m depth contour.

Divers take photographs and video footage of the benthic community along each transect. Images are analysed to determine the changes in percentage cover of a range of benthic categories such as corals, sponges and algae, through time and among locations on the reef. Divers also record the numbers of adults of most fish species are found at the reef slope habitat. The data obtained by the program have been explored using a range of statistical analyses to describe the temporal and spatial changes in benthic and fish communities.

Project 1.2 Birth, growth and survival of corals

To investigate the ultimate causes of changes in coral cover and community structure at the long-term monitoring sites, a supplementary study was established to quantify rates of birth (recruitment), growth and survival of two common groups of corals at Scott Reef. As a pilot

study in 2006, colonies in different size classes (colony diameter) of the coral *Acropora spicifera* were tagged at two sites at each of 4 locations. *A. spicifera* is common at Scott Reef and has a tabulate/branching growth-form similar to many of the most abundant corals on Indo-Pacific reefs (see Box 2). In 2008, with the commencement of the SRRP, colonies in the genus *Goniastrea* that had a massive growth form were also tagged at all study sites (see Box 2). These massive corals are also abundant across Scott Reef and on other Indo-Pacific reefs. The two common groups of corals were chosen because they have very different growth forms and were predicted to have contrasting rates of growth and survival, and different susceptibility to disturbances. For example, *Acropora* corals have rapid rates of growth but are particularly susceptible to disturbances such as cyclones or high water temperatures, while the *Goniastrea* corals were predicted to grow more slowly, but to have higher rates of survival and to be less susceptible to disturbance. Over 3000 colonies are now tagged across Scott Reef and are photographed annually for the calculation of rates of growth and survival.

Project 1.3 Coral and fish genetics

For most species that live on coral reefs, dispersal is achieved by pelagic larvae that have the potential to travel on ocean currents and migrate between distant patches of habitat. However, it is not clear how often dispersal among distant reefs occurs, nor how many survive the long journey to eventually contribute to populations. For coral-reef ecosystems, development of an understanding of patterns of "population connectivity" is crucial, as it allows an evaluation of the potential benefits of particular conservation strategies. In particular, the scale and strength of larval exchange within and among reefs is important for recovery after disturbance: populations that receive little input from immigrant larvae will be slow to recover compared with populations that receive a regular and large supply of immigrants (see Box 3). Because genetic differences accumulate when populations are reproductively isolated and do not "share" their genes through exchange of individuals, a spatial analysis of genetic variation provides an invaluable method for investigating patterns of population connectivity. The genetic connectivity of populations of corals and fishes that have different reproductive modes are being compared between Scott Reef and its neighbouring reefs with the expectation that contrasting life histories will yield insights into dispersal and colonisation patterns.

Project 1.4 Coral reproduction and recruitment

Reproduction and recruitment by corals involves the production of larvae and their subsequent settlement and metamorphosis into new coral colonies. This process underlies the maintenance of communities and facilitates their recovery from disturbances. Consequently, it is important to know the modes of reproduction and times of larval production for the majority of the corals on the reef. Around the predicted dates of coral spawning in autumn and spring, replicate samples are collected from species of spawning and brooding corals at locations across Scott Reef. Samples are examined using a microscope to determine the stages of development of eggs and/or sperm within each colony, from which inferences are made about the times of reproduction. Additionally, visual surveys of colonies

are used to determine whether polyps contained immature eggs, mature eggs, or planulae larvae, which provide further evidence for the time of spawning. To date, several hundred colonies have been sampled over two years.

The numbers of larvae that settle and metamorphose onto a reef can provide an indication of the 'health' of coral communities. Additionally, patterns of larval supply (recruitment) and coral cover together indicate the extent to which a stock-recruitment relationship exists for a reef, and the extent to which the new corals that maintain communities are produced from within the reef or supplied from others in the region. Knowledge about the distances over which larvae travel and the scales at which a stock-recruitment relationship exists is critical for managing coral reefs (see Box 3). To measure variation in the rates of larval settlement and recruitment at Scott Reef, settlement tiles have been attached to the reef approximately one month before the main period of coral spawning in autumn, and then collected approximately one month later. After collection, the numbers of hard corals that have settled on the tiles are counted under a microscope. Settlement tiles have been deployed prior to the mass spawning over two years.

2.4.3. Project 1: research highlights

Project 1.1 Long-term monitoring of coral and fish communities

Coral Communities

The impact of the 1998 bleaching event and the recovery of coral communities from this disturbance are a pervasive feature of the monitoring program at Scott Reef. However, these patterns of disturbance and recovery are not necessarily consistent throughout the reef system. For example, reductions in coral cover following bleaching were generally greatest at the locations that had the highest cover prior to the event (SL2, SS1, SS2 Fig. 2.4.3.1), while recovery (> 85% of original coral cover) was fastest at the locations that were least affected by bleaching (SL1, SL3, SL4) (Fig. 3.1.1). Recovery also varied among localities according to exposure to cyclone disturbances in 2004 and 2006 and among depths within localities. For example, at SL1 coral cover in the 1m depth habitat has recovered to only 21% of pre-bleaching levels, while at 9 m, coral is now 105% of pre-bleaching levels. At SL2, recovery ranged between 40% and 75% of pre-bleaching cover at all depths, while at SL3, recovery ranged from 40% in the 1m depth habitat to >135% of original cover in the 6 m and 9 m depth habitats.

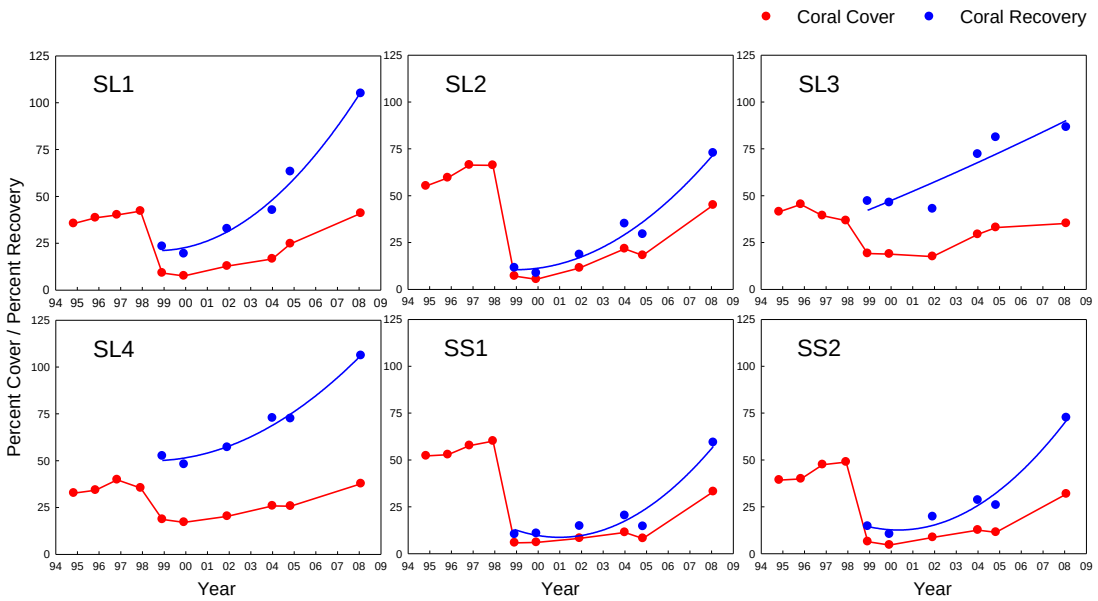


Fig. 2.4.3.1 Changes in the cover of hard corals (red) and their relative (%) recovery to pre-bleaching levels (blue), at the reef slope habitat (9 m depth) between 1994 and 2008. At 100% recovery the coral cover has returned to its pre-bleaching level**.**

These different patterns of change and recovery most likely reflect varying oceanographic conditions *(55, 56, 57)*, exposure to cyclones *(16, 18, 58, 59, 60)*, community structures *(61, 62, 63, 64)* and rates of larval supply *(65, 66, 67, 68, 69)* among localities. For example, there were smaller decreases in coral cover after the bleaching at locations (SL3, SL4) that were exposed to strong tidal currents and cooler oceanic water *(70)*. In contrast, the highest levels of mortality were at the lagoonal communities at North and South (SL2) Reefs, which were furthest from the cool oceanic waters and where there was limited flushing of hot water around the time of bleaching *(3, 70)*.

Following the bleaching event, recovery at some sites was slowed by exposure of communities to wave energy during storms and cyclones *(16, 18, 58, 59, 60)*. Whereas the bleaching in 1998 decreased coral cover across the entire reef system, Cyclones Fay and George had only localised impacts. The locations most affected by Cyclone Fay in 2004 were situated on the eastern side of Scott Reef (SL2, SS1, SS2), where wind and swell was greatest. In 2006, Cyclone George tracked south of Scott Reef, again producing a variable impact on coral communities. While decreases in coral cover similar to those after Cyclone Fay were not recorded, the smaller relative increases in coral cover at locations SL3 and SL4 between 2004 and 2008 were probably due to the impacts of Cyclone George, as supported by the patterns of growth and survival of tagged colonies at these locations (see Chapter 3.3).

For both temperature-induced bleaching and cyclone disturbances at Scott Reef, depth played a key role in determining the overall impact of disturbance. Very shallow locations (1m) were affected most strongly by the bleaching and cyclone activity, and have since shown relatively poor recovery. Deeper communities in habitats at 3 m, 6 m, and 9 m were less impacted by both bleaching and cyclone activity. This is likely the result of the strong attenuation of

surface water temperature, sunlight irradiance and wind driven water movement with increasing depth.

In addition to the influence of location on physical conditions, the community structure also determines the severity of the impact from disturbance. As various taxa of corals have different susceptibilities to disturbance, their relative abundances will influence changes in coral cover and community structure. For example, different families of coral have markedly variable responses to elevated water temperatures [56, 71, 72, 73]. As has been documented on other reefs, the branching Acroporidae were strongly affected by the 1998 bleaching at Scott Reef, while the massive Poritidae were only moderately affected. Relative decreases in the cover of the Poritidae were lower than for the Acroporidae because they were more likely to suffer only partial colony mortality (injury). As with the elevated water temperatures, different groups of corals also display different susceptibility to cyclone disturbances. Small encrusting or massive species are more resistant to water movement than larger branching or tabulate species [74], and this underlies variation in the survival of different taxonomic groups following cyclone impacts.

Changes in community structure following disturbance not only reflect their location and previous structure, but obviously also the severity of the event. At Scott Reef, bleaching has strongly influenced the subsequent rates of recovery; locations and depths that were worst affected by the bleaching have been the slowest to recover. Following the most severe disturbances, dramatic reductions in coral cover and the occupation of space by algae can further slow rates of recovery, if the algae exclude and outcompete coral recruits [75]. In the worst instances, acute disturbances (e.g. elevated water temperatures) coupled with chronic disturbances (e.g. degraded water quality) can result in a long-term shift in which algae replace corals as the dominant benthic organism [26, 31, 43, 76, 77]. However, at Scott Reef there has been little change in the cover of macroalgae following the bleaching, and most increases of algal cover have been composed of turfing and coralline algae that have comparatively little affect on coral recruitment and survival.

Despite the isolation of Scott Reef and the low number of neighbouring systems that can supply coral recruits, the recovery of Scott Reef coral communities across most depths has been relatively rapid. This may be due to the high water quality at Scott Reef, which provide an environment where corals have high rates of growth and survival, resulting in communities that are more resilient to disturbance [78, 79]. The coral communities at Scott Reef are expected to continue to return to their pre-bleaching state in the absence of major disturbances. The longer-term resilience of these communities will depend on maintaining good water quality, minimizing local stressors, and the magnitude of predicted increases in water temperatures and severity of cyclones arising from climate change [19, 47].

Fish Communities

In tropical waters, corals and fishes form a network of interdependencies that together have a profound influence on coral reef ecosystems. In order to understand the effects of disturbance, whether natural or anthropogenic, it is necessary to monitor these major

components of the system simultaneously, rather than in isolation. At Scott Reef, the long term monitoring program has shown how major disturbance events, such as bleaching and cyclones, have had effects on benthic communities that have then flowed through to fish assemblages. The coral bleaching that occurred in 1998 was unprecedented in scale and severity and reduced the cover of coral by approximately 75% over the entire reef [21, 53]. This had immediate and negative effects on abundances of those species that were obligate associates of live coral, either due to diet, such as butterfly fishes, or habitat preference, such as some planktivorous damselfishes. Such habitat specialists were a feature of the assemblage of fishes at Scott Reef prior to bleaching (Fig. 2.4.3.2). As the dead coral surfaces became overgrown by turfing algae and the structure of the corals degraded to rubble, the abundance of herbivorous species increased and there was a change in the assemblage to those species that prefer rubble habitats (Fig. 2.4.3.2). In more recent years, cover of hard corals has largely recovered and abundance of herbivores has declined to pre-bleaching numbers. However, unlike coral communities that are close to returning to pre-bleaching composition and structure, fish assemblages remain different from those prior to bleaching and remain dominated by more habitat generalists than specialists (Fig. 2.4.3.2). There are some signs that specialist species such as butterfly fishes may be increasing, but a return to a pre-bleaching assemblage of fishes may still require many years.

While changes in the coral communities were the obvious outcome of bleaching and cyclone disturbances, some of the observed changes in fish communities were not as simple to interpret. For example, the numbers of non-damselfish species steadily increased during the study. These were apparently unaffected by the major bleaching or cyclone disturbances. One possibility is that such patterns are the result of increasing fishing pressure on Scott Reef and reductions in large predatory reef fish and sharks over the last decade. Stocks of some of these species are now chronically over-fished [80]. Studies on other reef systems have shown that reduction in the abundance of large predatory fish changes the biomass, structure and abundance of the remainder of the fish community [81, 82], which might account for some of the changes at Scott Reef. 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 fishing pressure on stocks of predatory fishes.

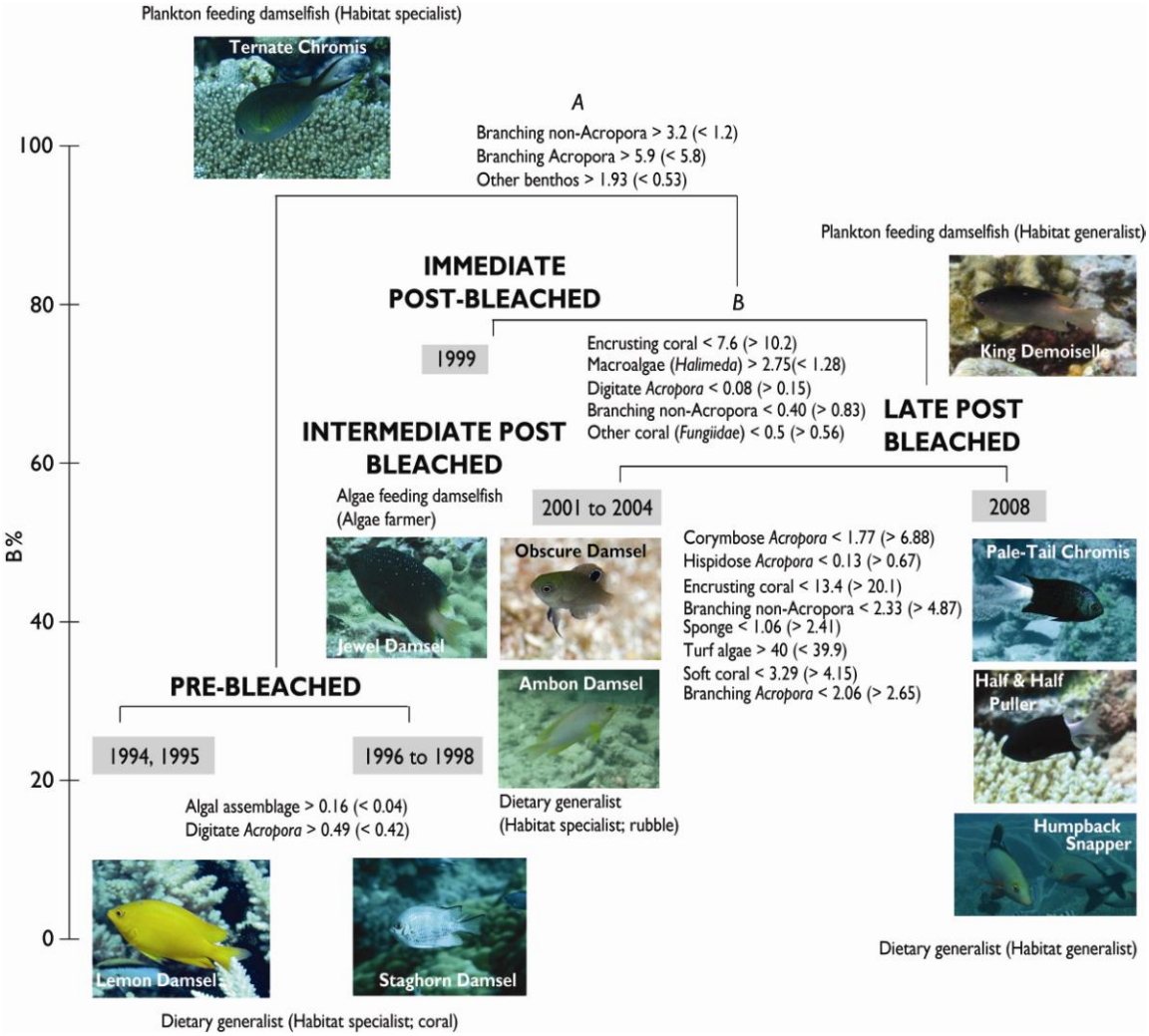


Fig. 2.4.3.2 Linkage tree showing the main fish species that distinguish the various pre- and post-bleach fish communities at Scott Reef. The percentage contribution thresholds of benthic groups correlated with these fish communities are also shown. Unbracketed and bracketed thresholds given at each node indicate that a left and right path, respectively, should be followed through the tree.

Project 1.2 Birth, growth and survival of corals

Tagged coral colonies at Scott Reef had high rates of growth and survival, except during periods of cyclone disturbance (Fig. 2.4.3.3 & 4). During 2008/9 when there were no cyclones, there were no clear differences in the growth and survival of either the branching or the massive corals (see Box 2) among locations or size classes; the exception was perhaps slower growth in the smallest (< 5cm) *Acropora spicifera* colonies. However, there were clear differences in growth and survival between different growth forms. Colonies of the branching coral *A. spicifera* grew much faster (2 to 9 cm yr^{-1}) and had slightly lower survivorship than the massive *Goniastrea spp.* corals (< 1cm cm yr^{-1}). This result is consistent with previous studies of these coral growth forms on other reefs [60, 83, 84, 85]. However, at Scott Reef, survivorship of both growth forms was higher than that reported for equivalent species at other reefs, and displayed less variation among size classes. Many studies have found that small colonies have

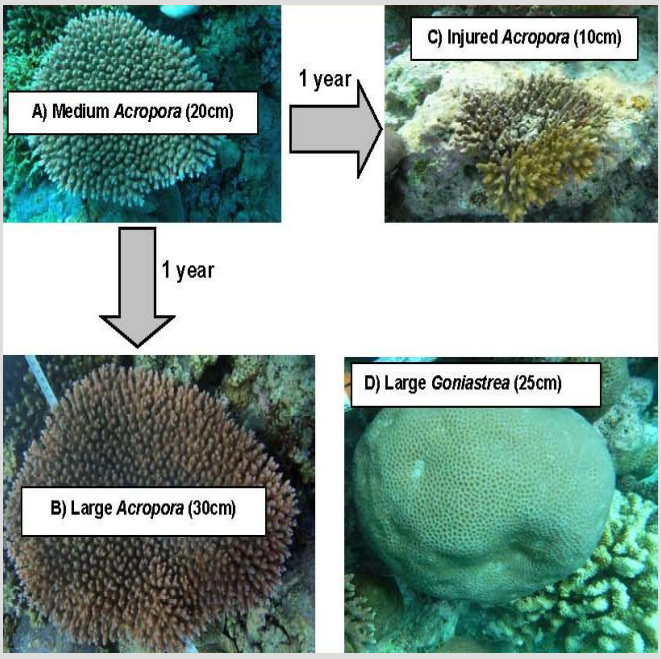
much lower survivorship than large colonies [83, 85], but at Scott Reef there was little difference in survival among the size classes of either growth form, even for the smallest (< 5cm) colonies (Fig. 2.4.3.3). For example, the survival of all size classes was >75% yr^{-1} for *A. spicifera*, and >95% yr^{-1} for *Goniastrea spp*., with the exception of 82% yr^{-1} for the smallest *Goniastrea spp* at one location (SL4). The high survival of all sizes of tagged corals may be due to the good water quality at Scott Reef, particularly the low sedimentation rates and cover of macro algae. Additionally, the density and cover of corals at Scott Reef has not yet reached a maximum following the mass-bleaching in 1998, so that small colonies are less likely to be exposed to competitive interactions with larger colonies that can result in their mortality [86].

BOX 2. HOW AND WHY CORAL COMMUNITIES CHANGE: BIRTH, GROWTH AND SURVIVAL

Long-term monitoring of coral reefs has traditionally documented changes in coral cover and community structure in response to natural disturbances. However, coral reefs are today exposed to a complex combination of natural and human disturbances, and it is becoming increasingly important to know both how and ***why*** *communities change through time [43, 87]. This requires measurement of the demographic processes (spawning, recruitment, growth, and survival) that cause changes in coral cover. Such data not only explain why changes have occurred, but also enables predictions to be made about the future and the longer-term impacts of disturbances on coral communities. For example, a severe cyclone may dramatically reduce coral cover by killing and injuring the largest colonies, which are the most susceptible to the wave energy produced by these storms. Communities will recover from this acute disturbance if there is an abundance of recruits and small colonies with high rates of survival. In contrast, chronic degradation of water quality may cause only small reductions in coral cover over several years, because there is relatively little impact on the largest corals. However, the long term future of the community may be threatened by reduction in rates of recruitment and survival of smaller corals due to increased levels of sedimentation and algal growth [88].*

Another advantage in collecting demographic data is that it can be used for computer modelling of populations [89, 90]. These models can summarise data to provide a simple measure of population 'health', such as the population growth rate (a population growth rate of 1 means the population is stable, or 0.5 means it will halve in size over a given period). Models also indicate which corals are most important for population maintenance and can be used to project population structure under different scenarios, such as years of calm conditions or periodic disturbance by cyclones [91, 92, 93, 94]. The results of population models are limited by their assumptions [95], so their results must be interpreted carefully. However, when combined with information about changes in physical conditions, coral cover and community structure, the suite of information provides a good understanding of how and why communities have responded a certain way to disturbances, and some idea of how they may change in the future.

Demographic data are being collected for two common groups of corals at Scott Reef, to help explain observed changes in coral cover and community structure at monitoring sites. Colonies of *Acropora spicifera* (Fig. A) and *Goniastrea spp.* (Fig. D) have been tagged at locations across Scott Reef. *Acropora* corals can grow quickly, rapidly increasing in size within a year (Fig. A to B), but are also most likely to be injured by disturbances such as cyclones, causing rapid reductions in size (Fig. A to C). Conversely, the more robust *Goniastrea spp.* (Fig. D) grow slower but are less susceptible to many disturbances.



The amount of space for recolonisation, good water quality, and the high rates of growth and survival of colonies may explain why Scott Reef has recovered quicker than some other coral reef from the catastrophic impacts of bleaching in 1998. Good water quality increases the resilience of coral communities to increasing sea-water temperatures and bleaching events [78, 79], and this is particularly important for isolated reefs that do not receive a regular supply of larvae from others in the region [96, 97].

Although not affected by degraded water quality, (in contrast to many of the world's reefs), Scott Reef is exposed to periodic disturbance by cyclones. In 2007, Cyclone George caused localised impacts at Scott Reef, affecting communities at two locations and slowing their recovery from previous disturbances. The impact of Cyclone George at these locations (SL3, SL4) was confirmed by the rates of growth and survival of tagged *Acropora spicifera,* and there was little or no evidence of impact at the sheltered locations SL1 and SL2 (Fig. 2.4.3.3 & 4). Additionally, at the locations affected by the cyclone, there were clear differences in rates of growth and survival among size classes, reflecting their varying susceptibility to this type of disturbance. For example, survival was lowest for the largest (>15 cm) colonies because they were most likely to be toppled over or fragmented by cyclonic waves (Fig. 2.4.3.3). Similarly, growth rates were much lower for the largest size classes at the exposed locations, although reduced growth was evident across all colony sizes at these locations (Fig. 2.4.3.4). Reductions in the rates of growth were also due to colony injury, which decreased the amount of live tissue between surveys and resulted in negative growth (Fig. 2.4.3. 4). For example, decreases in colony size due to injury resulted in a mean negative rate of growth for the largest colonies at one of the exposed (SL4) locations (Fig. 2.4.3.4). Importantly, many of the colonies that initially survived the cyclone died several months later from their injuries, so the full impact of the cyclone was not evident for more than a year after the disturbance [98].

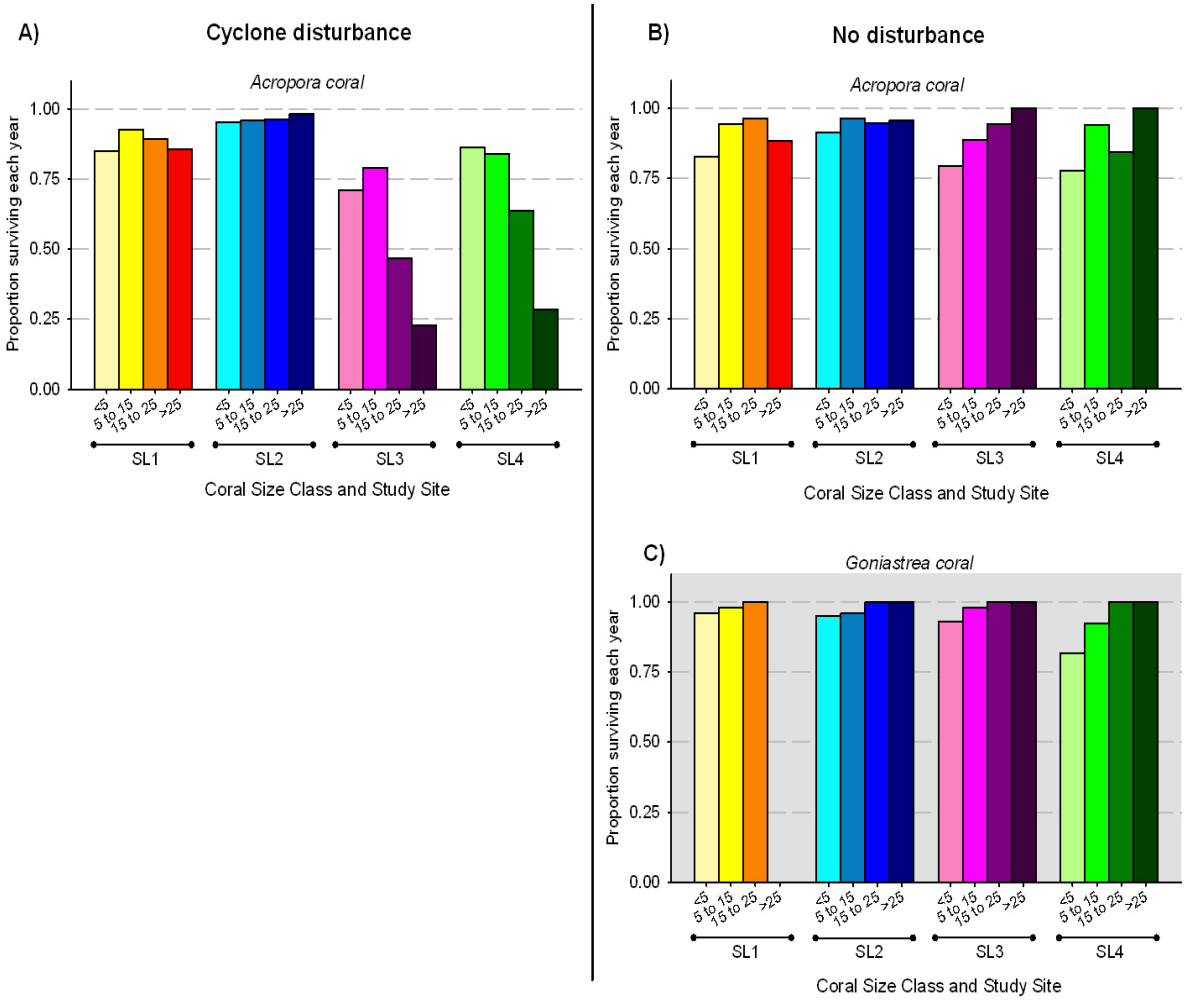


Fig. 2.4.3.3 Mean rates of survival for colonies of the fragile *Acropora spicifera*, and the massive *Goniastrea spp*., of different sizes (diameter) at different locations at Scott Reef. Cyclone George impacted communities at the end of the first survey year and at the start of the second (May 2007), so rates of survival under conditions of 'cyclone disturbance' were averaged over the two years (A). The rates of growth during the calm conditions of 'no disturbance' were for the period 2008/9 (B, C).

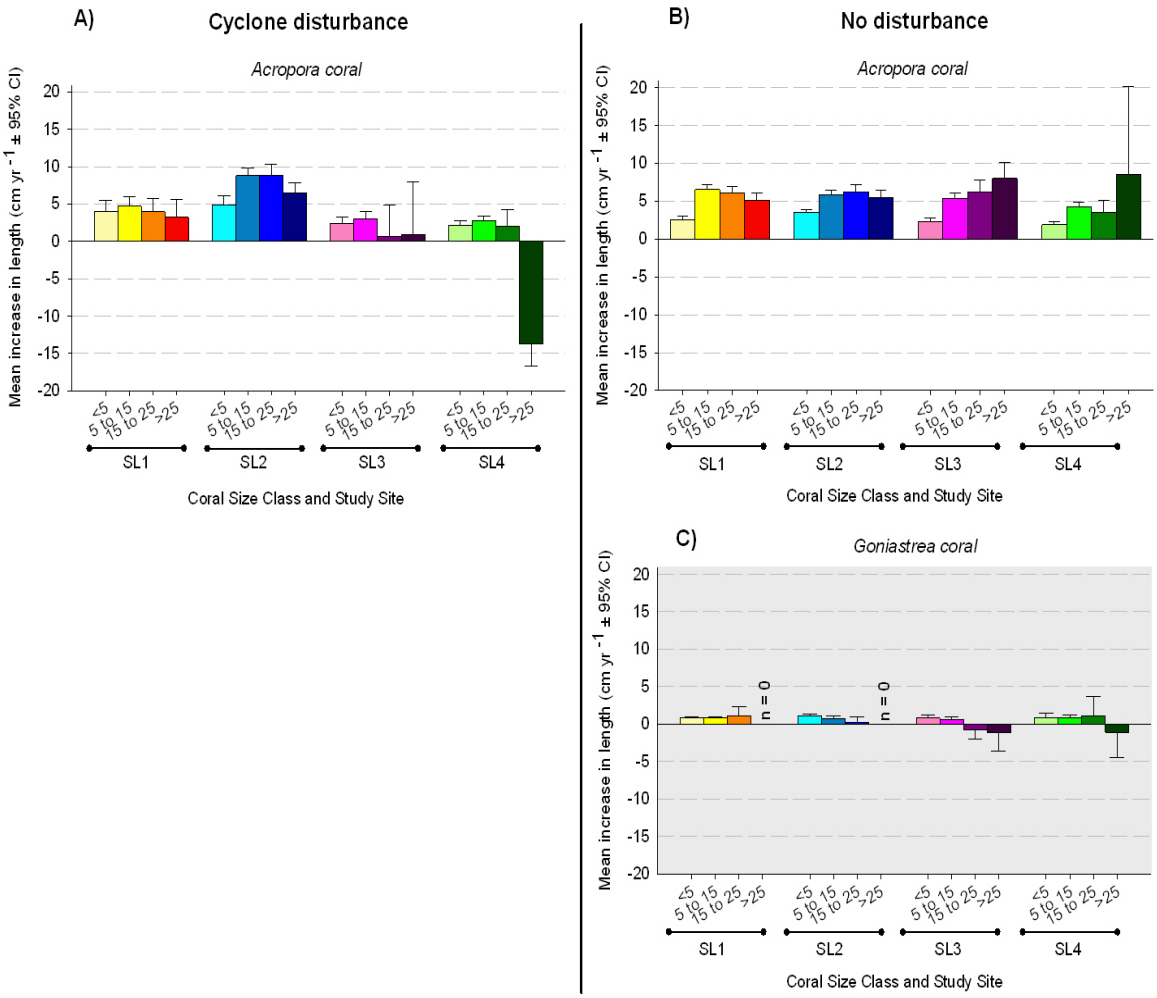


Fig. 2.4.3.4 Mean rates of growth for colonies of the fragile *Acropora spicifera*, and the massive *Goniastrea spp.*, of different sizes (diameter) at different locations at Scott Reef. Cyclone George impacted communities at the end of the first survey year and at the start of the second (May 2007), so rates of growth under conditions of 'cyclone disturbance' were averaged over the two years (A). The rates of growth during the calm conditions of 'no disturbance' were for the period 2008/9 (B, C).

Colonies of the massive *Goniastrea spp.* coral had not yet been tagged when the Cyclone George passed over Scott Reef, so the impact on this more robust species is not known. However, this massive coral is likely to be less affected by wave energy than the more fragile *Acropora spicifera*, particularly at large colony sizes. The trade-off between rapid growth and high survival in these two groups of corals is characteristic of different species and growth forms of corals. For example, branching corals such as the *Acropora* generally have high rates of reproduction and growth, but are among the most susceptible to disturbances such as elevated water temperature, cyclones and outbreaks of crown of thorns [51, 58, 71, 84, 99]. Conversely, robust massive corals such as the *Goniastrea* characteristically have low rates of reproduction and growth, but are less susceptible common disturbances, live longer and have slower rates of population turn-over. These differences in life history strategies are evident in the population growth rates (see Box 2) of the tagged corals at different locations at Scott Reef, throughout the disturbance regimes. For example, the population growth rates for *A. spicifera* at locations exposed to the cyclone ranged from 0.62 yr^{-1} to 0.88 yr^{-1} over two years (2006-2008), due to the high rates of mortality and colony injury, compared with between 1.0 yr^{-1} and 1.2 yr^{-1} at the sheltered locations; during the calm period that followed (2008-2009) population growth rates at all locations ranged between 1.1 and 1.2 yr^{-1}, indicating the potential for rapid increases in population size during good conditions.

Project 1.3 Connectivity of coral and fish among reef populations in north-western Australia

Recent research at Scott Reef has begun to not only describe patterns of population connectivity among the offshore coral reefs of the north-west, but also to identify the mechanisms driving these patterns and their consequences for the ecology of the reefs. This knowledge is crucial for the successful conservation of these threatened ecosystems (see Box 3). A study on two species of hard corals showed that there were genetic differences not only between the systems of Scott Reef and Rowley Shoals, between reefs within each system, and even between reef areas within the same reef [97, 100]. These results show that the majority of coral larvae may be retained close their natal (parent) reef patch, and are consistent with *in-situ* measurements of larval development and local hydrodynamics [4]. Additionally, there is a strong positive relationship between coral cover and number of new corals (recruits) over space and time, which also suggests that most recruits are produced locally (see Project 1.4). These results suggest that coral communities at Scott Reef rely on the reproductive output of corals within the same reef to provide new recruits every generation. Thus, to maximise the potential of reefs to recover from a disturbance, successful conservation zoning needs to be applied at the reef-scale (<10 km) so that a significant portion of the reproductive capacity of each reef is protected.

Fig. 2.4.3.5 The two coral species used in the genetic study of connectivity, *Seriatopora hystrix* (left) and *Acropora tenuis* (right).

Unlike coral larvae, many fish larvae are obligated to spend up to several weeks in the plankton before they are able to settle. But, most fish larvae are by no means passive particles. Late-stage larvae are able to not only sustain swimming speeds that are faster than average current speeds, but are also able to sense and swim towards reefs [101]. Because fish larvae feed on plankton, they may be able to extend their pelagic life in the open ocean without major energetic costs, thus increasing their chances of firstly encountering, and then surviving in, suitable habitat [102]. Thus, depending on the interplay between the behavioural abilities of larvae and their oceanographic environment, either localised or long-distance dispersal is a possibility.

We are now examining the relative extent of local and long distance dispersal in the damselfish, *Chromis margaritifer* (Fig. 2.4.3.6). Our study utilises ecological, oceanographic and genetic data to assess the strength and scale of larval connections within and among reefs of the Scott Reef and Rowley Shoals systems. Analysis of over 200 otoliths (Fig. 2.4.3.6) showed that spawning occurs throughout the year, that pelagic larval durations ranged between 16 to 42 days (mean of 35 days), and that larval durations were shorter at Scott Reef than at the Rowley Shoals. Oceanographic modelling suggested that although larvae could move between reef systems, the probability is low. A hierarchical sampling design revealed subtle but significant genetic structure that was primarily due to a weak genetic discontinuity between the two coral reef systems of Scott Reef and Rowley Shoals. These independent lines of evidence suggest that dispersal of *C. margaritifer* larvae occurs only infrequently over the 400 km of open ocean between the two reef systems. Thus, locally produced larvae maintain populations in each atoll reef system, although larvae disperse among reefs within the same system. At this latter scale, recovery after a disturbance should be rapid as long as reproductively viable (healthy) subpopulations remain on other reefs within each of the Scott Reef and Rowley Shoals system. Thus, these fish appear to be less vulnerable to local (reef-scale) disturbance than the hard corals, which have more limited dispersal, although protection of a significant portion of the breeding stocks within each system will be required for preservation of fish populations.

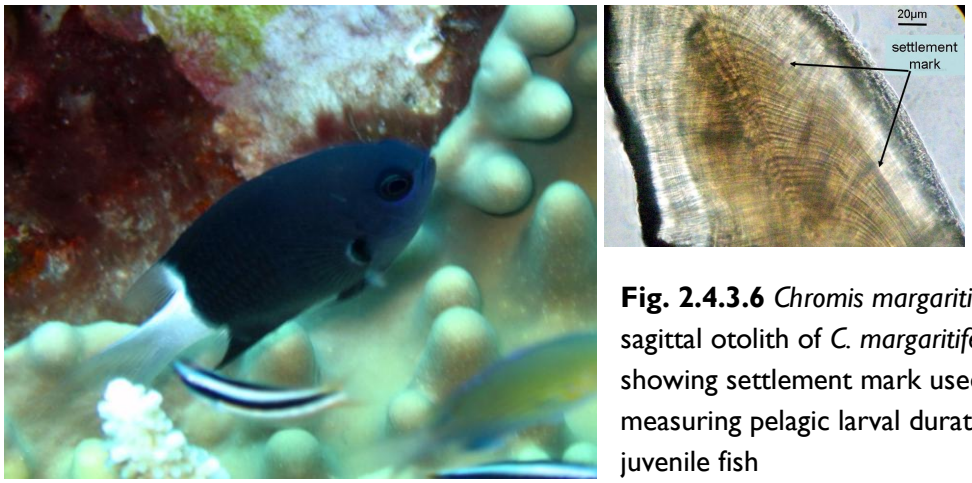


Fig. 2.4.3.6 *Chromis margaritifer* (left) and sagittal otolith of *C. margaritifer* (right) showing settlement mark used for measuring pelagic larval duration in juvenile fish

BOX 3. POPULATION CONNECTIVITY AMONG CORAL ATOLLS OF NORTH-WEST AUSTRALIA

"Population connectivity" refers to the extent to which individuals disperse within and among geographically separated populations. For most coral reef species, dispersal away from the parental habitat is achieved by a larval stage that lives in open water away from the reef. The duration of this pelagic stage, the swimming and sensory abilities of larvae, current patterns and the distances separating populations, all affect the extent of larval dispersal and exchange among populations on reefs [103]. This means that the strength and scale of dispersal often varies greatly among species and even within species over space and time [104].

Knowledge of patterns of larval connectivity among populations is essential for management of coral reefs [105, 106, 107]. For example, a reef or population that receives supplies of larvae from another source reef is likely to recover more rapidly from a severe disturbance (e.g. bleaching, cyclones). An effective management strategy in such a scenario would be to maintain the healthy source reef by designating it as a marine protected area. Alternatively, if a population depends on larvae produced by resident individuals for replenishment, it will be much less resilient to severe disturbance. In this situation, it would be important that a proportion of the local population is protected so that it can act as a source for resupply of new individuals in case of disturbance events. There are, however, immense practical challenges involved in tracking tiny larvae in the open ocean. For this reason, knowledge of patterns of larval connectivity is limited in marine systems, although it is the subject of a great deal of research effort worldwide.

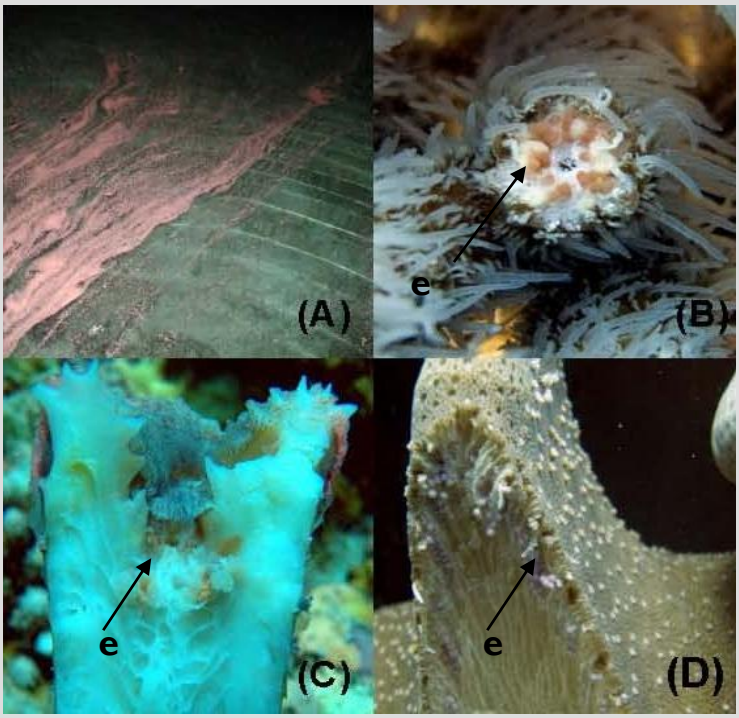
Scott Reef and the Rowley Shoals are offshore atoll systems that lie along the edge of continental shelf to the north-west of Australia and are separated by several hundreds of kilometres of open ocean. Within each system, there are three large reefs that are between 10 and 30 km apart. Until recently, it was assumed that Scott Reef and the Rowley Shoals were connected by a rapid unidirectional current that originates in the Indonesian Through-flow and moves poleward along the continental shelf margin. However, new oceanographic modelling of water flows suggests that transport of larvae between these systems will take at least one month, and since the larvae of hard corals may settle within days of being spawned, dispersal among reef systems will occur infrequently. Recent studies support this prediction; genetic differences between systems and among reefs within systems, together with a strong relationship between the amount of coral cover and the number of larvae that settle at a particular location, indicate that coral larvae rarely disperse between systems and that most originate from the local area [97, 100, 108]. The situation is more complex for the reef fishes that inhabit these systems. Unlike corals, which have a short planktonic life and are passively dispersed by currents, many larval reef fishes reside in the plankton for over a month and have well developed sensory and swimming abilities. These traits allow a greater opportunity for some transfer of individuals between reef systems. However, recent genetic analyses of a common damselfish show that this also occurs only very rarely. Similar to corals, most new individuals of this reef fish arriving from the plankton to benthic habitats have been produced by populations within the same reef system.

Project 1.4 Reproduction and settlement of corals

Mass spawning by corals is a spectacular event that involves the synchronous release of eggs and sperm by many/most corals on a reef during a single night of each year. Most corals on Indo-Pacific reefs reproduce by mass-spawning *(99, 109, 110, 111)* and the phenomenon is particularly prevalent on reefs around Australia, where it generally occurs a few nights after a full moon in spring (October / November) on the Great Barrier Reef *(109, 110, 112)*, and autumn (March/April) on West Australian reefs *(4, 113, 114, 115, 116)*. Mass spawning has been documented in autumn on many West Australian reefs, from the Abrolhos in the south, through Ningaloo and to Scott Reef in the north. However, recent research has discovered a second spawning event on northern reefs that occurs in spring at a similar time to the mass spawning event on the Great Barrier Reef. Although less prominent than the mass spawning in autumn, spawning by multiple colonies of some species during spring has been documented on reefs at Barrow Island, the Dampier Archipelago, Scott Reef *(4, 116)* and at the Rowley Shoals (see Box 4). Results to date suggest that the participation in the spring spawning decreases with increasing latitude, so that it does not occur as far south as Ningaloo Reef, although more surveys are required to confirm the geographical extent of secondary spawning.

Participation in a spring spawning by corals in Western Australia was first described at Scott Reef, where ongoing studies are providing the best insights into the phenomenon. Of 45 coral species surveyed at Scott Reef, 44 are known to spawn during autumn; 15 of these spawn during spring and 14 spawn during both seasons. Of the species that spawn twice a year, most have a larger proportion of colonies spawning in autumn than in spring, providing further confirmation that the main reproductive period occurs during autumn. However, there are some notable exceptions to this pattern. In four species, more than 30% of colonies were inferred to spawn in spring, suggesting their reproductive output during this period is similar, or greater than, during the autumn; recent evidence also suggests that one species (*Acropora millepora*) reproduces exclusively during spring. Additionally, a significant proportion of the massive *Porites* corals, which make an important contribution to reef structure, may also reproduce outside of the spawning period in autumn. As with some of the most common brooding corals (e.g. *Isopora brueggemanni, Seriatopora hystrix*) at Scott Reef, massive *Porites spp.* may reproduce over consecutive months from spring to autumn. Further surveys at Scott Reef should confirm these patterns of reproduction in common species, providing insights into the significance of the different reproductive schedules for population dynamics.

BOX 4. BIANNUAL SPAWNING BY CORALS OFF NORTH-WEST AUSTRALIA



Slick of coral spawn on the water's surface (a). Pigmented eggs (e) within species of *Acropora* (b), *Lobophyllia* (c) and soft coral(d)

Many coral communities spawn synchronously over a few nights each year, but some populations spawn at other times. Around Australia, coral communities have highly synchronous patterns of reproduction, mass-spawning during austral spring on the east coast and autumn on the west coast. However, preliminary research at a few locations off north-west Australia has documented a second spawning during spring, at a similar time to that of the east coast communities [A Heyward pers. comm. 4, 116].

Observations of biannual spawning are now supported by more recent work at the Rowley Shoals, one of Australia's largest groups of shelf atolls and most pristine reef systems. Based on the presence of pigmented eggs and the size of gametes within polyps (examined microscopically), 22% of 168 colonies sampled haphazardly at the Rowley Shoals participated in a multi-specific spawning event that produced large slicks of spawn (Fig. A) eight nights after the full moon in October 2008. Of the 51 species sampled, 37% were inferred to participate in this spring spawning, including species of Acropora *(Fig. B),* Diploastrea, Favites *and* Lobophyllia *(Fig. C); large and pigmented eggs were also observed in some soft corals (Fig. D). Within the region, populations of at least 25 species are known to spawn during both spring and autumn, but autumn remains the dominant spawning period. The extent to which communities at higher latitude reefs (e.g. Ningaloo Reef) also spawn during spring remains to be determined, but preliminary data suggest little or no participation in the spring spawning and a more protracted spawning around the autumn period.*

The larvae produced during the different reproductive periods at Scott Reef maintain the coral communities and facilitate their recovery following disturbances. Thus, the numbers of larvae that recruit into communities is an indication of their relative health, with a high and regular supply of recruits suggesting healthy communities. In the years after the mass-bleaching in 1998, rates of coral recruitment were particularly low (Fig. 2.4.3.7A). because few live corals remained on reefs and the reproductive output of the survivors was probably reduced by stress and injury *(117, 118)*. Additionally, multiple lines of evidence *(4, 97, 108)* suggest that other reef systems in the region (Ashmore Reef, Rowley Shoals) did not provide sufficient recruits to speed the recovery of communities at Scott Reef. Over subsequent years, the rates of recruitment increased gradually, and then more rapidly as these early recolonisers grew to adult size and further increased larval supply (Fig. 2.4.3.7A). By 2005, recruitment had increased at all locations at Scott Reef, and by 2008 the mean rate of recruitment (70 per tile) was higher than in the years before the bleaching (25 to 55 recruits per tile). Recruitment in 2009 occurred at similar, but slightly lower levels than in 2008.

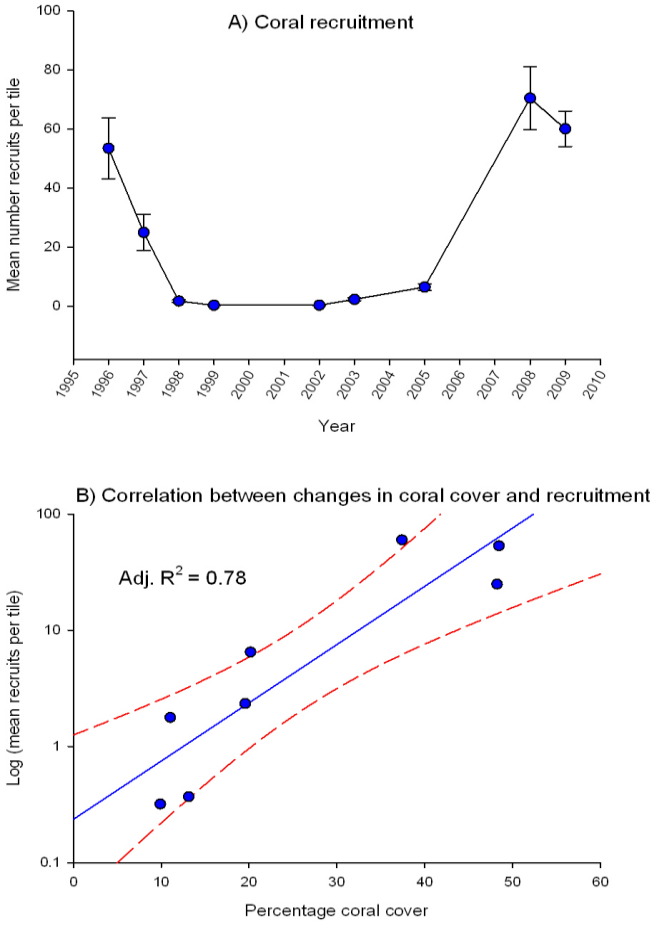


Fig. 2.4.3.7 (A) Changes in the rates of coral recruitment at Scott Reef from 1996 to 2009; the mass-bleaching occurred in 1998. (B) The relationship between changes in coral cover and recruitment through time at Scott Reef. High coral cover before the bleaching and in recent years was correlated to high recruitment; decreases in coral cover following the bleaching saw corresponding decreases in recruitment.

Rapid increases in coral recruitment in recent years reflect a lack of any major disturbance, increases in the number and size of adult corals, and the corresponding increases in coral cover at many sites. Indeed, there is a strong ($R^2 = 0.78$) correlation between coral cover and recruitment at Scott Reef over the entire period of monitoring. Changes in coral cover through periods of disturbance and recovery yielded similar changes in the rates of recruitment at Scott Reef Fig. 2.4.3.7B), indicating a strong stock-recruitment relationship for this reef system (i.e. a relationship between spawning stock of corals and the numbers of new recruits arriving from the plankton). This stock-recruitment relationship, coupled with information about larval ecology, coral genetics and oceanography *(4, 97, 108)* shows that that recovery of coral communities at Scott Reef following disturbances will largely be facilitated by the survivors remaining on reefs, and will not be rapidly increased by the supply of larvae from other reef systems in the region. This is not surprising given the isolation of Scott Reef, and these insights are particularly important for the management of similar reef systems in north-west Australia (See Box 3).

2.5. Publication of Research Outcomes

2.5.1. Scientific journal articles

Gilmour JP, Smith LD, Brinkman RM (2009) Biannual spawning, rapid larval development and evidence of self-seeding for corals on an isolated system of reefs. Marine Biology 156: 1297-1309

Underwood JN (2009) Genetic diversity and divergence among coastal and offshore reefs in a hard coral depend on geographic discontinuity and oceanic currents. Evolutionary Applications 2 222-233

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

2.5.2. Postgraduate research projects

None

2.5.3. Presentations and conferences

Underwood (2009) Dispersal among geographically isolated populations of coral reef fish: ecological freeways and evolutionary highways. Indo-Pacific Fish Conference, Perth 2009.

Underwood (2009) Dispersal among geographically isolated populations of coral reef fish: ecological freeways and evolutionary highways. Australian Marine Science Association, Adelaide July 2009.

2.6. References

1. Holloway P.E. (1995) Leeuwin current observations on the Australian North West Shelf, May–June 1993 *Deep-Sea Research Part I Oceanographic Research Papers* **42**: 285-305
2. Cresswell G., Frische A., Peterson J. & Quadfasel D. (1993) Circulation in the Timor Sea. *Journal of Geophysical Research* **98**: 14379-14389
3. Brinkman R., McKinnon A.D., Furnas M. & Patten M. (2009) *Understanding water column and pelagic ecosystem processes affecting South Reef Lagoon. AIMS SRRP Technical Report - Project 3. Report prepared for the Browse Joint Venture Partners*. Australian Institute of Marine Science, Perth
4. Gilmour J.P., Smith L.D. & Brinkman R.M. (2009) Biannual spawning, rapid larval development and evidence of self-seeding for corals on an isolated system of reefs. *Marine Biology* **156**: 1297-1309
5. Cooper T.F., Ulstrup K.E., Dandan S.S., Roger L., van Oppen M.J.H., Heyward A.J. & Hühl M. (2009) *Characterising the photophysiology of deep water corals at Scott Reef, Western Australia. Preliminary report prepared for the Browse Joint Venture Partners*. Australian Institute of Marine Science, Perth
6. Bryce C.W. (2007) A survey of the invertebrate marine resources at Scott and Seringapatam (& Browse Island) WA. *Australian Coral Reef Society*.Fremantle
7. ERM (2008) Baseline Review of Indonesian Fishers Identified at Scott Reef. Report prepared for Woodside Energy Ltd.
8. ERM (2009) Baseline Review of Indonesian Fishers Identified at Scott Reef. Report prepared for Woodside Energy Ltd.
9. Skewes T.D., Gordon S.R., McLeod I.R., Taranto T.J., Dennis D.M., Jacobs D.R., Pitcher C.R., Haywood M., Smith G.P., Poiner I.R., Milton D., Griffin D. & Hunter C. (1999) *Survey and Stock Size Estimates of the Shallow Reef (0-15 m) and Shoal Area (15-50 m Deep). Marine Resources and Habitat Mapping within the Timor Sea. Volume 2. Habitat Mapping and Coral Dieback*. Department of the Environment and Heritage, Canberra
10. Meekan M.G., Cappo M.C., Carleton J.H. & 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*. Prepared for the Australian Government Department of Environment and Heritage
11. Teichert C. & Fairbridge R.W. (1948) Some coral reefs of Sahul Shelf. *Geographical Review* **38**: 222-249
12. Berry P.F. & Marsh L.M. (1986) *History of investigation and description of the physical environment*. In: Berry P.F. (ed) *Records of the Western Australian Museum*, Western Australian Museum, Perth, pp 1-26
13. Done T., Williams D.M., Speare P., Turak E., Davidson J., De Vantier L.M., Newman S.j. & Hutchins (1994) *Surveys of coral and fish communities at Scott Reef and Rowely Shoals. Report to the Browse Joint Venture Partners*. Australian Institute of Marine Science, Final Report, Perth

14. Connell J.H. (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* **16 (Suppl)**: 101-113
15. Connell J.H., Hughes T.P. & Wallace C.C. (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs* **67**: 461-488
16. Tanner J.E., Hughes T.P. & Connell J.H. (1994) Species coexistence, keystone species, and succession: A sensitivity analysis. *Ecology* **75**
17. Gilmour J., Smith L., Underwood J. & Fitzgibon B. (2006) *Biological and Physical Environment at Scott Reef (2006), I: Biological report*. Australian Institute of Marine Science
18. Gilmour J.P. & Smith L.D. (2006) Category five cyclone at Scott Reef, northwestern Australia. *Coral Reefs* **25**: 200-200
19. Emanuel K. (2005) Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* **436**: 686-688
20. Smith L.D., Gilmour J.D. & Heyward A.J. (2008) Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. *Coral Reefs* **27**: 197-205
21. Halford A. & Caley M.J. (2009) Towards an understanding of resilience in isolated coral reefs. *Global Change Biology* **doi: 10.1111/j.1365-2486.2009.01972.x**
22. MacDonald I.A. & Perry C.T. (2003) Biological degradation of coral framework in a turbid lagoon environment, Discovery Bay, North Jamaica. *Coral Reefs* **22**: 523-535
23. Pandolfi J.M., Bradbury R.H., Sala E., Hughes T.P., Bjorndal K.A., Cooke R., McArdle D., McClenachan L., Newman M.J.H., Paredes G., Warner R.R. & Jackson J.B.C. (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science*
24. Grigg R.W. & Dollar S.J. (1990) *Natural and anthropogenic disturbances on coral reefs*. In: Dubinsky Z. (ed) *Ecosystems of the World 25: Coral Reefs*. Elsevier, Amsterdam, pp 439-452
25. Hughes T.P., Baird A.H., Bellwood D.R., Card M., Connolly S.R., Folke C., Grosberg R., Hoegh-Guldberg O., Jackson J.B.C., Kleypas J., Lough J.M., Marshall P., Nystrom M., Palumbi S.R., Pandolfi J.M., Rosen B. & Roughgarden J. (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* **301**: 929-933
26. Nystrom M., Folke C. & Moberg F. (2000) Coral reef distrubance and resilience in a human-dominated environment. *Trends in Ecology and Evolution* **15**: 413-417
27. Jackson J.B.C., Kirby M.X., Berger W.H., Bjorndal K.A., Botsford L.W., Bourque B.J., Bradbury R.H., Cooke R., Erlandson J., Estes J.A., Hughes T.P., Kidwell S., Lange C.B., Lenihan H.S., Pandolfi J.M., Peterson C.H., Steneck R.S., Tegner M.J. & Warner R.R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**: 629
28. Smith S.V., Kimmerer W.J., Laws E.A., Brock R.E. & Walsh T.W. (1981) Kaneohe bay sewage Hawaii USA diversion experiment perspectives on ecosystem responses to nurtritional peturbation. *Pacific Science* **35**: 279-395
29. Brodie J., Fabricius K., De'ath G. & Okaji K. (2005) Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. *Bulletin of Marine Science*: 266-278

30. De'ath G. & Moran P.J. (1998) Factors affecting the behaviour of crown-of-thorns starfish (Acanthaster planci L.) on the Great Barrier Reef: 1: Patterns of activity. *Journal of Experimental Marine Biology and Ecology* **220**: 83-106
31. Hughes T.P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**: 1547-1551
32. Walters L.J., Turner T., Kuffner I.B., Paul V.J., Ritson-Williams R., Grablow K., Settar C., Rivera G. & Hickey T.D. (2009) Coral-Algal-Urchin Interactions in Caribbean Waters. *Integrative and Comparative Biology* **49**: E321-E321
33. Glynn P.W. (1984) Widespread coral mortality and the 1982-83 El Nino warming event. *Environmental Conservation* **11**: 133-146
34. Wilkinson C. (2008) *Status of Coral Reefs of the World*. Australian Institute of Marine Science, Townsville
35. Harvell C.D., Mitchell C.E., Ward J.R., Altizer S., Dobson A.P., Ostfeld R.S. & Samuel M.D. (2002) Ecology - Climate warming and disease risks for terrestrial and marine biota. *Science* **296**: 2158-2162
36. Feely R.A., Sabine C.L., Lee K., Berelson W., Kleypas J., Fabry V.J. & Millero F.J. (2004) Impact of anthropogenic CO2 on the CaCO3 system in the oceans. *Science* **305**: 362-366
37. Anthony K.R.N., Kline D.I., Diaz-Pulido G., Dove S. & Hoegh-Guldberg O. (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America* **105**: 17442-17446
38. Silverman J., Lazar B., Cao L., Caldeira K. & Erez J. (2009) Coral reefs may start dissolving when atmospheric CO2 doubles. *Geophysical Research Letters* **36**: 5
39. Veron J.E.N., Stafford-Smith, Hoegh-Guldberg O., Obura D., Pearce-Kelly P., Spalding M., Sheppard C., Lenton T., Attenborough D., Caldeira K., CLarke A., Crabbe J., Fischlin A., Harding S., Jones R., Peterson d., Read P., Reid P.C., Roberts C.M., Teleki K., Taylor J., Turner J. & Rogers (2009) The Coral Reef Crisis: scientific justification for critical CO_2 threshold levels of < 350ppm[2]. Output of the technical working group meeting. The Royal Society, London
40. Hughes T.P., Bellwood D.R., Folke C., Steneck R.S. & Wilson J. (2005) New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology and Evolution*
41. Hoegh-Guldberg O., Anthony K.R.N., Berkelmans R., Dove S., Fabricus K., Lough J., P M., van Oppen M.J.H., Negri A. & Willis B.L. (2007) *Vulnerability of reef-building corals on the Great Barrier Reef to climate change*. In: Jonhson J.E.& Marshall P.A. (eds) *Climate Change and the Great Barrier Reef*. Great Barrier Reef Marine Park Authority and the Australian Greenhouse Office, Townsville, Australia, pp 271-307
42. Knowlton N. & Jackson J.B.C. (2008) Shifting baselines, local impacts, and global change on coral reefs. *Plos Biology* **6**: 215-220
43. Bellwood D.R., Hughes T.P., Folke C. & Nystroem M. (2004) Confronting the coral reef crisis. *Nature* **429**: 827-833
44. Veron J.E.N., Stafford-Smith, Hoegh-Guldberg O., Obura D., Pearce-Kelly P., Spalding M., Sheppard C., Lenton T., Attenborough D., Caldeira K., CLarke A., Crabbe J., Fischlin A., Harding S., Jones R., Peterson d., Read P., Reid P.C., Roberts C.M., Teleki

K., Taylor J., Turner J. & Rogers (2009) *The Coral Reef Crisis: scientific justification for critical CO_2 threshold levels of < 350ppm[2]. Output of the technical Royal Society working group meeting*, London

45. Fabricius K.E. (1995) Slow population turnover in the soft coral genera Sinularia and Sarcophyton on mid- and outer-shelf reefs on the Great Barrier Reef. *Marine Ecology Progress Series* **126**: 145-152
46. McFadden C.S. (1991) A comparative demographic analysis of clonal reproduction in a temperate soft coral. *Ecology* **72**: 1849-1866
47. Sheppard C.R.C. (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature* **425**: 294-297
48. Graham N.A.J., Wilson S.K., Jennings S., Polunin N.V.C., Robinson J., Bijoux J.P. & Daw T.M. (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conservation Biology* **21**: 1291-1300
49. Cole A.J., Pratchett M.S. & Jones G.P. (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries* **9**: 286-307
50. Wilson S.K., Burgess S.C., Cheal A.J., Emslie M., Fisher R., Miller I., Polunin N.V.C. & Sweatman H.P.A. (2008) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology* **77**: 220-228
51. Halford A., Cheal A.J., Ryan D. & Williams D.M. (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology* **85**: 1892-1905
52. Allen G.R. (1991) *Damselfishes of the world*. Mergus, Melle
53. Gilmour J.P., Travers M.J., Underwood J.N., McKinney D.W., gates E.N., Fitzgerald K.L. & Birrell C.L. (2009) *Long-term monitoring of shallow-water coral and fish communities at Scott Reef. AIMS SRRP Technical Report - Project 1. Report prepared for the Browse Joint Venture Partners*. Australian Institute of Marine Science, Perth
54. Syms C. & Jones G.P. (2001) Soft corals exert no direct effects on coral reef fish assemblages. *Oecologia* **127**: 560-571
55. 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
56. McClanahan T.R., Baird A.H., Marshall P.A. & Toscano M.A. (2004) Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Marine Pollution Bulletin* **48**: 327-335
57. Nakamura T. & van Woesik R. (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Marine Ecology Progress Series* **212**: 301
58. Fabricius K.E., De'ath G., Puotinen M.L., Done T., Cooper T.F. & Burgess S.C. (2008) Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. *Limnology and Oceanography* **53**: 690-704
59. Massel S.R. & Done T.J. (1993) Effects of cyclone waves on massive coral assemblages on the Great Barrier Reef: Meteorology, hydrodynamics and demography. *Coral Reefs* **12**

60. Wakeford M., Done T. & Johnson C.R. (2008) Decadal trends in a coral community and evidence of changed disturbance regime. *Coral Reefs* **27**: 1-13
61. Bak R.P.M. & Meesters E.H. (1999) Population structure as a response of coral communities to global change. *American Zoologist* **39**: 56-65
62. Hughes T.P. (1989) Community structure and diversity of coral reefs: The role of history. *Ecology* **70**: 275-279
63. Madin J.S., Black K.P. & Connolly S.R. (2006) Scaling water motion on coral reefs: from regional to organismal scales. *Coral Reefs* **25**: 635-644
64. Beltran-Torres A.U., Munoz-Sanchez L. & Carricart-Ganivet J.P. (2003) Effects of Hurricane Keith at a patch reef on Banco Chinchorro, Mexican Caribbean. *Bulletin of Marine Science* **73**: 187-196
65. Edmunds P.J. (2000) Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. *Marine Ecology Progress Series* **202**: 113-124
66. Harii S. & Kayanne H. (2003) Larval dispersal, recruitment and adult distribution of the brooding stony octocoral Heliopora coerulea on Ishaigaki Island, southwest Japan. *Coral Reefs* **22**: 188-196
67. Hughes T.P., Baird A.H., Dinsdale E.A., Harriott V.J., Moltschaniwskyj N.A., Pratchett M.S., Tanner J.E. & Willis B.L. (2002) Detecting regional variation using meta-analysis and large-scale sampling: Latitudinal patterns in recruitment. *Ecology* **83**: 436-451
68. Miller M.W., Weil E. & Szmant A.M. (2000) Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. *Coral Reefs* **19**: 115-123
69. Tamelander J. (2002) Coral recruitment following a mass mortality event. *Ambio* **31**: 51-57
70. 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
71. 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
72. McClanahan T.R. (2004) The relationship between bleaching and mortality of common corals. *Marine Biology* **144** 1239-1245
73. Marshall P.A. & Baird A.H. (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* **199**: 155-163
74. Madin J.S., O'Donnell M.J. & Connolly S.R. (2008) Climate-mediated mechanical changes to post-disturbance coral assemblages. *Biology Letters* **4**: 490-493
75. Birrell C.L., McCook L.M., Willis B.L. & Diaz-Pulido G. (2008) Effects of benthic algae on the replenishment potential of corals and the implications for the resilience of coral reefs. *Oceanography And Marine Biology: An Annual Review* **46**: 25-63
76. Bellwood D.R., Hoey A.S., Ackerman J.L. & Depczynski M. (2006) Coral Bleaching, reef fish community phase shifts and the resilliance of coral reefs. *Global Change Biology* **12**: 1587-1594
77. Hughes T.P., Rodrigues M.J., Bellwood D., Ceccarelli D., Hoegh-Guldberg O., McCook L., Moltschaniwskyj N.A., Pratchett M.S., Steneck R.S. & Willis B. (2007)

Phase Shifts, Herbivory, and the resislience of coral reefs to climate change. *Current Biology* **17**: 360-365

78. Wooldridge S.A. & Done T.J. (2009) Improved water quality can ameliorate effects of climate change on corals. *Ecological Applications* **19**: 1492-1499
79. Carilli J.E., Norris R.D., Black B.A., Walsh S.M. & McField M. (2009) Local stressors reduce coral resilience to bleaching. *Plos one* **4**: e6324
80. Cappo M., Meekan M.R., Perry M., McCauley R. & Harvey E.S. (2004) Traditional fishing puts the bite on sharks. *Australasian Science* **25**: 29-32
81. Sandin S.A. & Pacala S.W. (2005) Fish aggregation results in inversely density-dependent predation on continuous coral reefs. *Ecology* **86**: 1520-1530
82. DeMartini E.E., Friedlander A.M., Sandin S.A. & Sala E. (2008) Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Marine Ecology-Progress Series* **365**: 199-215
83. Babcock R.C. (1991) Comparative Demography of Three Species of Scleractinian Corals Using Age- And Size-Dependent Classifications. *Ecological Monographs* **61**: 225
84. Hughes T.P. & Connell J.H. (1999) Multiple stressors on coral reefs: A long-term perspective. *Limnology and Oceanography* **44**: 461-488
85. Hughes T.P. & Connell J.H. (1987) Population dynamics based on size or age? A reef-coral analysis. *The American Naturalist* **129**: 818-829
86. Tanner J.E., Hughes T.P. & Connell J.H. (1996) The role of history in community dynamics: A modelling approach. *Ecology* **77**
87. Hughes T.P. (1996) Demographic approaches to community dynamics: A coral reef example. *Ecology* **77**: 2256-2260
88. Hunte W. & Wittenberg M. (1992) Effects of eutrophication and sedimentation on juvenile corals: II. settlement. *Marine Biology* **114**
89. Caswell H. (1989) *Matrix population models: construction, analysis and interpretation.* Sinauer, Sunderland, Massachusetts
90. Ebert T.A. (1999) *Plant and Animal Populations. Methods in Demography.* Academic Press, New York
91. Done T. (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
92. Edmunds P.J. (2008) The effects of temperature on the growth of juvenile scleractinian corals. *Marine Biology* **154**: 153-162
93. Fong P. & Glynn P.W. (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
94. Edmunds P.J. (2005) The effect of sub-lethal increases in temperature on the growth and population trajectories of three scleractinian corals on the southern Great Barrier Reef. *Population Ecology* **146**: 350-364
95. Bierzychudek P. (1999) Looking backwards: Assessing the projections of a transition matrix model. *Ecological Applications* **99**: 1278
96. Ayre D.J. & Hughes T.P. (2004) Climate change, genotypic diversity and gene flow in reef-building corals. *Ecology Letters* **7**: 273-278

97. Underwood J.N., Smith L.D., van Oppen M.J.H. & Gilmour J.P. (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
98. Knowlton N., Lang J.C., Rooney M.C. & Clifford P. (1981) Evidence for Delayed Mortality in Hurricane-Damaged Jamaican Staghorn Corals. *Nature* **294**: 251-252
99. Harrison P. & Booth D.J. (2007) *Coral reefs: naturally dynamic ecosystems and increasingly disturbed ecosystems*. In: Connell S.D.& Gillanders B.M. (eds) *Marine Ecology*. Oxford University Press, Oxford, pp 316-377
100. Underwood J.N., Smith L.D., van Oppen M.J.H. & Gilmour J.P. (2007) Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. *Molecular Ecology* **16**: 771-784
101. Gerlach G., J A., Kingsford M.J., Black K.P. & Miller-Sims V. (2007) Smelling home can prevent dispersal of reef fish larvae. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 858-863
102. Leis J.M. (2002) Pacific coral-reef fishes: the implications of behaviour and ecology of larvae for biodiversity and conservation, and a reassessment of the open population paradigm. *Environmental Biology of Fishes* **65**: 199-208
103. Cowen R.K. & Sponaugle S. (2009) Larval dispersal and marine population connectivity. *Annual Review of Marine Science* **1**: 443-466
104. Cowen R.K., Gawarkiewicz G., Pineda J., Thorrold S.R. & Werner F.E. (2007) Population connectivity in marine systems an overview. *Oceanography* **20**: 3-21
105. McCook L.J., Almany G.R., Berumen M.L., Day J.C., Green A.L., Jones G.P., Leis J.M., Planes S., Russ G.R., Sale P.F. & Thorrold S.R. (2009) Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. *Coral Reefs* **28**: 353-366
106. Sale P.F., Cowen R.K., Danilowicz B.S., Jones G.P., Kritzer J.P., Lindeman K.C., Planes S., Polunin N.V.C., Russ G.R., Sadovy Y.J. & Steneck R.S. (2005) Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution* **20**: 74-80
107. Fogarty M.J. & Botsford L.W. (2007) Population Connectivity and Spatial Management of Marine Fisheries. *Oceanography* **20**: 112-123
108. Underwood J.N. (2009) Genetic diversity and divergence among coastal and offshore reefs in a hard coral depend on geographic discontinuity and oceanic currents. *Evolutionary Applications* **2** 222-233
109. Babcock R.C., Bull G.D., Harrison P.L., Heyward A.J., Oliver J.K., Wallace C. & Willis B.L. (1986) Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef Australia. *Marine Biology* **1986. 379-394.**
110. Harrison P., Babcock R., Bull G.D., Oliver J., Wallace C.C. & Willis B. (1984) Mass spawning in tropical reef corals. *Science* **223**: 1186-1189
111. Harrison P.L. & Wallace C.C. (1990) *Reproduction, dispersal and recruitment of scleractinian corals*. In: Dubinsky Z. (ed) *Ecosystems of the World: coral reefs*. Elsevier Publishers, Amsterdam, pp 133-207
112. Oliver J.K., Babcock B.C., Harrison P.L. & Willis B.L. (1988) Geographic extent of mass coral spawning: Clues to ultimate causal factors. *Proceedings of the Sixth International Coral Reef Symposium*

113. Babcock B.C., Willis B. & Simpson C.J. (1994) Mass spawning of corals on a high latitude coral reef. *Coral Reefs* **13**: 161-169

114. Simpson C.J. (1991) Mass spawning of corals on Western Australian reefs and comparisons with the Great Barrier Reef. *Journal of the Royal Society of Western Australia* **74**: 85-91

115. Rosser N.L. (2005) *Reproductive seasonality and biannual spawning of Acropora on two north-west Australian reefs*. Bachelor of Science with Honours. School of Biological Sciences and Biotechnology, Western Australia

116. Rosser N.L. & Gilmour J.P. (2008) New insights into patterns of coral spawning on Western Australian reefs. *Coral Reefs* **27**: 1-5

117. Baird A.H. & Marshall P.A. (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series* **237**: 133

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

3. Update of SRRP 1 sub-projects

3.1. Scales and frequencies of disturbance to coral communities: recovery following catastrophic bleaching and periodic cyclones in north-west Australia

Introduction

Coral reefs are dynamic systems that are increasingly subjected to disturbance events operating on a range of spatial and temporal scales. Disturbances are becoming more frequent, more severe, and more extensive in their geographical reach (Hoegh-Guldberg et al. 2007), and these new disturbance regimes represent a substantial threat to the long-term health and resilience of coral reefs. As global warming increases, sea surface temperatures are predicted to rise further (Wilkinson 2004), causing a pattern of increasingly frequent and severe coral bleaching and tropical cyclone events (Hoegh-Guldberg 2004; Sriver and Huber 2007). These changing disturbance regimes may ultimately result in the inability of coral communities to recover to previous levels of diversity and abundance. Consequently, there is now global concern that the synergistic effects of elevated seawater temperatures, storms, ocean acidification, overfishing, and degraded water quality may cause potentially irreversible changes to the integrity of coral reefs worldwide (Hughes et al. 2000; McManus et al. 2000; Pratchett et al. 2008; Wilkinson 2008).

Disturbances on coral reefs act across a range of temporal and spatial scales, driving different patterns of community response and recovery. Temporal effects range from acute impacts lasting hours or days to chronic, longer term impacts such as predation by *Acanthaster planci* starfish (Moran 1986; Sano et al. 1987). Spatial impacts range from the highly localised heterogenous damage associated with tropical cyclones (Cheal et al. 2002; Halford et al. 2004), to widespread mass mortality associated with temperature-induced bleaching (Berkelmans and Oliver 1999). These spatial and temporal scales of disturbance are closely tied to patterns of community structure, and the influence of bleaching and storms on coral community dynamics has been examined extensively (Done 1992; Edwards et al. 2001; Aronson et al. 2002; Cheal et al. 2002; Berkelmans et al. 2004; Graham et al. 2006). Several studies have shown that bleaching and cyclone disturbances are important drivers of coral reef community structure (Connell 1978; Hughes 1989; Bythell et al. 2000) and are potentially critical for the promotion of species diversity and structural complexity (Connell 1978; Karlson and Hurd 1993; Jones and Syms 1998).

Cyclone and bleaching disturbances influence these patterns of community structure via an array of physical and biological mechanisms. In the case of cyclone events, the primary impact of storm events is direct physical damage to colonies resulting in a reduction in live coral cover (Halford et al. 2004). In contrast, bleaching leaves the dead coral skeletons intact, where they subsequently become part of the reef structure itself as consolidated calcareous material or rubble (Sano et al. 1987). In addition to these coarse physical processes,

disturbances typically result in biological changes that range from individual sub-lethal effects to system-wide community transitions to an alternate state (Hughes 1994; Bellwood et al. 2004). In the past, coral reefs have been relatively resilient to these cyclic patterns of natural disturbance, with periods of recovery occurring on yearly to decadal timescales (Connell 1997). However, in more recent years, the scale, magnitude, and frequency of disturbance have increased, such that there is now serious concern about the global decline in coral reefs resilience.

In particular, historical patterns of post-disturbance recovery have led to the suggestion that coral reefs in the future may undergo permanent or long-term shifts from coral-dominated to algal-dominated states (McManus and Polsenberg 2006; Mumby et al. 2007). That is, if the system is driven beyond some critical threshold it may enter a new, non-reversible state that possesses its own characteristics of community structure, disturbance susceptibility and system resilience. In the Caribbean, the cumulative effects of cyclones, overfishing, and the mass-mortality of urchins has resulted in such a phase shift, to a state in which communities are now characterised by high algal cover and low coral cover (Bellwood et al. 2004; McManus and Polsenberg 2006). However, recent literature suggests that such phase shifts may not always be permanent (Idjadi et al. 2006; Mumby et al. 2007; Adjeroud et al. 2009) and that coral reefs may be more resistant to macroalgal replacement than previously thought (Bruno et al. 2009; Mumby 2009), provided there is a supply of new recruits and suitable habitat for settlement and survival. Importantly, future climate scenarios predict further increases in the frequency and severity of disturbances, and it remains unclear if coral reefs as we know them will be able to withstand the cumulative impacts of these forces (Hughes et al. 2003; McWilliams et al. 2005). Long-term studies that quantify community disturbance and recovery thus provide an important insight into the future resilience of coral reefs.

Scott Reef in north-west Australia is well suited to these studies of disturbance and recovery, given its offshore location and the absence of many major anthropogenic stressors that affect other coral reefs around the globe (e.g. commercial overfishing, degraded water quality); however there has been overexploitation of at least some stocks (e.g. trochus, sea cucumber, shark) by traditional fishers and the wider impact for on the ecological communities is uncertain. Moreover, during the last fifteen years of monitoring, the reef has been exposed to a series of major climate-driven disturbances events. In early 1998, temperature-induced mass bleaching occurred as a result of elevated sea water temperatures of 30-32° Celsius for a two month period. This major event was followed in early 2004 by category 5 Cyclone Fay which tracked directly across Scott Reef with wind speeds greater than 300km per hour, and in 2007 by category 2 Cyclone George with wind speeds greater than 90km per hour. From 2005 to 2007, three further cyclones tracked close to Scott Reef (Raymond in 2005, Clare in 2006, and Glenda in 2006), however these were relatively minor systems with effective local wind speeds of less than 70km per hour.

Here, we investigate how coral communities at Scott Reef were affected by this multi-faceted disturbance regime. The impacts of the major bleaching event and episodic cyclones were determined by quantifying changes in coral cover and community structure at a series of

locations from 1994 to 2008. The recovery trajectories of benthic cover and structure were analysed to determine patterns of change through time and space.

Methods

Scott Reef is a large offshore reef system consisting of three major atolls, North Reef, South Reef, and Seringapatam. The reef complex is located 270 km from the mainland of north-west Australia on the edge of the continental shelf (S14°04, E121°46). The nearest reefs are the Rowley Shoals 400 km to the south and the Ashmore system 240 km to the north (Fig. 3.1.1).

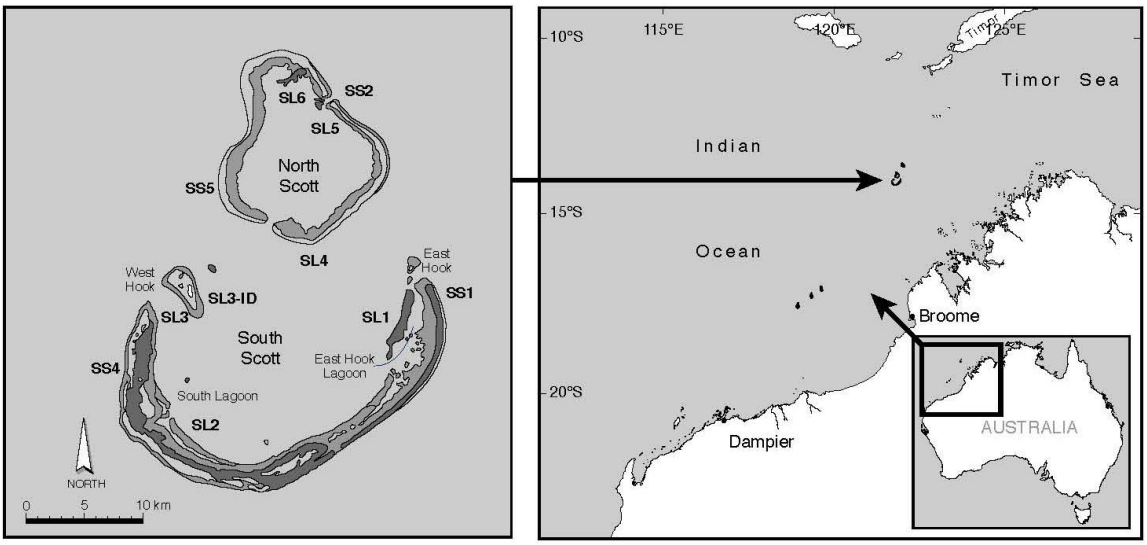


Fig. 3.1.1 Location of Scott Reef, north-west Australia.

In 1994, AIMS established a long-term monitoring program at Scott Reef to quantify spatial and temporal variation in benthic communities (Heyward et al. 1997). The monitoring design consisted of six study locations, with each location comprised of three replicate sites separated by approximately 300 m. At each site, five permanent 50 m transects were situated along the 9 m depth contour, marked at 10 m intervals and separated by approximately 10m. Four of the locations were located inside the relatively sheltered waters of the atoll system (SL1, SL2, SL3, SL4), while two locations were located outside the reef and exposed to open oceanic swells (SS1, SS2). Two of the sheltered inside locations (SL3, SL4) are moderately affected by the influence of oceanic waters as a result of their proximity to deepwater passages between North and South Reef.

Permanent transects were surveyed in 1994-1999, 2001, 2003, 2004, 2005, and 2008. During each survey, a 50m fibreglass tape was laid between permanent steel pickets, and the subsequent transect filmed using an underwater video camera held at a distance of 30cm from the substrata. The footage was analysed using a point sampling technique (Christie et al. 1996), whereby the video was paused at 40 regular intervals along each transect and the identity of the benthos under each of five fixed points was determined, producing a total of 200 points per transect. Organisms were identified to the greatest level of taxonomic detail achievable by the observers, and percent cover of each category was calculated at the transect level. For the purpose of analysis and discussion, the percent cover of benthic organisms were grouped into a series of 'benthic categories' based on a combination of

lifeform (morphology), taxonomic classification, reproductive strategy, and / or ecological relevance.

Benthic community analyses were conducted using the non-parametric techniques of Clarke (1993) and Clarke and Warwick (2001). Analyses were performed using PRIMER 6 software (Clarke and Gorley 2006). Percentage cover of benthic lifeforms were square-root transformed prior to analyses to reduce the effect of dominant species in the assemblage (Clarke and Green 1988). Transformed transect data were averaged to site level, giving three replicate sites for each location for each sampling year. In many analyses, data were further averaged across years into year periods (1994-1997, 1998-2001, 2002-2005, 2006-2009), representing periods of impact and recovery from disturbances.

Bray-Curtis similarities were calculated between each pair of samples, and the resemblance matrices were ordinated using non-metric multidimensional scaling (MDS) to display the key drivers of variation in community structure (Clarke and Gorley 2006). Analysis of Similarities (ANOSIM) was used to test the significance of differences between locations or years (Clarke and Green 1988; Clarke 1993). One and two-way crossed ANOSIM tests were computed using location and/or year category factors. The null hypothesis of no significant differences among groups was rejected when the significance level (p) was < 5%. The R-statistic was used to determine the extent of any significant difference. R values close to a value of one represent a situation where all samples within each group are more similar to each other than to any of the samples from other groups. R values close to zero imply that similarities within and between groups are the same. Where ANOSIM comparisons detected significant differences between locations and/or year periods, similarity percentage analysis (SIMPER) was used to identify the benthic categories that contributed most to the observed similarities and differences between groups i.e. those categories that typify and discriminate each group (Clarke 1993).

Results

Temporal changes in community structure

Communities at Scott Reef separated into groups associated with the four major periods of disturbance and recovery: pre-bleaching from 1994 to 1997, severe bleaching impact from 1998-2001, recovery & cyclones from 2002-2005, and further recovery & cyclones from 2006-2009 (Fig. 3.12).

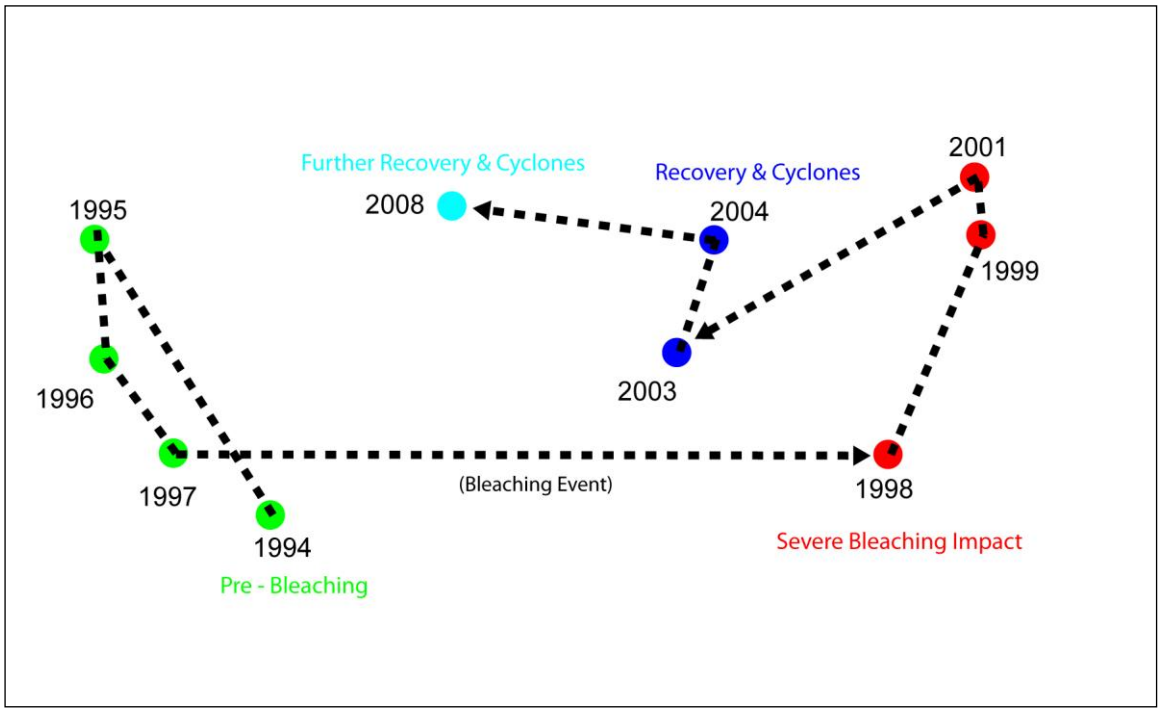


Fig. 3.1.2 MDS ordination of resemblance matrix values derived from benthic percent cover across all locations at Scott Reef from 1994 to 2008. Four disturbance periods are illustrated: pre-bleaching, severe bleaching impact, recovery & cyclones, and further recovery & cyclones. Similarities between communities in different years are represented by the distance between each year. Points that are close together represent communities that are more similar to each other than points that are further apart. The overlaid trajectory shows the transition of communities through periods of disturbance.

There were significant differences among the four disturbance periods at Scott Reef (2 Way ANOSIM across all locations: p = 0.1%, Global R statistic = 0.779), and all pairwise groups were significantly different from each other (Table 3.1.1).

Table 3.1.1 Pairwise comparisons in a two-way ANOSIM test carried out on benthic data at Scott Reef between 1994 and 2008 (significance level < 5%). Pairs are ranked in decreasing order of the R statistic. R values close to a value of one represent a situation where all samples within each group are more similar to each other than to any of the samples from other groups. R values close to zero imply that similarities within and between groups are the same.

Period	R Statistic	Significance Level %
94-97, 98-01	0.962	0.1
94-97, 02-05	0.892	0.1
98-01, 06-09	0.761	0.1
02-05, 06-09	0.756	0.1
94-97, 06-09	0.694	0.1
98-01, 02-05	0.461	0.1

In the years prior to the bleaching event, communities grouped closely together (Fig. 3.1.2). However, after the bleaching there was a significant shift (p = 0.1%) to an entirely different community, as reflected in the very high R statistic (0.962) for the 94-97 / 98-01 pair (Table 3.1.1). In 2002 to 2005 there was moderate recovery towards pre-bleaching structure, although Cyclone Fay impacted communities strongly in 2004. This entire period remained significantly different from both the pre-bleaching and severe bleaching periods (p = 01.%). The R statistic for the 94-97 / 02-05 pair was high (0.892), whereas R for the 98-01 / 02-05 pair was moderate (0.5), indicating that the recovery period was still far more similar to the severe bleaching period than the pre-bleaching period. Communities in the 2006-2009 period were also significantly different (p = 0.1%), however there was further recovery towards the pre-bleaching structure, as indicated by the R statistic for the 94-97 / 06-09 pair which had decreased to 0.694.

Table 3.1.2 Pairwise comparisons in a two-way ANOSIM test carried out on benthic data at Scott Reef for all years from 1994 and 2008. Pairs are ranked in decreasing order of the R statistic.

Location Pair	R Statistic	Significance Level %	Location Pair	R Statistic	Significance Level %
SL2, SL4	0.988	0.1	SL1, SL3	0.553	0.1
SL2, SS2	0.954	0.1	SL4, SS2	0.534	0.1
SL2, SL3	0.935	0.1	SL1, SS2	0.518	0.1
SL2, SS1	0.911	0.1	SL1, SL4	0.507	0.1
SL2, SL1	0.89	0.1	SL1, SS1	0.478	0.1
SL4, SS1	0.724	0.1	SL3, SL4	0.477	0.1
SL3, SS2	0.672	0.1	SS1, SS2	0.216	0.1
SL3, SS1	0.628	0.1			

Spatial differences in community structure

In addition to the difference between time periods, there were significant differences among locations at Scott Reef (2 Way ANOSIM across all periods: p = 0.1%, Global R statistic = 0.652), and all pairwise location groups were significantly different from each other (Table 3.1.2). Individual locations at Scott Reef followed a similar pattern of change through the four disturbance periods (Fig. 3.1.3). Communities that resided on the far left of the ordination prior to bleaching subsequently crossed to the far right of the plot directly after bleaching, and then slowly progressed back towards pre-beaching structure from 2002 onwards.

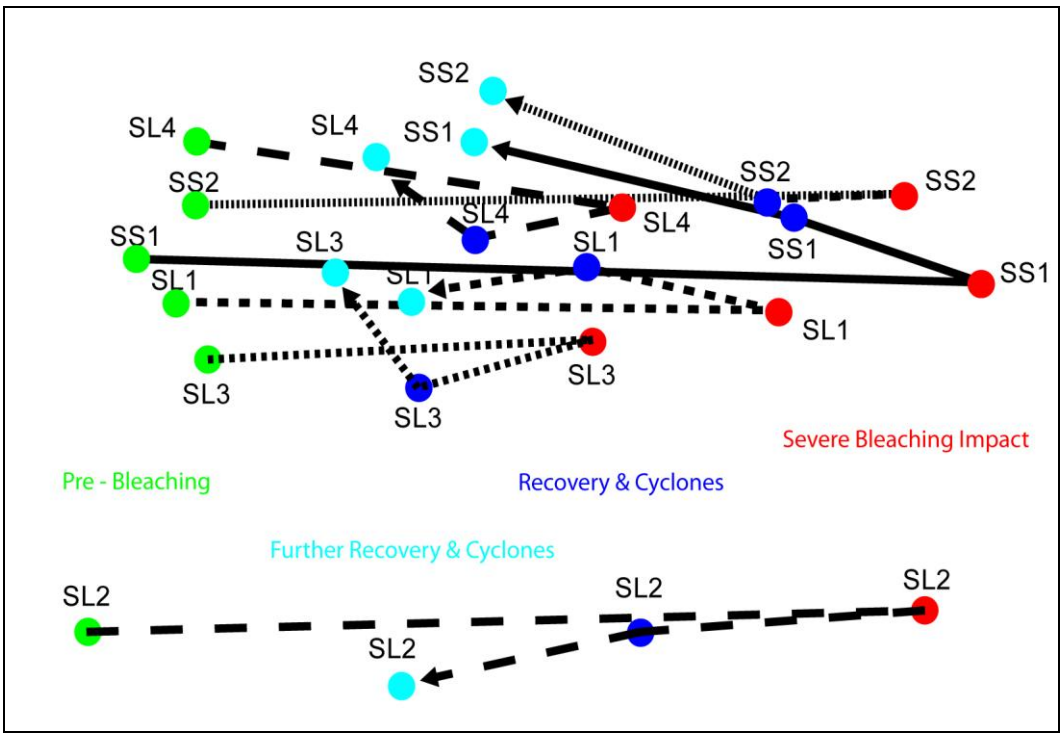


Fig. 3.1.3 MDS ordination of benthic communities at six Scott Reef locations (SL1, SL2, SL3, SL4, SS1, SS2) through the four major periods of disturbance and recovery.

The ordination shows that communities grouped strongly according to location. In particular, SL2 separated consistently from other locations (Fig. 3.1.3), grouping in a distinct band below all other locations, as reflected in the five highest pairwise R statistics (0.89 to 0.988) in Table 3.1.2. There was considerably less separation between other locations (R ranging from 0.216 to 0.724), however locations tended to maintain similar vertical positions in the ordination relative to each other through time (Fig. 3.1.3). Locations SS1 and SS2 consistently grouped very closely together, with an R statistic (0.216).

Based on the pairwise test results in Table 3.1.2, samples across all years grouped into four main location groups associated with their coarse geographical position: SS1/SS2 (outside

eastern slope), SL3/SL4 (northern lagoon), SL1 (East Hook), and SL2 (southern lagoon). These groupings occurred consistently through all disturbance periods, with the exception of the pre-bleaching period in which SL1 grouped with SL4, whereas SL3 remained separate. These data suggest that location-based effects are one of the primary drivers of community structure across Scott Reef, even in the face of severe and repeated disturbance.

Periods of impact and recovery: Pre-bleaching (1994-1997)

From 1994 to 1997 coral communities at Scott Reef remained in a relatively stable configuration with high levels of coral cover. In the absence of major disturbances there were only small changes in community structure, with the exception of a minor shift towards the increased dominance of Acroporidae corals. In April 1995 category 4 Cyclone Chloe tracked to the east of Scott Reef with winds of approximately 185km per hour, but coral communities suffered little impact.

Within this period there were significant differences among locations (1 Way ANOSIM: p = 0.1%, Global R statistic = 0.598). Based on pairwise test results, samples in the period grouped into four main location groups: SS1/SS2 (p = 0.3%, R = 0.206), SL1/SL4 (p = 0.1%, R = 0.467), SL3 (p = 0.1%, R = 0.898), and SL2 (p = 0.1%, R = 0.898). However, while the groupings were significantly different from each other, all locations grouped tightly in the MDS ordination with the exception of SL2 (Table 3.1.3[3]). Hard coral cover was high at location SL2 (62%) and the SS1/SS2 group (56/44%), and lower for the SL1/SL4 group (39/36%) and SL3 (41%) (Table 3.1.4[2]). Each location showed only minor changes in community structure within the 1994-1997 period, as illustrated by the consistent tracking patterns on the left of the MDS ordination (Table 3.1.4[3]).

Differences between location groups in the 1994-1997 period were driven by the different benthic categories that defined each group. The SS1/SS2 group was typified primarily by coralline algae, massive *Porites*, encrusting *Montipora*, soft coral, other benthos, and *Isopora palifera*, and the benthic categories that most discriminated the group from other locations were *Isopora brueggemanni*, coralline algae, turf algae, corymbose *Acropora*, sponge, soft coral, and abiotic benthos (Appendix 3.1.1).

The SL1/SL4 group was relatively similar, being typified by massive *Porites*, soft coral, abiotic benthos, encrusting *Montipora*, coralline algae and turf algae. The benthic categories that most discriminated the group from other locations were turf algae, coralline algae, soft coral, sponge, other algae, and corymbose *Acropora*. The single location in the SL3 group was also typified by similar benthos to the above two groups: abiotic benthos, turf algae, coralline algae, massive *Porites*, soft coral, Isopora palifera, and encrusting *Montipora*. Benthic categories that most discriminated the group from other locations were sponge, turf algae, coralline algae, other algae, abiotic benthos and *Isopora brueggemanni*.

In contrast to all of the above groups, SL2 was typified by a highly distinct assemblage (Table 3.1.4[3]) that was driven largely by branching *Acropora*, foliose coral, *Seriatopora hystrix*,

hispidose *Acropora*, turf algae, and encrusting *Montipora*. The benthic categories that most discriminated the group from other locations were foliose coral, branching *Acropora*, hispidose *Acropora*, massive *Porites*, soft coral, and coralline algae categories (Appendix 3.1.1).

Table 3.1.3 Changes in coral cover and community structure through time and space: Scott Reef, 1994-2008. Notes: [1] Typical community as shown by an indicative photo for the period. [2] Mean hard coral cover for each period, shown by location. [3] MDS of community structure for each period, shown by location (maximum stress 0.13). [4] Significant differences between locations for each period (1 Way ANOSIM). Legend: SL1 SL2 SL3 SL4 SS1 SS2

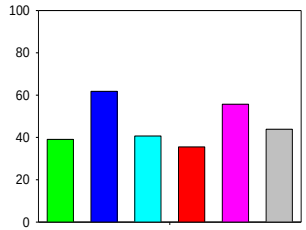
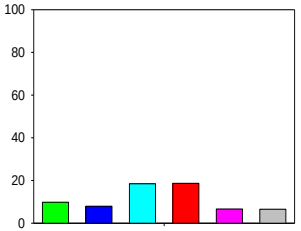
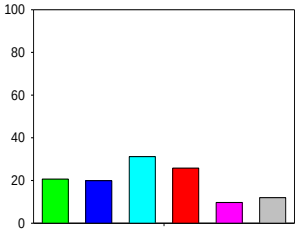
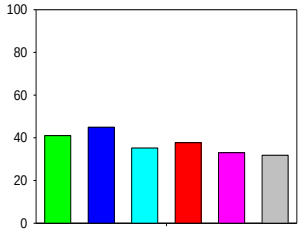
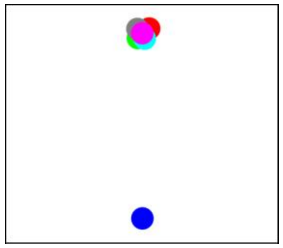
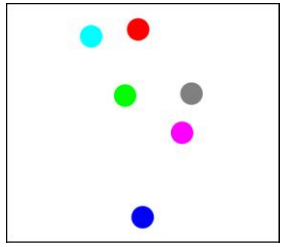
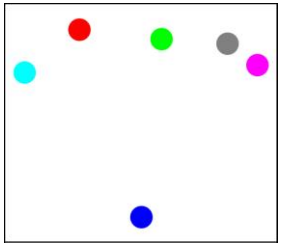
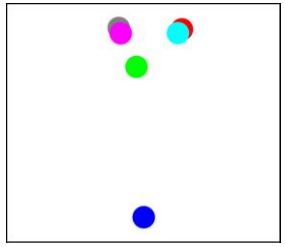
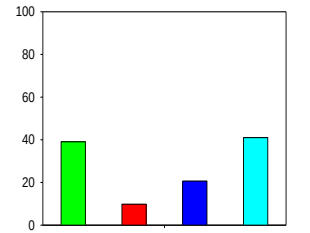
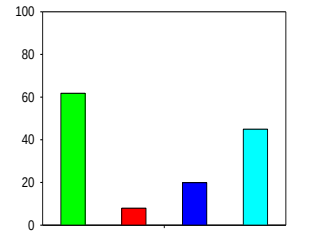
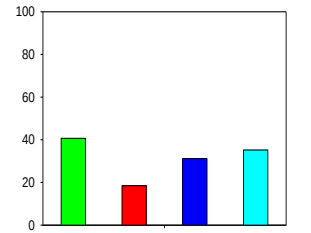
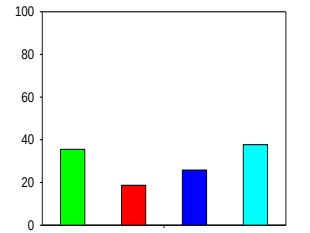
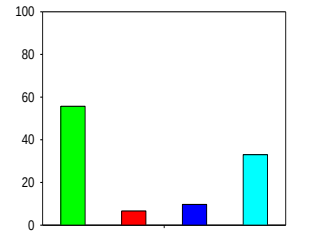
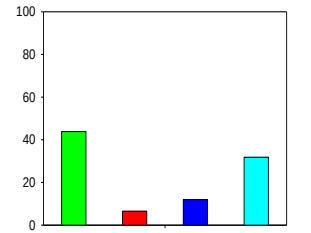
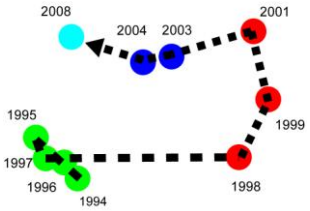
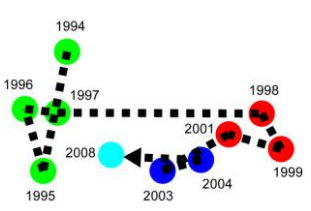
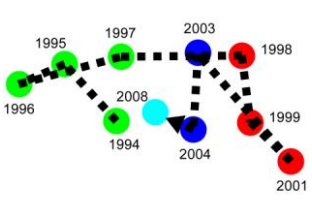
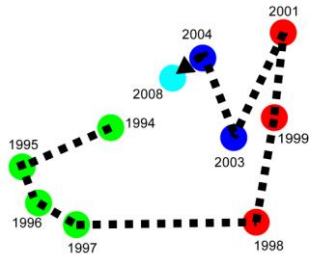
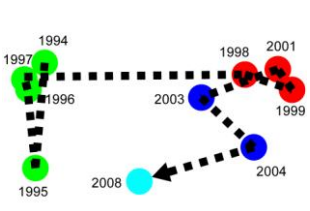
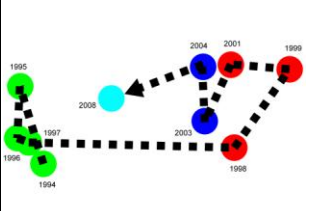
	1994-1997 Pre-Bleaching	1998-2001 Severe Bleaching Impact	2002-2005 Recovery & Cyclones	2006-2009 Further Recovery & Cyclones
Typical Community[1]				
Hard Coral Percent Cover[2]				
Community Structure[3]				
Location Differences[4]	There were significant differences among locations for the pre-bleaching period (1 Way ANOSIM: p = 0.1%, Global R statistic = 0.598). All pairwise location tests were significant (p = 0.1 to 0.3%, R statistic = 0.206 to 0.992).	There were significant differences among locations for the severe bleaching period (1 Way ANOSIM, p = 0.1%, Global R statistic = 0.698). All pairwise location tests were significant (p = 0.1 to 2%, R statistic = 0.267 to 0.986).	There were significant differences among locations for the recovery and cyclones period (1 Way ANOSIM, p = 0.1%, Global R statistic = 0.772). All pairwise location tests except SS1/SS2 were significant (p = 0.8 to 0.8%, R statistic = 0.52 to 0.996).	There were significant differences among locations for the second recovery and cyclones period (1 Way ANOSIM, p = 0.1%, Global R statistic = 0.947). Pairwise location tests could not be tested for meaningful significance due to a low number of test permutations (only one year was surveyed in this period).

Table 3.1.4 Changes in coral cover and community structure through space and time: Scott Reef, 1994-2008. Notes: [1] Typical community as shown by an indicative photo for the location. [2] Mean hard coral cover for each location, shown by period. [3] MDS of community structure for each location, shown by period (maximum stress 0.12). [4] Significant differences between periods for each location (1 Way ANOSIM). Legend: Pre-Bleaching Severe Bleaching Recovery & Cyclones Further Recovery & Cyclones.

	SL1 Lagoon	SL2 Lagoon	SL3 Lagoon	SL4 Slope	SS1 Slope	SS2 Slope
Typical Community[1]						
Hard Coral Percent Cover[2]						
Community Structure[3]						
Time Period Differences[4]	There were significant differences among time periods at SL1 (1 Way ANOSIM: p = 0.1%, Global R statistic = 0. 0.884). All pairwise time period tests were significant (p = 0.1 to 1.8%, R statistic = 0.622 to 0.987).	There were significant differences among time periods at SL2 (1 Way ANOSIM: p = 0.1%, Global R statistic = 0.867). All pairwise time period tests were significant (p = 0.1 to 1.8%, R statistic = 0.636 to 1.0).	There were significant differences among time periods at SL3 (1 Way ANOSIM: p = 0.1%, Global R statistic = 0.616). All pairwise time period tests were significant except 02-05/06-09 (p = 0.1 to 2.7%, R statistic = 0.295 to 0.919).	There were significant differences among time periods at SL4 (1 Way ANOSIM: p = 0.1%, Global R statistic = 0.5572). All pairwise time period tests were significant except 98-01/02-05 (p = 0.1 to 3.6%, R statistic = 0.362 to 0.873).	There were significant differences among time periods at SS1 (1 Way ANOSIM: p = 0.1%, Global R statistic = 0.886). All pairwise time period tests were significant (p = 0.1 to 1.8%, R statistic = 0.617 to 1.0).	There were significant differences among time periods at SS2 (1 Way ANOSIM: p = 0.1%, Global R statistic = 0.860). All pairwise time period tests were significant except 98-01/02-05 (p = 0.1 to 1.8%, R statistic = 0.959 to 1.0).

Periods of impact and recovery: Severe bleaching and early recovery (1998-2001)

In early 1998, a temperature-induced mass bleaching event occurred at Scott Reef as a result of sustained, elevated sea water temperatures. Widespread coral mortality occurred across Scott Reef causing a loss of more than 75% of all hard coral cover (Table 3.1.3[2]). Turfing algae rapidly colonised the newly available substrata, resulting in increases in algae cover of more than 185%. This did not include the macroalgae, the cover of which remained less than 1% across all locations after the beaching. Coral communities recovered poorly between 1998 and 2001, with only 25% mean recovery to pre-bleaching levels.

The bleaching also caused major changes in community structure, with all locations shifting to an entirely new community after bleaching (Table 3.1.4[3]). Major changes in benthic community structure were characterised by a large increase in turfing and coralline algae, the reduced cover of branching, submassive, encrusting and soft corals, and an increase in massive corals (Appendix 3.1.1).

Changes in coral community structure were driven largely by variation in the abundance of corals from the families Acroporidae, Pocilloporidae, Poritidae, and Faviidae. Whereas pre-bleaching communities were primarily characterised by branching *Acropora* (47%) and other branching corals (9%), communities after the bleaching event were largely characterised by the high abundance (45%) of massive *Porites* corals.

Within the severe bleaching period there were significant differences among locations (1 Way ANOSIM, p = 0.1%, Global R statistic = 0.698). Based on the pairwise test results, samples in the period grouped into four main location groups: SS1/SS2 (p = 2%, R = 0.267), SL3/SL4 (p = 0.7%, R = 0.382), SL1 (p = 0.1%, R = 0.852), and SL2 (p = 0.1% R = 0.852). These groups matched those in the earlier pre-bleaching period, with the exception of the SL3/SL4 and SL1 grouping, which switched from the previous grouping of SL1/SL4 and SL3. After the bleaching, communities spread apart strongly in multidimensional space as they were differentially affected by the disturbance (Table 3.1.4[3]). The clear distinction between SL2 and all other locations that was observed prior to the bleaching was maintained in this period.

SL2 and SS1/SS2 were impacted very strongly by the bleaching (Table 3.1.4[2]), experiencing >85% relative decreases in cover, while SL1, SL3, and SL4 were affected less strongly (47-77%). Hard coral cover was highest for the SL3/SL4 group (18/19%), followed by SL1 (10%), SL2 (8 %), and the SS1/SS2 group (7/7 %) (Table 3.1.4[2]). These changes in percent cover from the previous period reflect markedly different locational responses to the bleaching event.

Overall changes in community structure after the bleaching were driven by the new benthic categories that defined each of the location communities. The SS1/SS2 group was primarily typified by turf algae, coralline algae, massive *Porites*, other algae, abiotic benthos, and soft coral, and the benthic categories that discriminated the group most from other locations were coralline algae, turf algae, other algae, abiotic benthos, soft coral, and encrusting *Montipora* (Appendix 3.1.2).

The SL3/SL4 group was relatively similar, being typified by turf algae, coralline algae, massive *Porites*, abiotic benthos, soft coral, encrusting *Montipora*, and encrusting coral. The benthic categories that most discriminated the group from other locations were coralline algae, turf algae, branching *Acropora, Isopora brueggemanni*, massive *Porites*, abiotic benthos, and encrusting *Montipora*.

In contrast, location SL1 stood out from the other groups, being typified by turf algae, coralline algae, massive *Porites*, other algae, abiotic benthos, and soft coral, and discriminated from other locations by other algae, coralline algae, turf algae, abiotic benthos, soft coral, and encrusting *Montipora*.

SL2 group continued to remain highly distinct from all other locations, being typified predominately by turf algae, coralline algae, other coral, abiotic benthos, foliose coral, and other algae, and discriminated from other locations by coralline algae, turf algae, massive *Porites*, soft coral, other coral, abiotic benthos, and encrusting *Montipora* (Appendix 3.1.2).

Periods of impact and recovery: Post-bleaching and cyclone disturbance (2002-2005)

From 2002 to 2005 coral cover started to increase more rapidly with 43% recovery to mean pre-bleaching levels. However, in early 2004 category 5 Cyclone Fay tracked directly over Scott Reef, with wind speeds greater than 300 km per hour. The storm caused severe damage to coral communities on the exposed eastern side of Scott Reef, resulting in decreases in coral cover at SL2, SS1 and SS2.

Coralline and turfing algae remained the dominant benthic groups in the period (46% and 25% respectively) and levels of soft corals remained low (3%). The branching *Acropora* returned to 31% of previous levels, whereas massive *Porites* and tabulate corals returned to 75% and 97% of their previous cover respectively. Community structure in the 2002-2005 period remained very different to the pre-bleaching period, particularly at locations that were previously dominated by branching corals. The period was characterised by only minor changes in structure across all locations (Table 3.1.4[3]). Consequently, changes in community structure between the 1998-2001 and 2002-2005 periods were the least significant of all periods due to the low net increases in recovery and very similar combinations of typifying benthic categories (Appendix 3.1.1).

Within the 2002-2005 recovery period there were significant differences among locations (1 Way ANOSIM, p = 0.1%, Global R statistic = 0.772), and all pairwise location tests except SS1/SS2 were significant (p = 0.8 to 0.8%, R statistic = 0.52 to 0.996). Based on the pairwise test results, samples in the period grouped into four main location groups: SL3/SL4 (p = 0.8%, R = 0.520), SL1 (p = 0.8%, R = 0.988), SL2 (p = 0.8%, R = 0.988), and SS1/SS2 (p = 59.5%).

These location groups matched those in the previous period, reflecting the ongoing influence of the bleaching on community structure and the habitat-driven effects associated with each

location. With the exception of SL2 and SL4, communities at each location continued to move further apart as they tracked away from their pre-bleaching structure (Table 3.1.4[3]). As in all previous periods, locations SL2 and SL4 tracked a consistent distance apart from each other through time.

Cover of hard corals (Table 3.1.4[2]) was highest at the SL3/SL4 group (31/26 %), followed by SL1 (21%) and SL2 (20%). The SS1/SS2 group had the lowest cover (10/12%). All groups maintained their position relative to each other when compared with the previous disturbance period; SL3/SL4 continued to have the highest cover of all groups, followed by SL1, SL2, and the SS1/SS2 group.

Changes in community structure in 2002-2005 were driven by the benthic categories that defined each of the location communities. The SS1/SS2 group was primarily typified by turf algae, coralline algae, massive *Porites*, abiotic benthos, encrusting coral, and encrusting *Montipora*, and the benthic categories that most discriminated the group from other locations were soft coral, abiotic benthos, coralline algae, turf algae, massive *Porites*, and corymbose *Acropora* (Appendix 3.1.3).

Similarly, the SL3/SL4 group was typified by turf algae, coralline algae, abiotic benthos, massive *Porites*, soft coral, and encrusting coral, however the benthic categories that most discriminated the group from other locations were turf algae, coralline algae, *Isopora brueggemanni*, massive *Porites*, *Seriatopora hystrix*, soft coral and branching *Acropora*.

The single location in the SL1 group was typified primarily by turf algae, coralline algae, massive *Porites*, soft coral, abiotic benthos, encrusting coral, corymbose *Acropora* and encrusting *Montipora*. The benthic categories that most discriminated the group from other locations were coralline algae, turf algae, soft coral, encrusting *Montipora*, corymbose *Acropora*, and *Seriatopora hystrix*.

In contrast to all of the above groups, SL2 was typified predominately by turf algae, coralline algae, other coral, encrusting coral, *Seriatopora hystrix*, foliose coral, abiotic benthos and corymbose *Acropora*. The benthic categories that most SL2 from other locations were turf algae, other coral, coralline algae, foliose coral, soft coral, and abiotic benthos.

Periods of impact and recovery: Post-bleaching and further cyclone disturbance (2006-2009)

From 2006 to 2009 benthic communities continued to recover to pre-bleaching levels of cover and structure against a backdrop of frequent, low-intensity disturbance. In 2007, Cyclone George tracked close to Scott Reef causing minor localised damage, predominately to the exposed, shallow coral communities at SL3 and SL4. Between 2005 and 2007, three further cyclones tracked close to Scott Reef (TC Raymond 2005, TC Clare 2006, and TC Glenda 2006) however these were relatively small systems and did not cause major disturbance effects. In late 2008, NOAA Coral Reef Watch issued a bleaching alert for Scott

Reef as a result of sustained periods of higher than average water temperature, however there was no evidence of coral bleaching during this period.

In 2008, a decade after the bleaching, mean hard coral cover at Scott Reef had increased to 37%, a recovery of 81% to pre-bleaching levels (42%). Recovery of soft corals was substantially slower, with cover in the period (9%) approximately half (48%) of that prior to bleaching. Locations which had the highest relative decreases in percent cover after the bleaching (SL2, SS1, and SS2) had still not returned to pre-bleaching cover by 2008, whereas locations that had the lowest decreases in cover after the bleaching (SL1, SL3, SL4) had recovered to similar or greater levels of coral cover.

Within the 2006-2009 period, all communities began to track strongly towards pre-bleaching structure, as individual locations approached points in multidimensional space close to values in 1994-1997 (Table 3.1.3[3]). Locations also clustered more closely towards the tight spatial distribution that was seen prior to bleaching (Table 3.1.4[3]). Community structure in the period was distinguished from that prior to the bleaching by an increased cover of coralline algae, turfing algae, and tabulate corals, and a decreased cover of branching *Acropora*, soft corals and branching non-*Acropora* (Appendix 3.1.1). Turf and coralline algae remained the dominant benthic groups across all locations, with higher percent cover than pre-bleaching levels. Notable changes between the previous period and the 2006-2009 period were the substantial increases in tabulate corals and sponges. Tabulate corals increased across most locations to a mean cover of 5% compared to <1% prior to bleaching. Sponges also had large relative increases in cover, to a mean of 3% compared to <1% before bleaching.

Within the 2006-2009 period there were significant differences among locations (1 Way ANOSIM, p = 0.1%, Global R statistic = 0.947). Pairwise location tests could not be tested for meaningful significance due to a low number of test permutations (only one year was surveyed in this period). However, visual examination of the MDS plot in this period indicated that samples in the period grouped into the same four location groups seen in the previous two periods: SS1/SS2, SL3/SL4, SL1, and SL2 (Table 3.1.4[3]). Hard coral cover (Table 3.1.4[2]) was highest at SL2 (45%), followed by SL1 (41%), the SL3/SL4 group (35/38%) and SS1/SS2 group (33/32%). Locations changed their percent cover relative to each other when compared with the previous period as they tracked back towards original levels of pre-bleaching cover.

Associated changes in community structure in the 2006-2009 period are reflected in the benthic categories that defined each of the location communities. The SS1/SS2 group was primarily typified by turf algae, coralline algae, abiotic benthos, encrusting *Montipora*, massive *Porites*, tabulate *Acropora*, Pocilloporidae, and encrusting coral, and the benthic categories that most discriminated the group from other locations were coralline algae, soft coral, abiotic benthos, tabulate *Acropora*, *Seriatopora hystrix*, massive *Porites*, and encrusting *Montipora* (Appendix 3.1.4).

The single location in the SL1 group was similar to the SS1/SS2 group, being typified primarily by turf algae, coralline algae, tabulate *Acropora*, massive *Porites*, soft coral, encrusting

Montipora, branching *Acropora*, and sponge. The benthic categories that most discriminated the group from other locations were coralline algae, abiotic benthos, soft coral, and tabulate coral.

The SL3/SL4 group was typified by turf algae, abiotic, coralline algae, massive *Porites*, soft coral, encrusting *Montipora*, encrusting coral, and other massives. The benthic categories that most discriminated the group from other locations were coralline algae, soft coral, tabulate *Acropora*, massive *Porites*, *Isopora brueggemanni*, abiotic benthos, and turf algae.

In contrast to all of the above groups, SL2 was typified predominately by turf algae, tabulate *Acropora*, abiotic benthos, branching *Acropora*, coralline algae, other coral, hispidose *Acropora*, and foliose coral. The benthic categories that most discriminated the group from other locations were other coralline algae, other coral, hispidose *Acropora*, massive *Porites*, foliose coral, soft coral, and branching *Acropora*.

Discussion

Benthic communities at Scott Reef are in a long phase of recovery after temperature-induced bleaching and cyclone disturbance over the last 15 years. Recent data from 2008 indicate that most communities show strong signs of recovery to pre-bleaching levels of percent cover and community structure.

The thermal-induced bleaching in 1998 was catastrophic and killed more than 75% of corals across the Scott Reef system (Smith et al. 2008a). This single large-scale disturbance event has been the most important driver of change in benthic communities at Scott Reef since monitoring began in 1994 and the impacts of the bleaching are still evident in all communities across Scott Reef. In addition to the mass bleaching, episodic cyclones have also played a key role in structuring communities at different locations. In 2004 category 5 Cyclone Fay severely damaged coral communities at several locations, further slowing rates of recovery. Soon after, category 2 Cyclone George tracked close to the reef in 2007, but the lower intensity of the system caused less severe and more localised impacts. In 2008, the cumulative impact of these three major disturbance events, each operating on different spatial and temporal scales, remains the primary influence on the cover and structure of benthic communities at Scott Reef since monitoring began.

The recovery of coral communities at Scott Reef has been relatively rapid, despite the geographic isolation of the reef and the low number of neighbouring systems that can supply coral recruits. Post-disturbance recovery timeframes of one to two decades have been reported in other studies (Connell 1997; Halford et al. 2004; Emslie et al. 2008), and very isolated reefs such as the Maldives and Chagos have shown various levels of recovery after the 1998 beaching (Graham et al. 2008; Sheppard et al. 2008). Benthic assemblages at Scott Reef are therefore relatively consistent with other reefs with regards to the recovery of coral cover and structure after disturbance. This contrasts with a recent French Polynesian study

which found that while coral cover recovered rapidly after multiple large-scale disturbances, the community structure remained plastic (Adjeroud et al. 2009).

Importantly, many of these other studies examined reefs that are considerably larger or more interconnected than the Scott Reef system. Scott Reef is highly isolated and Halford and Caley (2009) note that the reef may be more comparable to the Seychelles than other systems. Given that the Seychelles recovered poorly after the bleaching event (Graham et al. 2006), it is important to understand potential reasons for the strong recovery of Scott Reef communities over the last decade.

Smith et al. (2008a) suggest that the relatively pristine offshore waters that surround Scott Reef provide an environment that is suitable for fast coral growth and survival, thereby promoting increased system resilience (Carilli et al. 2009; Wooldridge and Done 2009). Halford and Caley (2009) also suggest that the deeper lagoon habitats at Scott Reef represent potential refugia for the shallow water communities that are under threat from the increasing effects of disturbance. However, these refugia can only be effective if the deep and shallow communities at Scott Reef have functionally connected populations of common species.

Scale and frequency of disturbance

The frequency and intensity of bleaching and cyclone events are predicted to increase as a result of climate change (Hoegh-Guldberg et al. 2007), and these parameters will play an increasingly important role in the future resilience of reefs worldwide.

At Scott Reef, the bleaching in 1998 caused widespread coral mortality across an entire reef system. The impact of the bleaching varied among locations, but was consistent among sites within locations, suggesting that conditions responsible for the bleaching operated on spatial scales of kilometres (Smith et al. 2008a). Thus, the bleaching was a severe and acute disturbance acting over large spatial-scales.

In contrast, cyclones caused acute disturbances of moderate severity that acted over local scales causing heterogeneous impacts to benthic communities across different locations (Gilmour and Smith 2006). Cyclones are relatively frequent in the region with at least one cyclone tracking close to Scott Reef each year, but their impacts to communities are likely restricted to once every five or ten years, and impacts as severe as those from Cyclone Fay (a category 5 cyclone) are less common. Thus, cyclones were periodic acute disturbances of moderate severity acting over local scales.

Spatial effects

Significant differences in the structure of benthic communities have existed between locations at Scott Reef since monitoring began in 1994. These spatial patterns are the result of the particular combination of community structure, aspect and history at each location and

remain evident throughout the monitoring program against a constantly changing backdrop of multiple disturbance events.

Different patterns of impact and recovery are visible in the trajectories of change for each location. Locations that had the highest relative decreases in percent cover after the bleaching (SL2, SS1, and SS2) had not returned to pre-bleaching cover by 2008. In contrast, locations that had the lowest decreases in cover after the bleaching (SL1, SL3, SL4) had recovered to similar or greater levels of coral cover. In general, hard coral cover and structure at SL1, SL3, SL4, and SS2 is relatively similar in 2008 to that prior to the bleaching, whereas locations SL2 and SS1 are still on the path to full recovery.

After the broad-scale spatial effects of the bleaching event, changes in community structure and recovery were driven primarily by the differential exposure of locations to local-scale cyclone forces. The impact of Cyclone Fay varied considerably according to the relative exposure of each site; locations on the eastern flank that were exposed to waves generated by the cyclone were impacted most strongly (SS1, SS2, SL2), while those at the top of the lagoon that had a sheltered aspect were less affected (SL1, SL3, SL4). The impact of Cyclone George in 2006 was less severe than Fay, however it also produced highly localised effects on community structure; the cyclone negatively impacted the recovery of SL3 and SL4 communities and caused further shifts in community structure. Other locations at Scott Reef were impacted less severely by Cyclone George and their recovery trajectories continued towards their pre-bleaching state.

Impact and mortality

As noted above, different patterns of mortality and recovery after disturbance among locations at Scott Reef reflect the particular combination of physical and biological parameters including water temperature, tidal flow, eddies and currents, wind and swell exposure, larval supply, existing community structure, colony size, and growth form at each location. At SL3 and SL4, local hydrodynamic conditions including strong tidal currents helped to maintain cooler water temperatures during the bleaching and reduce the impact on coral communities (Steinberg et al. 2003). Close proximity to the deep water channel between North and South Reefs and the potential for cold water intrusions and upwelling (Steinberg et al. 2006) may have also reduced impacts of bleaching at SL4 . In contrast, extended water retention times in the lagoon (Steinberg et al. 2003) may have exacerbated the bleaching impact at SL2. Site aspect and exposure to wave energy have also played an obvious role in determining the impact of tropical cyclones on coral communities at Scott Reef; physical locations with high exposure to storm swells and wind were affected strongly, while other nearby locations suffered only minor damage.

Both bleaching and cyclone events exert differential impacts on taxonomic groups and growth morphologies, and differences in life history traits among these groups of corals influence their susceptibility to disturbances and their rates of recovery. In turn, these life history strategies drive system-wide changes in community structure, with the potential for previously

abundant but highly susceptible species to be replaced by suites of other species after disturbance (Ostrander et al. 2000; Aronson et al. 2002). Corals have a range of susceptibility responses to bleaching, and in general, branching and tabulate corals from the *Acropora* genus and the family Pocilloporidae have the highest bleaching rates and subsequent rates of mortality (Marshall and Baird 2000; Loya et al. 2001; Baird and Marshall 2002; McClanahan et al. 2004). In contrast, encrusting and massive species from the families Poritidae and Faviidae are typically less likely to bleach, while a complex of other less common taxa may suffer only minor bleaching effects. At Scott Reef, the Acroporidae were strongly affected by the 1998 bleaching while the Poritidae were only moderately affected, and it is likely that the Poritidae were more resistant to bleaching as a result of experiencing partial rather than whole colony mortality (Brown and Suharsono 1990; Loya et al. 2001). Impact and recovery from disturbances clearly affected community structure through time (McClanahan et al. 2007) and both the bleaching and cyclone events impacted the locally common branching *Acropora* more than other corals. However, while *Acropora* corals show high mortality rates after disturbance, these species are also able to recover more rapidly, with accelerating levels of cover achieved via fast growth rates and strong recruitment (Glynn 1993). In the absence of further disturbance, the branching *Acropora* are likely to return to dominate benthic cover.

Recovery

The capacity of coral reef communities to recover after disturbance is determined by many factors, including scale and severity of the disturbance, previous history of disturbance, coral cover and community structure, subsequent disturbances, and the demographic rates of recruitment, growth and survival (Colgan 1981; Brown and Suharsono 1990; Glynn 1993; Hughes and Connell 1999; Hughes et al. 2000; Ostrander et al. 2000; Aronson et al. 2002). At Scott Reef, disturbance impacts were clearly influenced by pre-bleaching cover, and these levels were important in determining overall recovery (Smith et al. 2008a). Locations with the highest pre-bleaching levels of coral cover suffered the highest rates of mortality, and subsequently the largest changes in community structure. Locations that were worst affected by the bleaching recovered more slowly, while those that were least affected recovered quickly. In addition, after the bleaching most surviving corals were small and contributed to only low levels of cover and recruitment. Subsequently, even though the secondary impact of Cyclone Fay was severe, the impact appeared relatively minor due to the very low levels of cover and a community structure that was highly modified due to bleaching. Similarly, very high algal cover after bleaching reduced the ability of new corals to re-colonise, further compounding the slow rates of recovery. Clearly, in systems affected by multiple disturbances, the cascading effects of pre-existing structure may span periods of disturbance and modify future trajectories of recovery. These complex patterns of recovery illustrate the degree to which recent or historical disturbance can play a major role in shaping the current structure of benthic communities (Hughes 1989; McClanahan et al. 2007).

Recovery was also tied strongly to recruitment, as low rates of recovery can result from reduced adult stock after catastrophic mortality. Coral recovery is usually driven by the arrival of new individuals on the reef (Connell 1997), however recruitment at Scott Reef was

reduced by more than 95% after the bleaching (unpublished data). This massive decline in recruitment was the result of severe mortality combined with minimal larval input from exogenous reef systems. Early increases in coral cover were therefore driven primarily by the growth of survivors of the bleaching, rather than the recruitment and growth of new corals (Smith et al. 2008b). Thereafter, there were size-associated increases in cover, and reproductive maturation and fecundity, resulting in additional cycles of recruitment and growth.

In 2008, community structure at Scott Reef was relatively similar to that in the pre-bleaching period from 1994-1997. Major differences between the two periods included an increased cover of tabulate corals and coralline and turfing algae, and the reduced cover of branching *Acropora* and soft corals. The high cover of tabulate *Acropora* corals in recent years may reflect processes of succession whereby the previously dominant branching *Acropora* have been unable to maintain their earlier ecological position due to high susceptibility to disturbance. Similarly, the brooding coral *Isopora brueggemanni* appears highly susceptible to thermal bleaching and cyclone disturbance. This species was dominant before the bleaching, and is likely to return to dominance in the community at some point in the future as a result of very high growth rates and strong local recruitment. In contrast, massive *Porites* corals were impacted less strongly by the bleaching, however their low growth rates and reproductive output have resulted in a protracted period of recovery. The degree to which all of these species and the community in general return to their previous levels of cover and structure will depend on future disturbances at Scott Reef. Residual impacts of the major bleaching event, combined with the predicted increases in local cyclone severity due to climate change (Walsh and Pittock 1998), may cause compounding effects that compromise overall system resilience and modify trajectories of recovery.

Conclusion

Over historical timeframes, coral reef systems have been resilient to major disturbances (Pandolfi et al. 2003), however the increasing frequency and scale of disturbance (Hughes et al. 2003) has important implications for the resilience of coral reefs worldwide. The offshore nature of the Scott Reef system, combined with the absence of commercial fishing and many direct human stressors, means it is relatively unaffected by anthropogenic impacts that are common on other coral reefs. However, the most notable exception is traditional fishing of some prized stocks, which includes the overfishing of sea cucumbers, trochus, and reef sharks. Communities at Scott Reef ten years after the bleaching showed resilience to a climate-driven disturbance regime that acted over multiple spatial and temporal scales. However, isolated coral reefs remain highly vulnerable to disturbance (Graham et al. 2006) and the resilience of coral communities at Scott Reef will be severely tested by predicted increases in the frequency and scale of future disturbance.

References

Adjeroud M, Michonneau F, Edmunds PJ, Chancerelle Y, Lison de Loma T, Penin L, Thibaut L, Vidal-Dupiol J, Salvat B, Galzin R (2009) Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef. Coral Reefs 28: 775-780

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

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

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

Berkelmans R, De'ath G, Kininmonth S, Skirving WJ (2004) A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. Coral Reefs 23: 74-83

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

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

Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90: 1478–1484

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

Carilli JE, Norris RD, Black BA, Walsh SM, McField M (2009) Local Stressors Reduce Coral Resilience to Bleaching. Public Library of Science One 4(7): e6324

Cheal AJ, Coleman G, Delean S, Miller I, Osborne K, Sweatman H (2002) Responses of coral and fish assemblages to a severe but short-lived tropical cyclone on the Great Barrier Reef, Australia. Coral Reefs 21: 131-142

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

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. PRIMER-E, Plymouth

Clarke KR, Green RH (1988) Statistical design and analysis for a 'biological effects' study. Marine Ecology Progress Series 46: 213-226

Clarke KR, Warwick RM (2001) Change in Marine Communities: An Approach to Statistical Analysis and Interpretation (2nd ed.) PRIMER-E. Plymouth

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 (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 (1992) Constancy and change in some Great Barrier Reef coral communities: 1980–1990. American Zoologist 32: 655-662

Edwards AJ, Clark S, Zahir H, Rajasuriya A, Naseer A, Rubens J (2001) Coral Bleaching and Mortality on Artificial and Natural Reefs in Maldives in 1998, Sea Surface Temperature Anomalies and Initial Recovery. Marine Pollution Bulletin 42: 7-15

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

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

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

Graham NAJ, McClanahan TR, MacNeill MA, Wilson SK, Polunin NVC, Jennings S, Chabanet P, Clark S, Spalding MD, Letourneur Y, Bigot L, Galzin R, Ohman MC, Garpe KC, Edwards AJ, Sheppard CRC (2008) Climate warming, marine protected areas and the ocean-scale integrity of coral reef systems. Public Library of Science One 3 e3039

Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef systems. Proceedings of the National Academy of Sciences USA 103: 8425-8429

Halford A, Caley MJ (2009) Towards an understanding of resilience in isolated coral reefs. Global Change Biology doi: 10.1111/j.1365-2486.2009.01972.x

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

Heyward AJ, Halford A, Smith L, Williams D (1997) Coral reefs of North West Australia: Baseline monitoring of an oceanic reef ecosystem Proceedings 8th International Coral Reef Symposium, Panama, pp 289-294

Hoegh-Guldberg O (2004) Coral reefs in a century of rapid 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, Hatziolos 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

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, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301: 929-933

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

Hughes TP, Connell JH (1999) Multiple stressors on coral reefs: A long-term perspective. Limnology and Oceanography 44: 461-488

Idjadi JA, Lee SC, Bruno JF, Precht WF, Allen-Requa L, Edmunds PJ (2006) Rapid phase-shift reversal on a Jamaican coral reef. Coral Reefs 25: 209-211

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

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

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 199: 155-163

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

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

McManus JW, Menez AB, Kesner-Reyes KN, Vergara SG, Ablan MC (2000) Coral reef fishing and coral-algal phase shifts: implications for global reef status. ICES Journal of Marine Science 57: 572-578

McManus JW, Polsenberg JF (2006) Coral-algal phase shifts on coral reefs: ecological and environmental aspects. Progress in Oceanography 60: 263-279

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

Moran P (1986) The Acanthaster phenomenon. Oceanography and Marine Biology - An Annual Review 24

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

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

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

Pratchett MS, Baird AH, Bradbury DM, Coker DJ, Cole AJ, Wilson SK (2008) Protracted declines in coral cover and fish abundance following climate-induced coral bleaching on the Great Barrier Reef. Proceedings Eleventh International Coral Reef Symposium

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

Sheppard CRC, Harris A, Sheppard ALS (2008) Archipelago – wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean. Marine Ecology Progress Series 362: 109–117

Smith LD, Gilmour JP, Heyward AJ (2008a) Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. Coral Reefs 27: 197-205

Smith LD, Gilmour JP, Heyward AJ (2008b) Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. Coral Reefs 27: 197-205

Sriver RL, Huber M (2007) Observational evidence for an ocean heat pump induced by tropical cyclones. Nature 477: 577–580

Steinberg C, Brinkman R, Bird J, McLean C (2003) Biological and Physical Environment at Scott Reef: 1994-2003, III: Physical Environment. Australian Institute of Marine Science

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

Walsh K, Pittock AB (1998) Potential Changes in Tropical Storms, Hurricanes, and Extreme Rainfall Events as a Result of Climate Change. Climatic Change 39: 199-213

Wilkinson C (2004) Status of coral reefs of the world: 2004 Volume 1. Australian Institute of Marine Science, Townsville, Queensland

Wilkinson C (2008) Status of Coral Reefs of the World. Australian Institute of Marine Science, Townsville

Wooldridge SA, Done TJ (2009) Improved water quality can ameliorate effects of climate change on coral. Ecological Applications 19: 1492–1499

Appendices

Appendix 3.1.1 Benthic categories that typify and discriminate time periods across all locations at Scott Reef. Typifiers are shown in grey; discriminators in white. Benthic categories are listed in decreasing order of importance. Categories marked with an asterix contribute inconsistently to the differences between year periods.

	1994-1997 Pre-Bleaching	1998-2001 Bleaching Impact	2002-2005 Recovery & Cyclones	2006-2009 Recovery & Cyclones
1994-1997	Algae Coralline Soft Coral Massive *Porites* Algae Turf Abiotic benthos Encrusting *Montipora* Other Benthos Encrusting Coral *Isopora palifera* *Seriatopora hystrix* Branching *Acropora*			
1998-2001	Algae Turf Algae Coralline* Encrusting *Montipora* *Isopora palifera* Branching *Acropora* Soft Coral Algae Other* *Isopora brueggemanni** *Seriatopora hystrix* Other Benthos Submassive Coral Abiotic benthos	Algae Turf Algae Coralline Massive *Porites* Abiotic benthos Soft Coral		
2002-2005	Algae Turf Algae Coralline Algae Other* *Isopora palifera* *Isopora brueggemanni** Other Benthos Encrusting *Montipora* Soft Coral* Branching *Acropora** Sponge* *Seriatopora hystrix*	Algae Coralline Algae Turf Abiotic benthos* Algae Other* Encrusting Coral Encrusting *Montipora** *Seriatopora hystrix** Branching *Acropora** Digitate *Acropora* Tabulate *Acropora** Corymbose *Acropora**	Algae Turf Algae Coralline Massive *Porites* Abiotic benthos Soft Coral Encrusting Coral Encrusting *Montipora*	
2006-2009	Algae Turf Algae Other Tabulate *Acropora* Other Benthos *Isopora brueggemanni** Algae Coralline* Soft Coral Sponge* *Isopora palifera* Abiotic benthos* *Seriatopora hystrix*	Algae Turf Tabulate *Acropora* Abiotic benthos Algae Coralline* Pocilloporidae Encrusting *Montipora* Branching *Acropora* Sponge Corymbose *Acropora* Algae Other* *Seriatopora hystrix**	Tabulate *Acropora* Algae Turf Algae Coralline Encrusting *Montipora* Abiotic benthos* Pocilloporidae Branching *Acropora** Sponge Corymbose *Acropora* *Isopora palifera** *Seriatopora hystrix**	Algae Turf Algae Coralline Massive *Porites* Abiotic benthos Encrusting *Montipora* Tabulate *Acropora* Soft Coral Sponge Pocilloporidae Encrusting Coral

Appendix 3.1.2 Benthic categories that typify and discriminate locations in the 1994-1997 period at Scott Reef. Typifiers are shown in grey; discriminators in white. Benthic categories are listed in decreasing order of importance. Categories marked with an asterix contribute inconsistently to the differences between locations.

	SL1 Lagoon	SL2 Lagoon	SL3 Lagoon	SL4 Slope	SS1 Slope	SS2 Slope
SL1	Massive *Porites* Soft Coral Abiotic benthos Encrusting *Montipora* Algae Coralline Algae Turf Algae Other Other Benthos					
SL2	Soft Coral Branching *Acropora* Foliose Coral Algae Coralline Massive *Porites* Hispidose *Acropora* Other Coral Algae Other	Branching *Acropora* Foliose Coral *Seriatopora hystrix* Hispidose *Acropora* Algae Turf Encrusting *Montipora* Other Benthos Other Coral				
SL3	Algae Other Sponge Algae Turf Algae Coralline Abiotic benthos *Isopora palifera* Soft Coral *Isopora brueggemanni**	Abiotic benthos Foliose Coral Hispidose *Acropora* Branching *Acropora* Algae Other Sponge* Algae Coralline Other Coral	Abiotic benthos Algae Turf Algae Coralline Massive *Porites* Soft Coral *Isopora palifera* Encrusting *Montipora* Other Benthos			
SL4	Algae Other Algae Turf Algae Coralline Soft Coral Sponge* Abiotic benthos *Isopora palifera* Corymbose *Acropora*	Soft Coral Branching *Acropora* Foliose Coral Hispidose *Acropora* Massive *Porites* Algae Other Algae Coralline Other Coral	Soft Coral Sponge* Algae Other Abiotic benthos* Corymbose *Acropora** *Isopora brueggemanni** Massive *Porites* Branching *Acropora*	Soft Coral Massive *Porites* Algae Turf Abiotic benthos Algae Coralline Encrusting *Montipora* Other Benthos *Isopora palifera*		
SS1	*Isopora brueggemanni* Algae Turf Algae Coralline Algae Other Corymbose *Acropora** Sponge* Soft Coral Submassive Coral*	*Isopora brueggemanni* Foliose Coral Branching *Acropora* Algae Coralline Hispidose *Acropora* Massive *Porites* Other Coral Algae Other	*Isopora brueggemanni* Algae Turf Abiotic benthos Sponge* Corymbose *Acropora** Algae Other Algae Coralline* Other Coral*	*Isopora brueggemanni* Soft Coral Algae Other Algae Turf Corymbose *Acropora** Algae Coralline* Abiotic benthos Sponge*	Algae Coralline Massive *Porites* Encrusting *Montipora* Soft Coral Abiotic benthos *Isopora brueggemanni** Other Benthos *Isopora palifera*	
SS2	Algae Coralline *Isopora brueggemanni** Algae Other Algae Turf Abiotic benthos *Isopora palifera* Sponge* Submassive Coral*	Foliose Coral Branching *Acropora* Algae Coralline Hispidose *Acropora* Soft Coral Other Coral Massive *Porites* Algae Other	Abiotic benthos Algae Coralline *Isopora brueggemanni** Sponge* Algae Other* Corymbose *Acropora** Encrusting *Montipora* Algae Turf	Algae Coralline Algae Other Abiotic benthos *Isopora brueggemanni** Soft Coral Sponge* Algae Turf Corymbose *Acropora**	*Isopora brueggemanni* Corymbose *Acropora** Algae Other Sponge* Algae Coralline* Algae Turf Soft Coral Branching *Acropora*	Algae Coralline Encrusting *Montipora* Massive *Porites* Soft Coral Algae Turf Other Benthos *Isopora palifera* Encrusting Coral

Appendix 3.1.3 Benthic categories that typify and discriminate locations in the 1998-2001 period at Scott Reef. Typifiers are shown in grey; discriminators in white. Benthic categories are listed in decreasing order of importance. Categories marked with an asterix contribute inconsistently to the differences between locations

	SL1 Lagoon	SL2 Lagoon	SL3 Lagoon	SL4 Slope	SS1 Slope	SS2 Slope
SL1	Algae Turf Algae Coralline Massive *Porites* Algae Other Abiotic benthos Soft Coral					
SL2	Algae Other Algae Turf* Algae Coralline* Massive *Porites* Other Coral Soft Coral Abiotic benthos Encrusting *Montipora**	Algae Turf Algae Coralline Other Coral Abiotic benthos Foliose Coral Algae Other				
SL3	Algae Other Algae Coralline* Branching *Acropora* Algae Turf* *Isopora brueggemanni* Abiotic benthos *Isopora palifera* *Goniastrea*	Algae Turf* Algae Coralline* Soft Coral Other Coral *Isopora brueggemanni* Massive *Porites* Abiotic benthos Branching *Acropora**	Algae Turf Algae Coralline Abiotic benthos Massive *Porites* Soft Coral *Isopora brueggemanni* Encrusting *Montipora* Encrusting Coral			
SL4	Algae Other Algae Coralline Algae Turf* Soft Coral Massive *Porites* Abiotic benthos* Encrusting *Montipora* Encrusting Coral	Massive *Porites* Soft Coral Algae Turf Algae Coralline Other Coral Abiotic benthos Encrusting *Montipora* Algae Other	Algae Coralline Algae Turf* Branching *Acropora** *Isopora brueggemanni* Massive *Porites* Abiotic benthos Encrusting *Montipora* Encrusting Coral	Algae Turf Algae Coralline Massive *Porites* Soft Coral Abiotic benthos Encrusting *Montipora* Encrusting Coral		
SS1	Algae Coralline Algae Other Algae Turf* Abiotic benthos Soft Coral Encrusting *Montipora** Other Benthos* Massive Other	Algae Coralline Other Coral Massive *Porites* Foliose Coral Algae Other* Algae Turf Abiotic benthos Other Benthos*	Algae Coralline Branching *Acropora* *Isopora brueggemanni* Abiotic benthos Soft Coral Algae Other Algae Turf* Corymbose *Acropora*	Soft Coral Algae Coralline Algae Turf* Abiotic benthos Algae Other Encrusting *Montipora* Massive *Porites* Encrusting Coral	Algae Turf Algae Coralline Massive *Porites* Algae Other*	
SS2	Algae Other Algae Coralline Algae Turf* Abiotic benthos Massive Other Encrusting *Montipora** Soft Coral Other Benthos*	Algae Coralline Algae Turf* Massive *Porites* Other Coral Foliose Coral Algae Other Soft Coral Encrusting *Montipora*	Algae Coralline Algae Turf Branching *Acropora* *Isopora brueggemanni* Abiotic benthos Soft Coral *Isopora palifera* Corymbose *Acropora*	Algae Coralline* Algae Turf* Soft Coral Abiotic benthos Massive *Porites* Encrusting *Montipora* Massive Other Encrusting Coral	Algae Coralline Algae Turf* Algae Other Abiotic benthos Other Benthos* Encrusting *Montipora** Soft Coral* Massive *Porites**	Algae Turf Algae Coralline Massive *Porites* Abiotic benthos Soft Coral

Appendix 3.1.4 Benthic categories that typify and discriminate locations in the 2002-2005 period at Scott Reef. Typifiers are shown in grey; discriminators in white. Benthic categories are listed in decreasing order of importance. Categories marked with an asterix contribute inconsistently to the differences between locations

	SL1 Lagoon	SL2 Lagoon	SL3 Lagoon	SL4 Slope	SS1 Slope	SS2 Slope
SL1	Algae Turf Algae Coralline Massive *Porites* Soft Coral Abiotic benthos Encrusting Coral Corymbose *Acropora* Encrusting *Montipora*					
SL2	Algae Coralline Other Coral Massive *Porites* Algae Turf Soft Coral Foliose Coral *Seriatopora hystrix* Abiotic benthos*	Algae Turf Algae Coralline Other Coral Encrusting Coral *Seriatopora hystrix* Foliose Coral Abiotic benthos Corymbose *Acropora*				
SL3	*Isopora brueggemanni* *Seriatopora hystrix* Branching *Acropora* Abiotic benthos Algae Turf Encrusting *Montipora** Algae Coralline Submassive Coral	Algae Turf Other Coral *Isopora brueggemanni* Soft Coral Abiotic benthos Algae Coralline* Branching *Acropora** Foliose Coral	Algae Turf Algae Coralline Abiotic benthos Soft Coral Massive *Porites* Encrusting Coral Branching *Acropora* *Seriatopora hystrix*			
SL4	Abiotic benthos Massive *Porites* *Seriatopora hystrix* Algae Turf Algae Coralline* Encrusting *Montipora* Corymbose *Acropora* Soft Coral	Massive *Porites* Algae Turf Soft Coral Other Coral Abiotic benthos Foliose Coral Algae Coralline* Encrusting *Montipora**	Massive *Porites* *Isopora brueggemanni** Branching *Acropora* Algae Coralline* Abiotic benthos* Algae Turf* Encrusting *Montipora** *Seriatopora hystrix**	Algae Turf Algae Coralline Massive *Porites* Abiotic benthos Soft Coral Encrusting *Montipora* Encrusting Coral *Goniastrea*		
SS1	Soft Coral Corymbose *Acropora* Abiotic benthos* Encrusting *Montipora* Algae Coralline Algae Turf* Massive Other Encrusting Coral*	Algae Coralline Other Coral Foliose Coral Massive *Porites* *Seriatopora hystrix* Algae Turf Abiotic benthos* Corymbose *Acropora*	Branching *Acropora* Soft Coral *Isopora brueggemanni* Algae Turf Abiotic benthos *Seriatopora hystrix* Algae Coralline Corymbose *Acropora*	Soft Coral Abiotic benthos Algae Coralline Massive *Porites* Algae Turf *Seriatopora hystrix* *Goniastrea* Algae Other	Algae Turf Algae Coralline Massive *Porites* Abiotic benthos Encrusting Coral	
SS2	Corymbose *Acropora* Soft Coral Algae Coralline Abiotic benthos* Encrusting *Montipora** Algae Turf* Encrusting Coral Tabulate *Acropora*	Algae Coralline Other Coral Massive *Porites* Foliose Coral *Seriatopora hystrix* Algae Turf Abiotic benthos Tabulate *Acropora*	Branching *Acropora* Abiotic benthos *Isopora brueggemanni* *Seriatopora hystrix* Algae Turf Algae Coralline Soft Coral Tabulate *Acropora*	Abiotic benthos Soft Coral Algae Coralline Algae Turf Massive *Porites* *Seriatopora hystrix* *Goniastrea* Submassive Coral	Abiotic benthos Algae Turf* Algae Other Encrusting *Montipora* Algae Coralline* Soft Coral* Massive *Porites** Encrusting Coral	Algae Turf Algae Coralline Massive *Porites* Abiotic benthos Encrusting Coral Encrusting *Montipora*

Appendix 3.1.5 Benthic categories that typify and discriminate locations in the 2006-2009 period at Scott Reef. Typifiers are shown in grey; discriminators in white. Benthic categories are listed in decreasing order of importance. Categories marked with an asterix contribute inconsistently to the differences between locations.

	SL1 Lagoon	SL2 Lagoon	SL3 Lagoon	SL4 Slope	SS1 Slope	SS2 Slope
SL1	Algae Turf Algae Coralline Tabulate *Acropora* Massive *Porites* Soft Coral Encrusting *Montipora* Branching *Acropora* Sponge					
SL2	Algae Coralline Other Coral Soft Coral Massive *Porites* Hispidose *Acropora* Abiotic benthos Foliose Coral *Seriatopora hystrix*	Algae Turf Tabulate *Acropora* Abiotic benthos Branching *Acropora* Algae Coralline Other Coral Hispidose *Acropora* Foliose Coral				
SL3	Abiotic benthos Tabulate *Acropora* *Isopora brueggemanni* Algae Coralline *Isopora palifera* Algae Turf Corymbose *Acropora* *Seriatopora hystrix*	Hispidose *Acropora* Soft Coral Other Coral *Isopora palifera* Tabulate *Acropora* *Isopora brueggemanni** Massive *Porites* Foliose Coral	Algae Turf Abiotic benthos Algae Coralline Massive *Porites* Soft Coral Encrusting *Montipora* Encrusting Coral Massive Other			
SL4	Tabulate *Acropora* Algae Coralline Massive *Porites* Abiotic benthos Branching *Acropora* *Isopora palifera* Digitate *Acropora* Soft Coral	Massive *Porites* Soft Coral Tabulate *Acropora* Other Coral Hispidose *Acropora* Branching *Acropora* Foliose Coral *Isopora palifera*	Massive *Porites* *Isopora brueggemanni* Branching *Acropora** Tabulate *Acropora** Abiotic benthos* Algae Coralline* Algae Turf* Soft Coral*	Algae Turf Massive *Porites* Soft Coral Abiotic benthos Algae Coralline Encrusting *Montipora* Sponge Encrusting Coral		
SS1	Soft Coral Abiotic benthos Branching *Acropora* Algae Coralline *Seriatopora hystrix* Tabulate *Acropora* Foliose Coral *Goniastrea*	Algae Coralline Other Coral Hispidose *Acropora* Foliose Coral Branching *Acropora* Encrusting *Montipora* Massive *Porites* Algae Turf	Algae Coralline Soft Coral *Isopora brueggemanni* Tabulate *Acropora* *Isopora palifera* Algae Turf *Seriatopora hystrix* *Goniastrea*	Algae Coralline Soft Coral Tabulate *Acropora* Massive *Porites* *Seriatopora hystrix* *Goniastrea* Abiotic benthos Foliose Coral	Algae Turf Algae Coralline Abiotic benthos Encrusting *Montipora* Tabulate *Acropora* Massive *Porites* Pocilloporidae Encrusting Coral	
SS2	Tabulate *Acropora* Abiotic benthos Branching *Acropora* Soft Coral Algae Coralline Encrusting Coral Encrusting *Montipora* Foliose Coral	Algae Coralline Other Coral Hispidose *Acropora* Branching *Acropora* Massive *Porites* Foliose Coral Encrusting *Montipora* *Seriatopora hystrix*	Algae Coralline *Isopora brueggemanni* Abiotic benthos Soft Coral *Isopora palifera* *Seriatopora hystrix* Algae Turf Corymbose *Acropora*	Algae Coralline Soft Coral Massive *Porites* Tabulate *Acropora* *Seriatopora hystrix* Abiotic benthos Pocilloporidae Encrusting *Montipora*	*Seriatopora hystrix** Abiotic benthos Tabulate *Acropora* Soft Coral Sponge Encrusting Coral Algae Coralline Massive *Porites**	Algae Turf Algae Coralline Encrusting *Montipora* Massive *Porites* Abiotic benthos Sponge Pocilloporidae Tabulate *Acropora*

3.2. Climate induced disturbance effects on coral reef fish communities at an isolated atoll system in the north-east Indian Ocean

Introduction

Coral reefs are the most diverse ecosystem within the marine environment and provide habitat for thousands of species, including up to one-third of all known species of marine fishes (Moberg and Folke 1999). 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 can alter their structural components (Connell 1997; Hughes and Connell 1999; McCulloch et al. 2003; Connell et al. 2004; Wilson et al. 2006) such as the coral bleaching associated with high sea temperatures, and frequent and intense tropical storms (Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007; IPCC 2007; Veron 2008). Reefs have evolved in a regime subjected to disturbances and have the capability to respond and recover to these events. However, this capability may be compromised in the future due to climate change that could result in more frequent environmental conditions favourable for coral bleaching and a greater frequency and intensity of tropical storms (IPCC 2007). This will allow shorter times for reefs to recover between disturbance events (Hughes et al. 2003) and could ultimately result in reefs switching to alternate states where they are dominated by organisms other than corals (Norström et al. 2009). For these reasons, a great deal of research now involves monitoring programs that track changes in the status of coral reef communities and assess their ability to resist alternate states and recover from disturbance-induced changes (Syms and Jones 2000; Holbrook et al. 2008).

The effects of disturbance on coral-dominated communities flow through to the assemblages of fishes that live on reefs. For many 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). 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). This variation in response of coral reef fishes to disturbance requires an analytical approach that can tease apart changes in measures of abundance and species richness and relate these to the key ecological processes that are essential for maintaining coral reef resilience (Green and Bellwood 2009). Such multivariate statistical techniques are now available (Clarke et al. 2008; Emslie et al. 2008) and are able to

highlight how a species response to disturbance may depend on their habitat dependency (McKinney 1997; Hughes et al. 2000; Kotze and O'Hara 2003).

The Scott Reef system is an isolated group of coral reef atolls that lie in the Indian Ocean at the edge of the continental shelf off 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). 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 between Scott Reef and 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 Great Barrier Reef.

Monitoring studies offer one means to examine the processes of disturbance, recovery and resilience on coral reefs. AIMS initiated long-term monitoring at Scott Reef in 1994 and this Chapter updates the progress of this program for fish communities. The monitoring program records 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 abundance, species richness and diversity of reef fishes change in response to major disturbances over a 15-year study period? (2) Do the abundances of functional groups of fishes show predictable patterns of decline and recovery in response to disturbance? (3) Does disturbance cause greater variation in the species composition of fish assemblages within than among locations at Scott Reef? (4) What are the species and functional groups that change in response to disturbance?

Materials and Methods

Study area and sampling regime

The Scott Reef system is composed of Seringapatam, North Reef and South Reef in the eastern Indian Ocean at the edge of the Australian continental shelf and is biogeographically important as it intersects the Indonesian and north-west Australian faunal provinces. Scott Reef rises from a water depth of *ca* 450 m and is located on the slope to the east of the Scott Plateau, occupying an area of 800 km^{-2} (Jones 1973).

To quantify the changes in the fish communities at Scott Reef, permanently marked transects were censused in the same period (October to January) at seven locations during 12 surveys between 1994 and 2008. During each survey, the abundances of fish species were estimated by divers along transects of fixed width (Halford and Thompson 1994). Two transect sizes were used, with the relatively large and mobile fish species from 9 families (Acanthuridae, Chaetodontidae, Labridae, Lethrinidae, Lutjanidae, Scaridae, Serranidae, Siganidae and Zanclidae) surveyed along a 50 m x 5 m corridor and the smaller, more site-attached species from the family Pomacentridae being sampled along the same transects, but using a 50 m x 1 m corridor. 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 the larger mobile and small sedentary species. For each transect we calculated the density of each individual fish species and the total density of fishes, total number of species and Shannon diversity (Log_n). The percentage contribution of each of fifty life-form categories 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). Fish species were classified into seven functional groups based on published data of their feeding behaviour, diet and habitat associations (see Appendix 1 for full species list and functional group classification). Species that rely heavily on coral for food or shelter were classified as coral dependent and included both obligate and facultative coral feeders (Pratchett 2005; Wilson et al. 2006). The classification of herbivorous species followed Green *et al*. (2009) while that for detritivores (including epilithic algal matrix feeders), invertivores, omnivores and piscivores followed Froese & Pauly (2009) and Wilson *et al*. (2003). Fish were also assigned according to other functional classifications that differed mainly in the assignment of corallivores as obligate or facultative and they also recognized that herbivorous species do not constitute an ecologically uniform group and thus differ in terms of how they feed, what they consume, and their impact on the underlying substratum (Green and Bellwood 2009).

Long-term trends of fish faunal characteristics

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, species richness, Shannon diversity index (Log_n), average taxonomic distinctness (Clarke and Warwick 1998), 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 examines if the fish abundance was different between 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 regard as non-independent. The model also allowed for different variance structures per reef location.

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 R2, Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and the (restricted) log-likelihood test. For all most 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.

Generalized additive models (GAM) were used to examine the relationship between percent of coral and fish density (Guisan et al. 2002). This statistical analysis can model the predictor (independent) variables as linear, non-linear or polynomial terms. The relationships explored included: (1) Cover of live hard coral versus species richness, number of fish, Shannon diversity, average taxonomic distinctness, and abundance of Pomacentridae, non-Pomacentridae and functional groups (2) Cover of algae versus species richness, number of fish, average taxonomic distinctness and abundance of functional groups (3) Branching coral versus density of obligate corallivores and (4) Encrusting coralline algae versus density of obligate corallivores. The relationship between percent of cover either coral or algae with other variables were plotted showing the actual observed data, and the mean, lower and upper confidence fitted from the GAM.

Multivariate analysis of fish and benthos

Each of the following analyses were done using the PRIMER v6 multivariate statistics package (Clarke and Gorley 2006) with the PERMANOVA+ for PRIMER add-on module (Anderson et al. 2008).

Prior to analysis, the density of each fish species and the percentage contribution of each life-form category in each replicate sample were $Log_n(x+1)$ and square-root transformed, respectively, then used to construct Bray-Curtis similarity matrices. The Log 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). Square-root transformation is appropriate for the percentage

contribution data. The Bray-Curtis distance matrix derived from mean transformed values was subjected to hierarchical agglomerative clustering with group average linking (CLUSTER), 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 each location grouped together for a particular year and thus do not differ significantly in their species composition. This analysis is a permutation test that determines whether any significant group structure exists within a set of samples for which there is no *a priori* grouping hypothesis (Clarke et al. 2008). When used in conjunction with CLUSTER analysis, a SIMPROF test is performed at each node of the dendogram to ascertain whether the particular group of samples being subdivided contains significant internal differences, except in those cases when a test carried out at a broader division returned a non-significant result. This routine thus provides a sound basis for identifying those points in the clustering procedure at which further subdivision of samples is unwarranted. These year group categories were then subsequently used as *priori* hypotheses in CAP analysis and ANOSIM tests. The null hypothesis that there were no significant differences among groups were rejected if the significance level (p) associated with the test statistic (π) was < 0.01.

Canonical Analysis of Principal Coordinates (CAP; Anderson et al. 2008) was used to explore the effect of the year groups and reef locations on the fish community composition. CAP is a constrained ordination technique and is an appropriate method to apply after unconstrained techniques (Anderson and Willis 2003). CAP is a 2-step process combining two existing multivariate techniques: Principal Coordinate analysis (PCO) followed by a Canonical Correlation Analysis (CCorA) on un-scaled orthonormal PCO axes. The contributions of the various fish species to the first CAP axis was inferred from its correlation to the original variables, and tested using both the Root and Trace statistics with 9999 permutations (Anderson and Robinson 2003). To identify those species that contributed most to the multivariate pattern, we isolated those species which had a strong correlation (> 0.5) between the original data and the first CAP axis.

Pairwise comparisons of the species composition of fishes between year categories (4 levels: 1994-1998, 1999-2001, 2003-2004 and 2006-2008) and reef locations (6 levels) were examined using the two-way crossed analysis of similarities (ANOSIM) tests (Clarke and Warwick 2001; Clarke and Gorley 2006). 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 (PERMANOVA) test

(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).

The RELATE procedure (Clarke and Gorley 2006) was used to quantify the extent to which the pattern of rank orders between the ichthyofaunal compositions of the various samples in the biotic similarity matrix, derived from density data for use in the cluster and nMDS ordination analyses, paralleled those in a distance matrix constructed from the contributions of benthic life-form categories for those same samples. RELATE was also used to determine whether the distance matrix constructed from density data at the species level was related to matrices derived using density data from either a higher taxonomic level (family) or from the various functional groups of fishes. The correlation between two matrices was considered significant if the associated *P* value was < 0.05 and the Spearman rank correlation (ρ) was used to assess the extent to which the multivariate structure of the two matrices agreed. BIOENV was used to elucidate which mean values of the twelve benthic categories, or combination of those categories, were best correlated with the pattern of fish species compositions for all locations collectively (Clarke and Ainsworth 1993).

Linkage Tree (LINKTREE) was used to explore which benthic category or combination of categories were most tightly linked with the progressive separation of the groups identified by the classification procedure described above. LINKTREE (Clarke et al. 2008) is a non-metric modification of the multivariate regression tree (MRT) technique (De'Ath 2002). A binary "linkage tree" was constructed that reflects how samples from an underlying (fixed) resemblance matrix were most naturally split into successively smaller groups, based on maximising the *R*-statistic (Clarke 1993). At each branching node of the tree, the quantitative thresholds of the benthic category(s) from a complementary sample x category data matrix that best mirror that division were also provided. The complementary sample x category data matrix employed contained the untreated (true) percentage contributions for the twelve benthic life-form categories averaged for each combination of location and year. The notation associated with those category thresholds (e.g. category A < x [> y], where x and y are quantitative percentage contributions of benthic category A), indicates whether a left (< x) or right path ([> y]), should be followed at each branching node.

A Similarity Profiles (SIMPROF) test was also used in conjunction with LINKTREE to terminate construction of the tree at those nodes where there was no significant structure among the remaining samples. Specifically, a SIMPROF test is performed at each node of the tree to ascertain whether the particular group of samples being subdivided contains significant internal differences, except in those cases when a test carried out at a broader division returned a non-significant result (Clarke et al. 2008). Larger values of the test statistic π than expected provide evidence that significant group structure is present among the samples. The LINKTREE and SIMPROF routines thus produced a linkage tree with terminal nodes

comprising groups of samples that precisely represent the groups identified by the classification procedure (along with the benthic categories) and their true quantitative thresholds, that were most tightly linked with the separation of those groups.

Results

Temporal trends in fish faunas

Trends in fish communities at Scott Reef were dominated by the response of fishes to the catastrophic bleaching event that removed 75% of all live coral cover in early 1998. This response was most striking in the fishes that were obligate associates of live coral. Numbers of these declined from a high in 1997 to lows from 2001 through 2004. A modest increase in these fishes has occurred in the last two years of the study (Fig. 3.2.1). A similar decline in planktivores occurred following the bleaching event, although in contrast to coral dependent species, numbers of these fishes rebounded 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. Algal overgrowth of coral also traps detrital material and as a consequence the abundance of detrital-feeding species also increased after the bleaching event, but have not declined and have remained higher than at pre-bleaching levels throughout the monitoring program. In contrast to these trophic groups, numbers of omnivores, invertivores and piscivores displayed no obvious response to the bleaching event in 1998. The latter two groups have increased in abundance throughout the study.

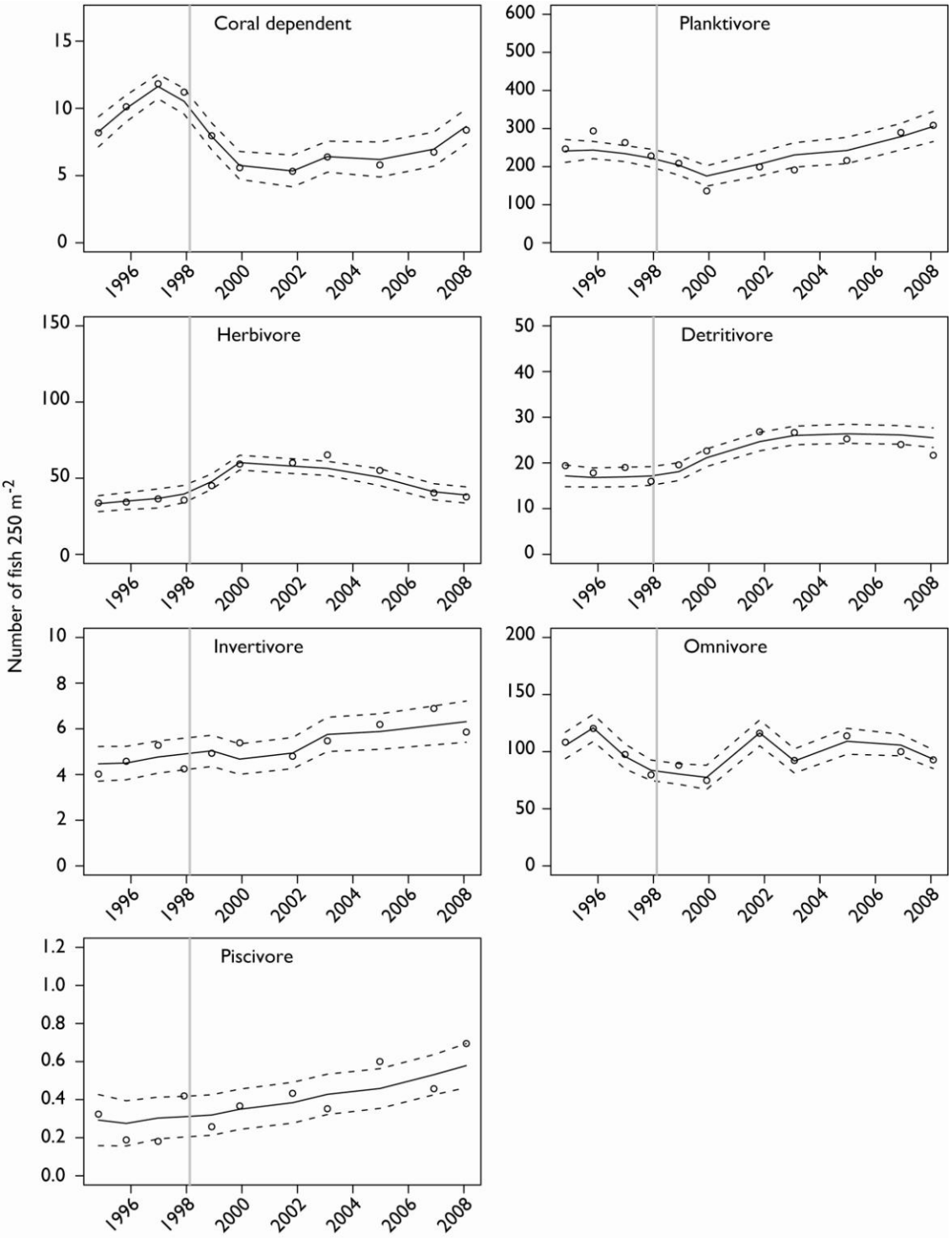


Fig. 3.2.1 Mean (± 95% C.I.) densities of functional groups of fishes at Scott Reef between 1994 and 2008. Solid lines are general additive mixed model (GAMM) fits, dashed lines indicate 95% confidence intervals, circles are the observed men densities and grey line indicates period of coral bleaching. All analyses were conducted at the transect level.

These general patterns in abundance were complicated by significant interactions between location and year (Figs. 3.2.2, 3.2.3). Sigmoidal trends in the densities of coral-dependent

species were more pronounced at the locations of SS1, SS2 and SS3 that were more exposed to wave and wind action than at the inner locations that were protected from these factors (Fig. 3.2.2). Densities of coral dependent species at all locations tended to be lowest during the three year period following the 1998 coral bleaching, except in the case of SL3, where numbers remained low and showed no trend for increase or decrease throughout the study period.

Mean densities of planktivores tended to be lowest in 1999, except at SL1 and SL2 where overall numbers were much lower than in other locations and in both, there was little variation in numbers through time (Fig. 3.2.2). The most rapid increase in abundance of planktivores occurred at SL3 between 1999 and 2008. For herbivores and detritivores, mean densities were greater at SL2 than at all other locations, whereas densities of detritivores remained consistently low at SL3 and SS3 for the duration of the study (Fig. 3.2.3). Although densities of herbivores, and to a lesser extent, detritivores, tended to be greater in the period immediate following the 1998 coral bleaching event, there was a striking increase in herbivore abundance at SL2 through to 2002 and an equally rapid subsequent decline.

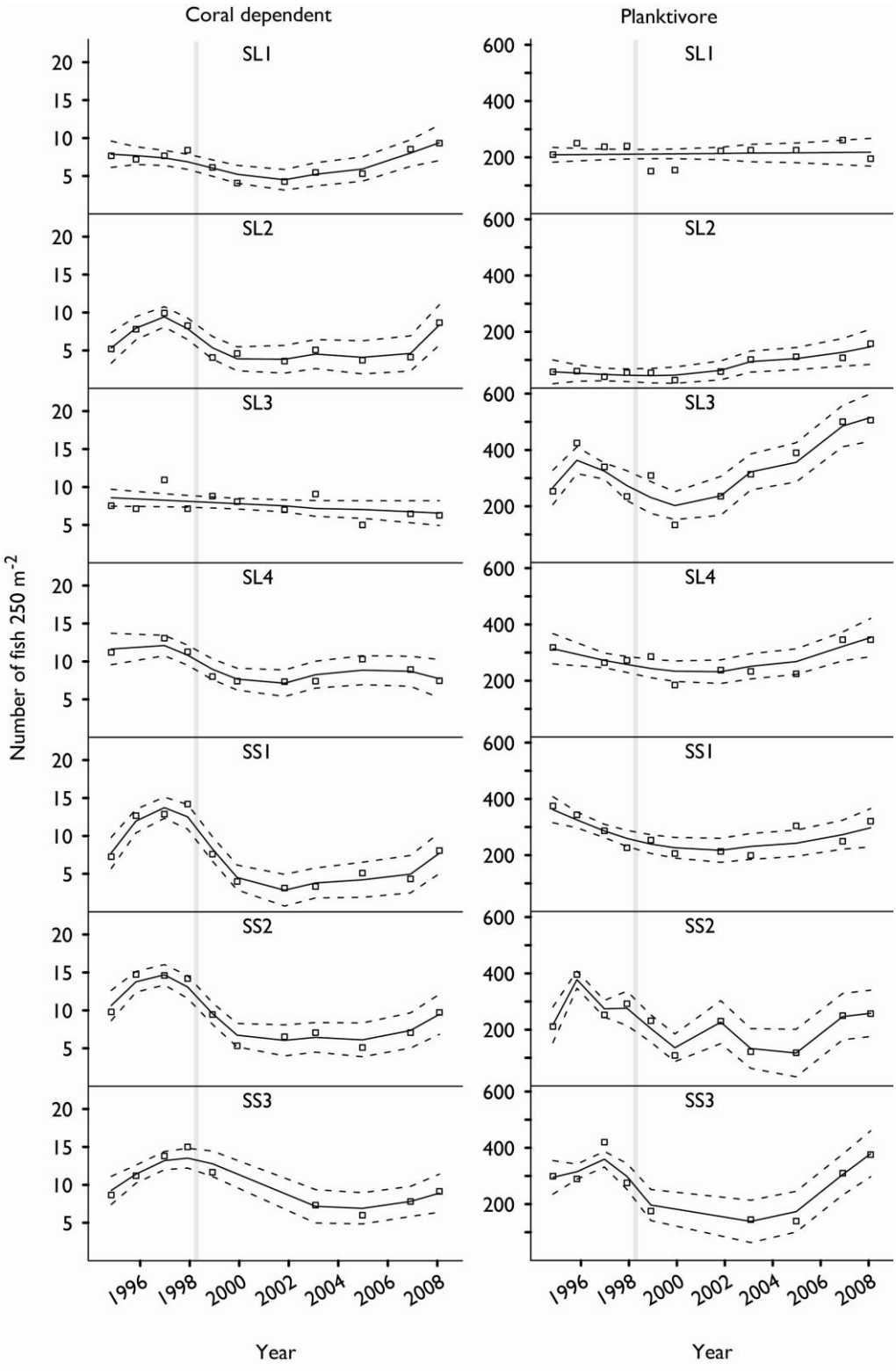


Fig. 3.2.2 Mean (± 95% C.I.) densities of coral dependent and plankton feeding fishes at seven locations at Scott Reef between 1994 and 2008. Solid lines are general additive mixed model (GAMM) fits, dashed lines indicate 95% confidence intervals, circles are the observed men densities and grey line indicates period of coral bleaching. All analyses were conducted at the transect level.

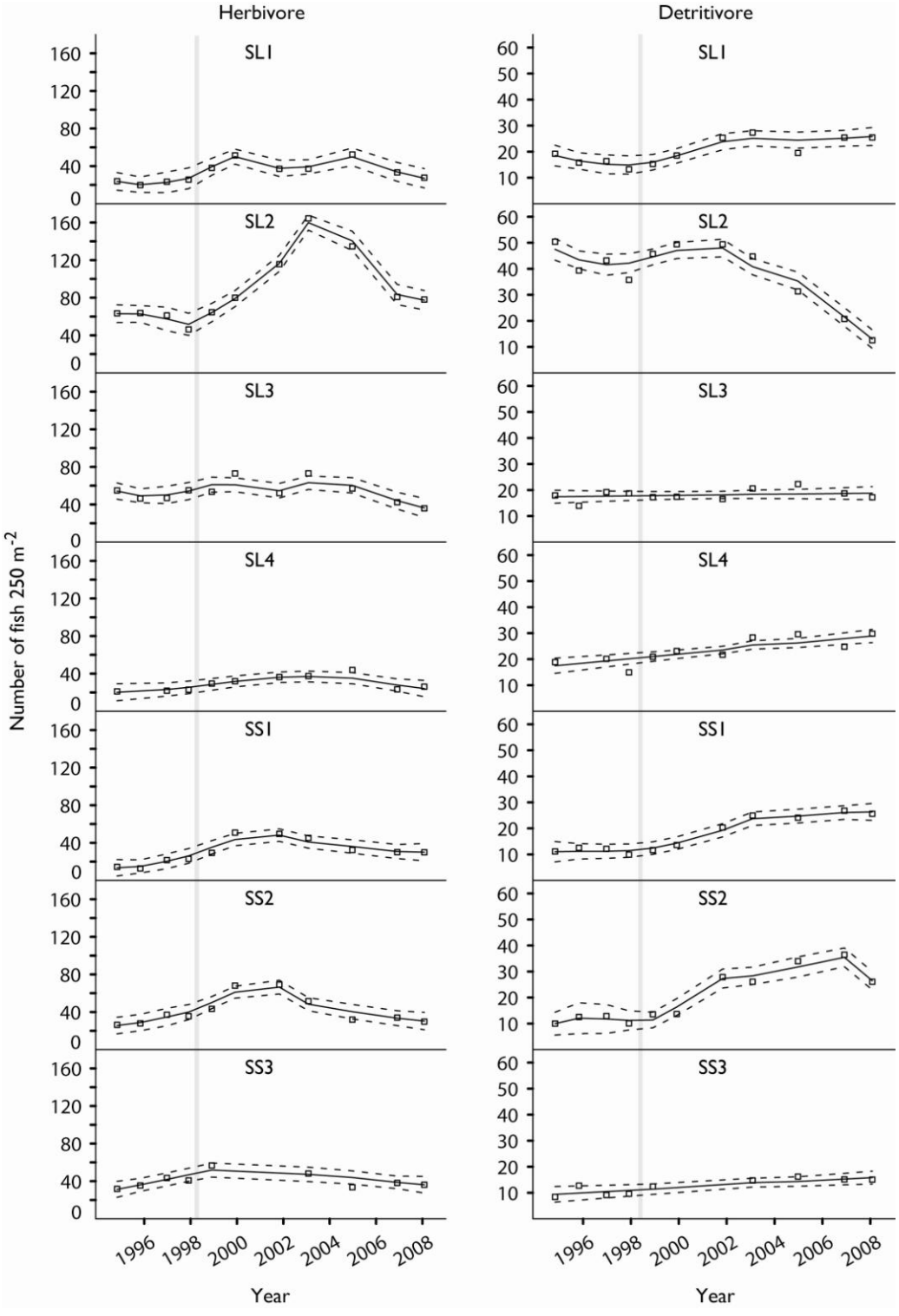


Fig. 3.2.3 Mean (± 95% C.I.) densities of herbivorous and detritus-feeding fishes at seven locations at Scott Reef between 1994 and 2008. Solid lines are general additive mixed model (GAMM) fits, dashed lines indicate 95% confidence intervals, circles are the observed men densities and grey line indicates period of coral bleaching. All analyses were conducted at the transect level.

Temporal trends in densities of both pomacentrid and non-pomacentrid fishes, the number of fish species and the diversity of fishes were fitted by GAAM models with interactions between location and year. The trend in the mean densities of damselfishes (Pomacentridae) was non-linear ($p < 0.0001$) with values declining from 1995 through 1999 before returning to higher levels in subsequent years (Fig. 3.2.4). In contrast, the densities of other fishes (non-Pomacentridae) and numbers of species increased throughout the entire 15 year study period, with the trend being greater for non-pomacentrids ($p < 0.0001$) than number of species ($p < 0.001$). Shannon diversity increased from a low of 2.22 in 1994 to a high of 2.43 in 1999 and then remained at about 2.3 through 2008 (Fig 3.2.4).

The densities and number of fish species varied significantly among locations and years (Figs. 3.2.5, 3.2.6). At SL2, the abundance of pomacentrids peaked in 2002 and then declined through 2008 (Fig. 3.2.5). This contrasted with the trends for all other locations, particularly SL3, where damselfish abundance decreased between 1995 and 1999 and then rose steadily from 2001 to 2008. The mean densities of other fishes increased steadily throughout the study period except at SL2, where densities peaked in 1999 and then decreased until 2008 (Fig. 3.2.5). The mean number of species recorded by the study increased at SL1, SL2, and SL3 (all $p < 0.0001$). However, in the case of SS2, numbers remained at about 25 throughout the study period ($p > 0.05$), and at. SS1 and SS3, only increased towards the end of the study period (Fig. 3.2.6).

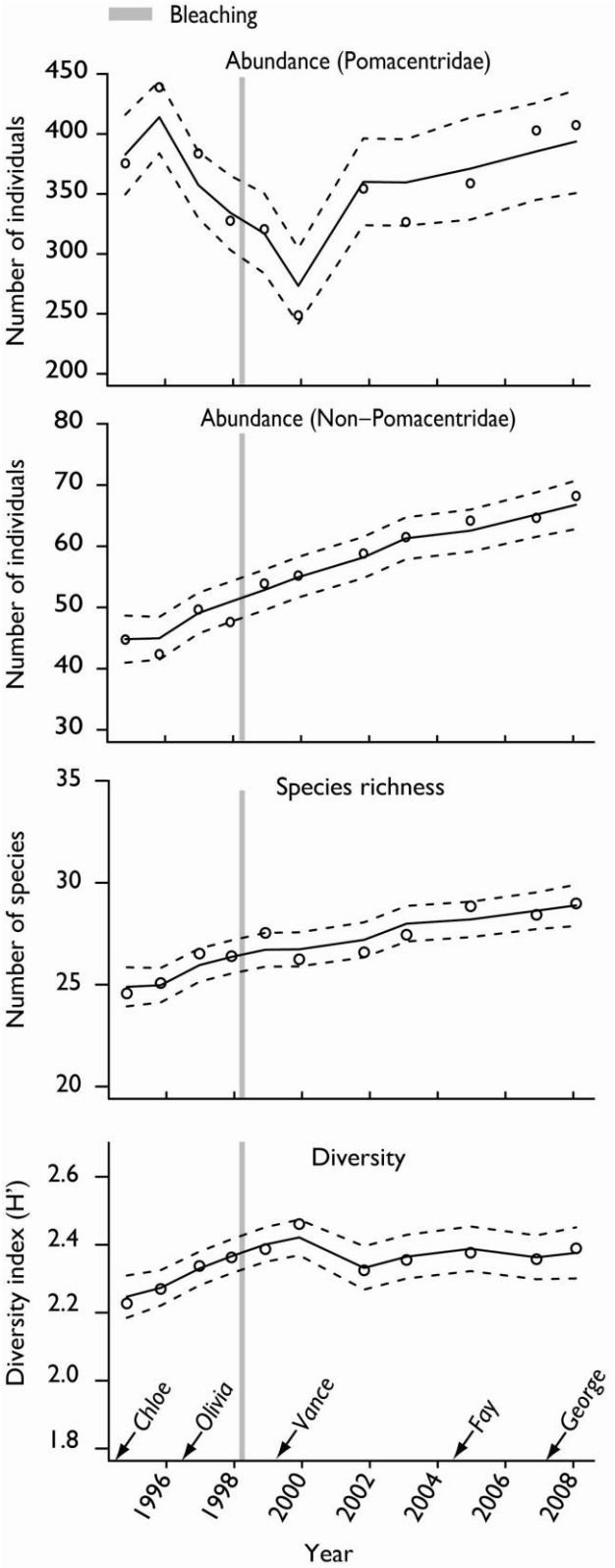


Fig. 3.2.4 Mean densities of pomacentrid and non-pomacentrid fishes, species richness and Shannon diversity of fishes at Scott Reef between 1994 and 2008. Solid lines are general additive mixed model (GAMM) fits, dashed lines indicate 95% confidence intervals, circles are the observed men densities and grey line indicates period of coral bleaching. All analyses were conducted at the transect level.

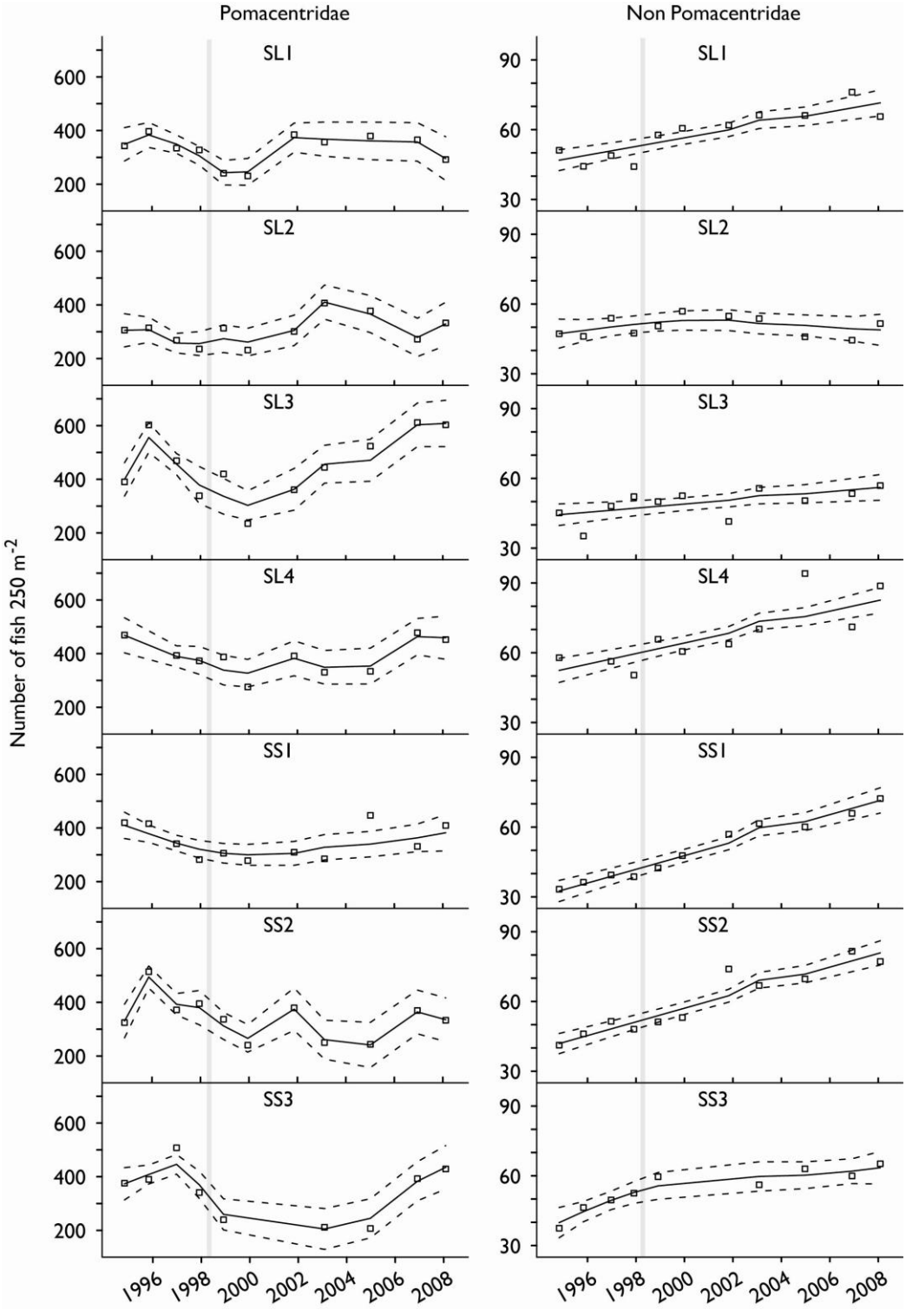


Fig. 3.2.5 Mean (± 95 C.I.) densities of pomacentrid and non-pomacentrid fishes at each of the seven locations at Scott Reef between 1994 and 2008. Solid lines are general additive mixed model (GAMM) fits, dashed lines indicate 95% confidence intervals, circles are the observed men densities and grey line indicates period of coral bleaching. All analyses were conducted at the transect level.

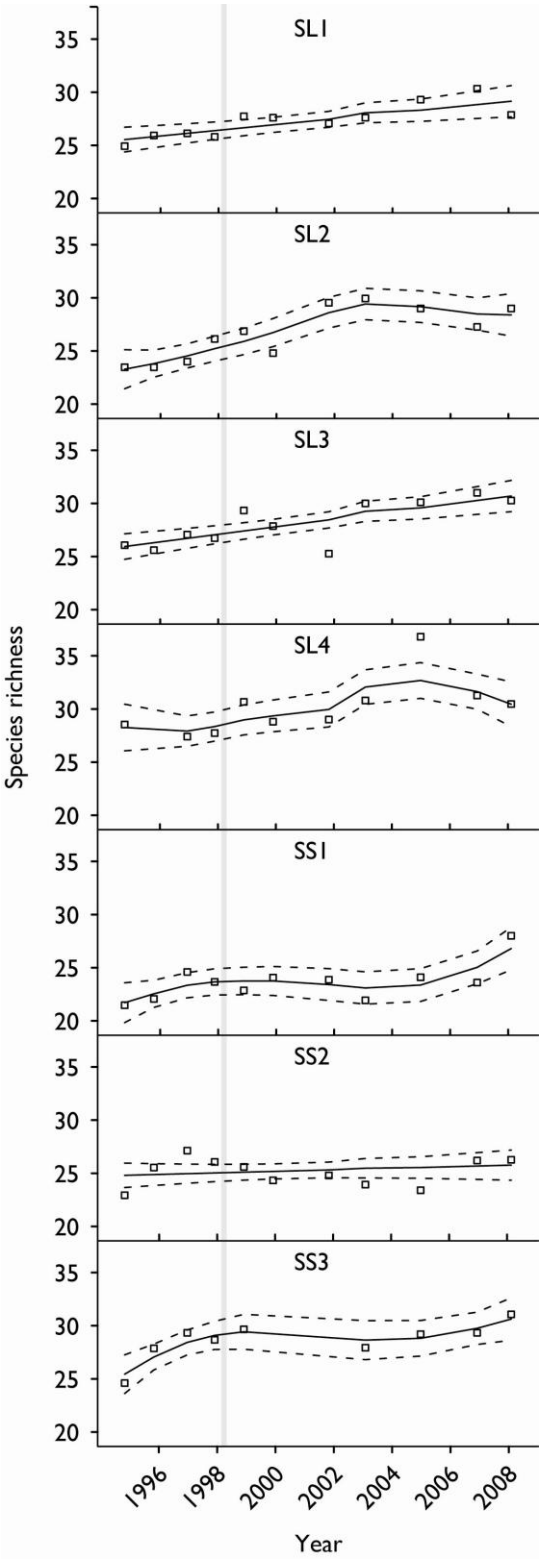


Fig. 3.2.6 Mean (± 95 C.I.) numbers of fish species at seven locations at Scott Reef between 1994 and 2008. Solid lines are general additive mixed model (GAMM) fits, dashed lines indicate 95% confidence intervals, circles are the observed men densities and grey line indicates period of coral bleaching. All analyses were conducted at the transect level.

Modeling of the relationships between species richness and density of fishes and the cover of both live hard coral and algae resulted in statistically significant ($p < 0.0001$) dome shaped curves (Fig. 3.2.7). The numbers of fish species and densities peaked at about 30 and 40% coral cover, respectively, and the decline in the number of fishes was sharper at lower than higher coral cover. The saturation points for number of species and densities occurred with algal covers of about 50 and 40%, respectively. Average taxonomic distinctness decreased linearly with increases in coral cover, whereas the reverse situation occurred with increasing algal cover (Fig. 3.2.7). The total abundance of coral-dependent species increased linearly with coral cover and declined linearly with algal cover (Fig. 3.2.8). GAM indicated that there were significant asymptotic relationships for planktivores with coral cover and scrapers with algal cover ($p < 0.0001$).

Given the strong relationship between fish abundance and diversity and cover of coral and algae, the temporal trajectories of change for the various functional groups of fishes were investigated. The 'best' model that fitted the temporal trend of the densities of each function group was equivalent to the number of fish species, that is a GAAM with an interaction between location and year. All functional groups had a significant temporal trend (all $p < 0.0001$), except in the case of piscivores ($p=0.37$).

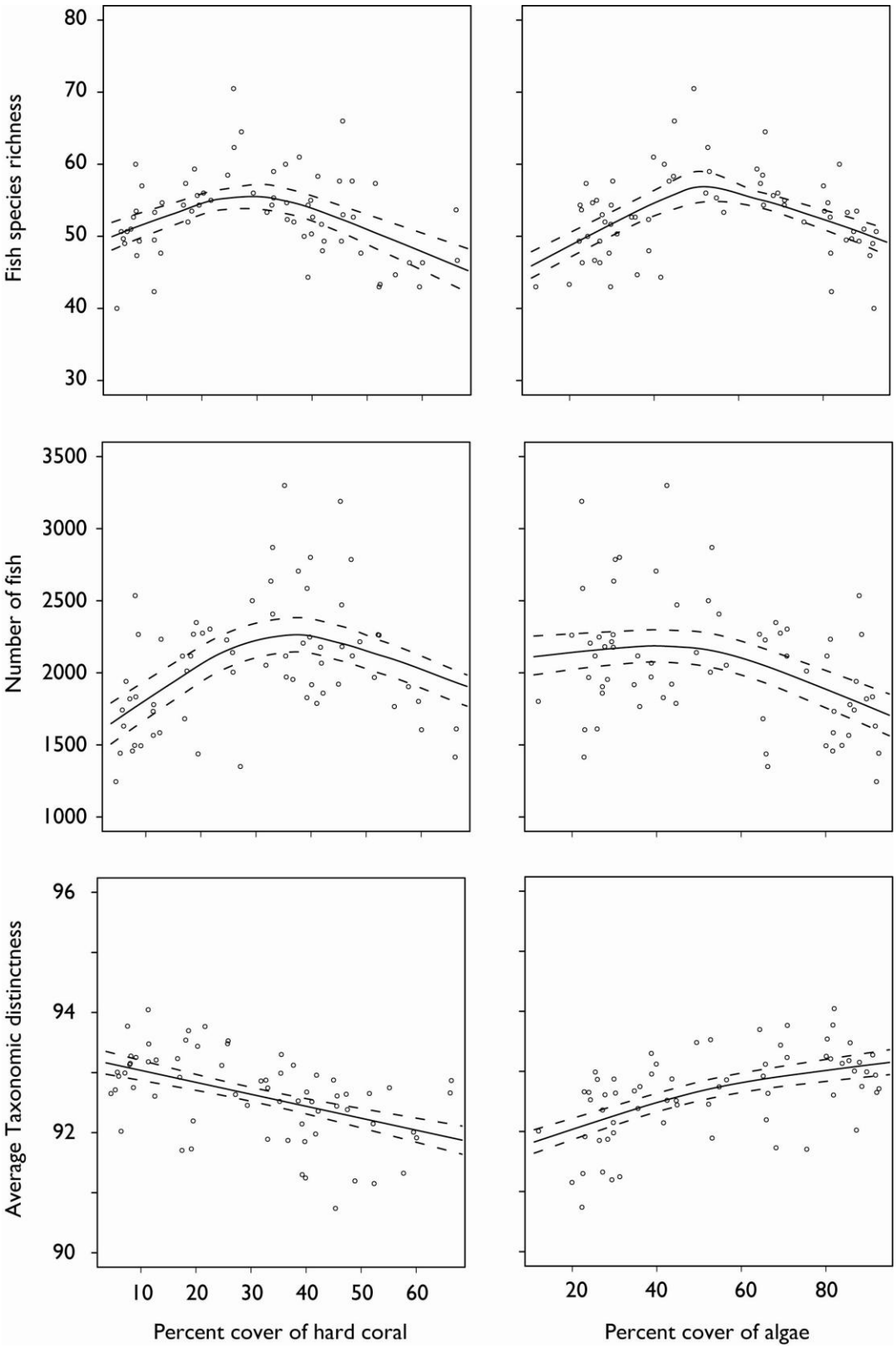


Fig. 3.2.7 Species richness, density of fishes and average taxonomic distinctness vs the cover of live hard coral and algae. Lines are general additive model (GAM) fits and dashed lines indicate 95% confidence limits, circles are the observed means.

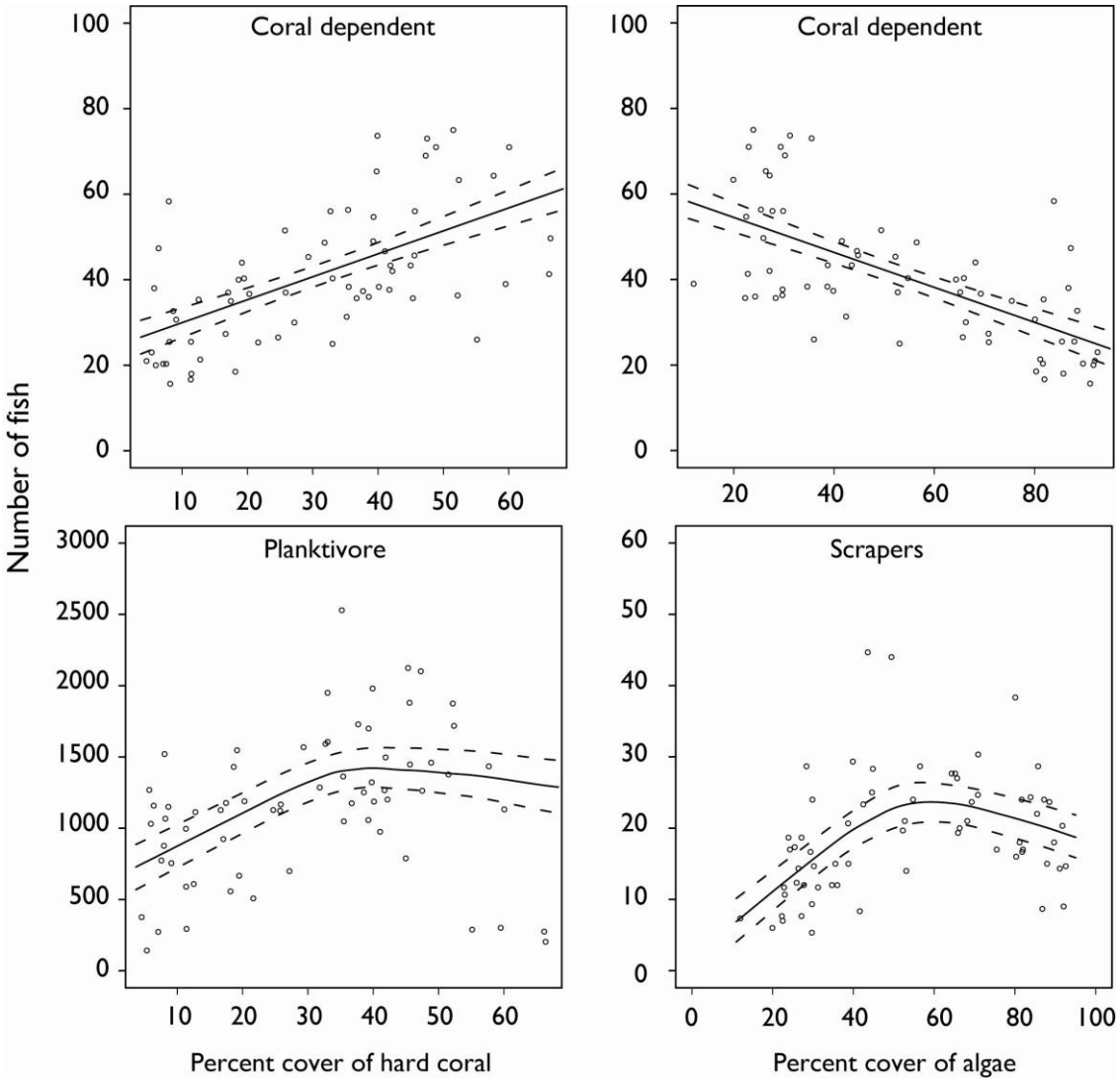


Fig. 3.2.8 Total abundance of coral dependent and planktivorous species vs coral cover and coral dependent and herbivorous scraper species vs algal cover. Lines are general additive model (GAM) fits and dashed lines indicate 95% confidence limits and circles are the observed mean abundance.

Faunal composition

The combined use of CLUSTER and SIMPROF revealed significant structure in the reef fish communities at Scott Reef and the samples were divided into distinct pre-bleach, immediate post-bleach and late post-bleach communities (Fig. 3.2.9A). Non-metric multidimensional scaling (nMDS) ordination of the same data showed the trajectory of faunal change through time and indicated that the late post-bleach community was tracking away from earlier pre-bleach communities (Fig. 3.2.9B). ANOSIM confirmed that these differences were statistically significant ($P < 0.001$) with a Global R-statistic of 0.544. Pair-wise ANOSIM comparisons

showed that the species composition of the fish faunas in each period differed significantly from that in each other period (all $P < 0.001$), with *R*-statistic values ranging from 0.191 for 1997/98 *vs* 1999 to 0.785 for 1994/96 *vs* 2008 (Table 3.2.1). *R*-statistic values for comparisons between faunas of temporally contiguous periods were far less than those that were widely-separated.

Table 3.2.1 Global R-statistic values for pairwise two-way ANOSIM comparisons carried out on data for reef fish species at Scott Reef between 1994 and 2008.

Period	1994 to 1996	1997 to 98	1999	2001 to 03	2004 to 06
1997 to 98	0.194**	-	-	-	-
1999	0.614***	0.191*	-	-	-
2001 to 03	0.748***	0.587***	0.449***	-	-
2004 to 06	0.774***	0.667***	0.648***	0.286***	-
2008	0.785***	0.668***	0.605**	0.590***	0.260**

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

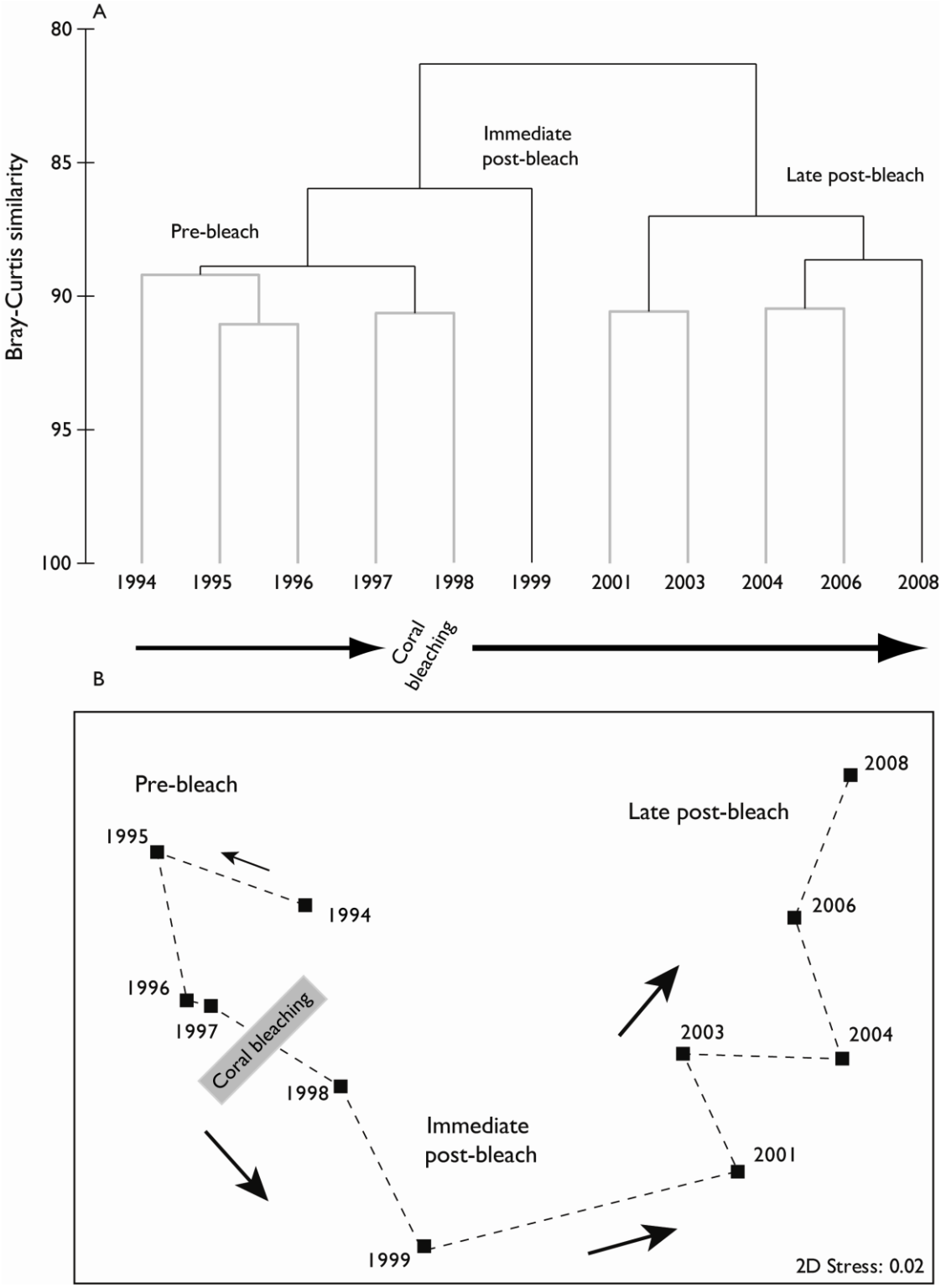


Fig. 3.2.9 CLUSTER analysis (A), with SIMPROF of the species compositions of reef fish communities at Scott Reef between 1994 and 2008. Solid lines indicate groups that SIMPROF determined were significantly different from each other and (B) Non-metric multidimensional scaling (nMDS) ordination showing the trajectory of change in the structure of fish communities at Scott Reef between 1994 and 2008.

Damselfishes were largely responsible for the differences in species composition among the six periods (identified in Fig. 3.2.9A, Table 3.2.2). Species that were characteristic of all time periods included *Pomacentrus lepidogenys*, *P. vaiuli* and *P. phillipinus*. The fauna between 1994 and 1996 was distinguished from that in all other periods by greater abundances and frequencies of occurrence of *Pomacentrus moluccensis* and the staghorn damsel *Amblyglyphidodon curacao*, which are both omnivores, whereas the period 2001 to 2003 was distinguished by a greater density and frequency of occurrence of the algal feeding/farming species *Pomacentrus adelus* and the omnivorous *Pomacentrus amboinensis*. The fauna in 2008 was distinguished by relatively greater contributions of the planktivores *Chromis margaritifer* and *Chromis xanthura* and the omnivorous humpback snapper *Lutjanus gibbus*.

The four contrasting temporal trends for densities of the key fish species identified by the above SIMPER analysis were modeled with GAAMs and are illustrated in Fig. 3.2.10. The mean densities of *Chromis ternatensis* and *Chromis atripes* decreased following the 1998 bleaching event through to 2004 before increasing to 2008, whereas *Amblyglyphidodon curacao* and *Pomacentrus moluccensis* maintained a decreasing trend through the bleaching event to 2008. Densities of *Chrysiptera rex* and *Pomacentrus adelus* increased immediately following the 1998 bleaching and remained high through to 2004 before decreasing to 2008. The fourth trend is illustrated by *Chromis margaritifer* and *Pomacentrus amboinensis,* whose densities both increased immediately following the bleaching and maintained that trend and are now even greater than prior to the bleaching. Furthermore, although densities of *Chromis xanthura* decreased slightly following the bleaching, they are now at their highest level of the study period.

Relationship between fish and benthic compositions

There was a significant match in temporal patterns of reef fish faunas and the benthos ($P < 0.001$). Results of BIOENV demonstrated that overall, the pattern was most highly correlated with that of lobate soft coral (ρ 0.497), and that the correlation was improved by the inclusion of fungiids, encrusting corals, branching *Acropora* and non-*Acropora*, digitate *Acropora*, corymbose *Acropora*, hispidose *Acropora*, soft coral, macroalgae (mainly *Halimeda*), sponge and the category other benthos, which included corallimorphians, ascidians and hydroids (ρ 0.87, $P < 0.001$).

The selection of these eleven benthic categories by BIOENV provided the basis for their subsequent use in the LIKTREE routine. Within each of the year groups (identified above using CLUSTER and SIMPROF), linkage tree was used to distinguish which of the benthic categories were related to composition of reef fish (Fig. 3.2.11). The paths through the tree were defined by thresholds for the benthic categories and provide a way for detecting which of the benthic categories were most important for separating the reef fish faunas at Scott Reef through a 15 year period of change. The pre-bleached fish community was characterized by greater contributions of branching *Acropora* and non-*Acropora* corals, whereas the intermediate post-bleach fish community (2001 to 2004) was distinguished from the late-

bleached community (2008) by reduced contributions of corymbose and hispidose *Acropora*, encrusting corals and sponges but a greater contribution of turfing algae (Fig. 3.2.11).

Table 3.2.2. Species identified by SIMPER as typifying the fish assemblages of reefs in the six time-periods (shaded boxes) and 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 from that of another are indicated by the initials of that period.

Period	1994 to 1996	1997 to 1998	1999	2001 to 2003	2004 to 2006	2008
1994 to 1996	*Pomacentrus lepidogenys* *Pomacentrus vaiuli* *Pomacentrus philippinus* *Chromis ternatensis* *Ctenochaetus* spp. *Plectro. lacrymatus* *Chrysiptera rex* *Chromis margaritifer*					
1997 to 1998	*Pom. moluccensis* 94/96 *Ambly. curacao* 97/98 *Chrom margaritifer* 94/96 *Chromis lepidolepis* 94/96 *Chromis atripes* 97/98 *Chrom amboinensis* 97/98	*Pom. lepidogenys* *Chromis ternatensis* *Pom. philippinus* *Pomacentrus vaiuli* *Ctenochaetus* spp. *Plectr. lacrymatus*				
1999	*Pomacentrus adelus* 99 *Chrom margaritifer* 94/96 *Ambly. curacao* 94/96 *Chromis lepidolepis* 94/96 *Pom. moluccensis* 94/96 *Chromis atripes* 99 *Chromis ternatensis* 94/96	*Pomacentrus adelus* 99 *Pom. moluccensis* 97/98 *Chrom margaritifer* 97/98 *Ambly. curacao* 97/98 *Chrom amboinensis*97/98 *Chrom lepidolepis* 97/98 *Chrom ternatensis* 97/98	*Plectro. lacrymatus* *Pom. philippinus* *Ctenochaetus* spp. *Pom. lepidogenys* *Pomacentrus vaiuli* *Chlororus sordidus* *Chromis ternatensis*			
2001 to 2003	*Chromis ternatensis* 94/96 *Pom. moluccensis* 94/96 *Pom. adelus* 01/03 *Ambly. curacao* 94/96 *Chrom margaritifer* 01/03 *Chromis lepidolepis* 94/96 *Pom. amboinensis* 01/03	*Chrom ternatensis* 97/98 *Ambly. curacao* 97/98 *Pom. adelus* 01/03 *Pom. moluccensis* 97/98 *Chrom margaritifer* 01/03 *Chromis lepidolepis* 01/03 *Pom. amboinensis* 01/03	*Pomacentrus adelus* 01/03 *Chromis ternatensis* 99 *Chromis margaritifer* 01/03 *Pom. moluccensis* 99 *Chromis lepidolepis* 01/03 *Ambly. curacao* 99 *Pom. amboinensis* 01/03	*Pom. philippinus* *Pom. lepidogenys* *Chrysiptera rex* *Ctenochaetus* spp. *Pomacentrus vaiuli* *Plectro. lacrymatus* *Chlororus sordidus*		
2004 to 2006	*Chromis ternatensis* 94/96 *Pom. moluccensis* 94/96 *Ambly. curacao* 94/96 *Pom. adelus* 04/06 *Chrom margaritifer* 04/06 *Chromis weberi* 04/06 *Pom. amboinensis* 04/06 *Chromis atripes* 04/06	*Chrom ternatensis* 97/98 *Pom. moluccensis* 97/98 *Ambly. curacao* 97/98 *Pom. adelus* 04/06 *Chrom margaritifer* 04/06 *Chromis weberi* 04/06 *Chrom lepidoleppis* 04/06 *Ambly. aureus* 97/98	*Pomacentrus adelus* 04/06 *Chromis weberi* 04/06 *Chromis ternatensis* 99 *Pom. moluccensis* 99 *Chromis margaritifer* 04/06 *Ambly. curacao* 99 *Chromis lepidoleppis* 04/06 *Ambly. aureus* 99	*Pomacentrus adelus* 01/03 *Chromis ternatensis* 04/06 *Pom. moluccensis* 04/06 *Pom. amboinensis* 01/03 *Chromis margaritifer* 04/06 *Chromis weberi* 04/06 *Lutjanus gibbus* 04/06 *Ambly. aureus* 04/06 *Plec lacrymatus* 01/03	*Pom. philippinus* *Pom. lepidogenys* *Chrysiptera rex* *Ctenochaetus* spp. *Pomacentrus vaiuli* *Plectro. lacrymatus* *Chromis xanthura* *Chromis margaritifer*	
2008	*Pom. moluccensis* 94/96 *Ambly. curacao* 94/96 *Chromis margaritifer* 08 *Chromis weberi* 08 *Chromis ternatensis* 94/96 *Chromis atripes* 08 *Chrom lepidoleppis* 94/96 *Chromis xanthura* 08 *Lutjanus gibbus* 08	*Ambly. curacao* 97/98 *Pom. moluccensis* 97/98 *Chromis margaritifer* 08 *Chromis weberi* 08 *Chromis lepidoleppis* 08 *Chrom ternatensis* 97/98 *Chromis atripes* 08 *Chromis xanthura* 08 *Lutjanus gibbus* 08	*Chromis margaritifer* 08 *Pom. moluccensis* 99 *Chromis weberi* 08 *Chromis lepidoleppis* 08 *Ambly. curacao* 99 *Chromis atripes* 08 *Chromis ternatensis* 08 *Chromis xanthura* 08 *Lutjanus gibbus* 08	*Chromis ternatensis* 08 *Pomacentrus adelus* 01/03 *Pom. moluccensis* 08 *Chromis weberi* 08 *Chromis margaritifer* 08 *Pom. amboinensis* 01/03 *Chromis lepidoleppis* 08 *Chromis xanthura* 08 *Lutjanus gibbus* 08 *Plec lacrymatus* 01/03	*Chromis weberi* 04/06 *Chromis ternatensis* 08 *Pomacentrus adelus* 04/06 *Poma. amboinensis* 04/06 *Chromis margaritifer*08 *Chromis xanthura* 08 *Ambly. aureus* 08 *Acanthurus nigrofuscus* 04/06 *Lutjanus gibbus* 08	*Pom. philippinus* *Pom. lepidogenys* *Chrysiptera rex* *Pomacentrus vaiuli* *Ctenochaetus* spp. *Chromis margaritifer* *Chromis xanthura* *Chromis ternatensis* *Chlororus sordidus*

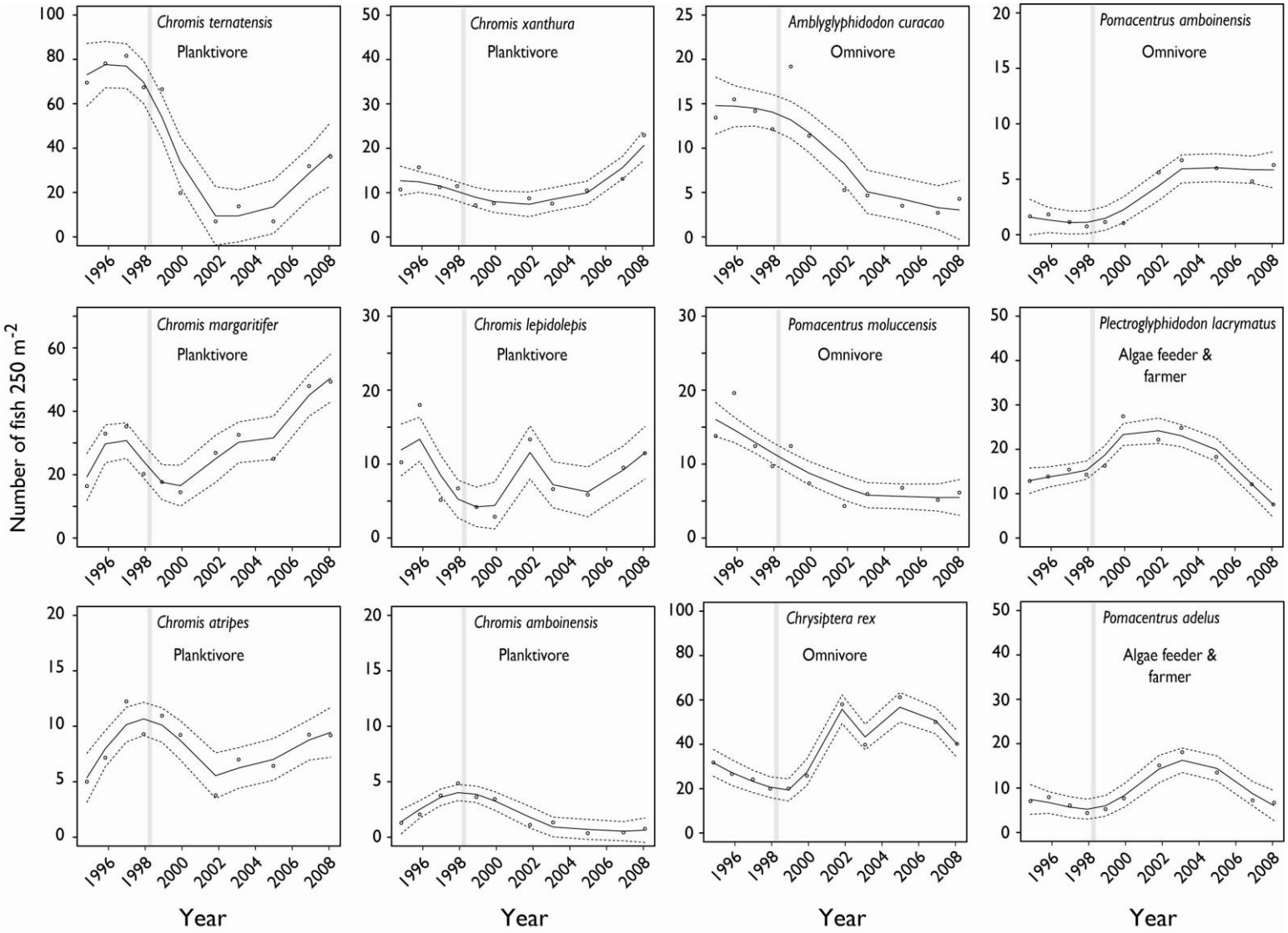


Fig. 3.2.10 Mean (± 95 C.I.) densities of fish species identified by SIMPER as distinguishing particular time periods at Scott Reef between 1994 and 2008. Solid lines are general additive mixed model (GAMM) fits, dashed lines indicate 95% confidence intervals, circles are the observed men densities and grey line indicates period of coral bleaching. All analyses were conducted at the transect level.

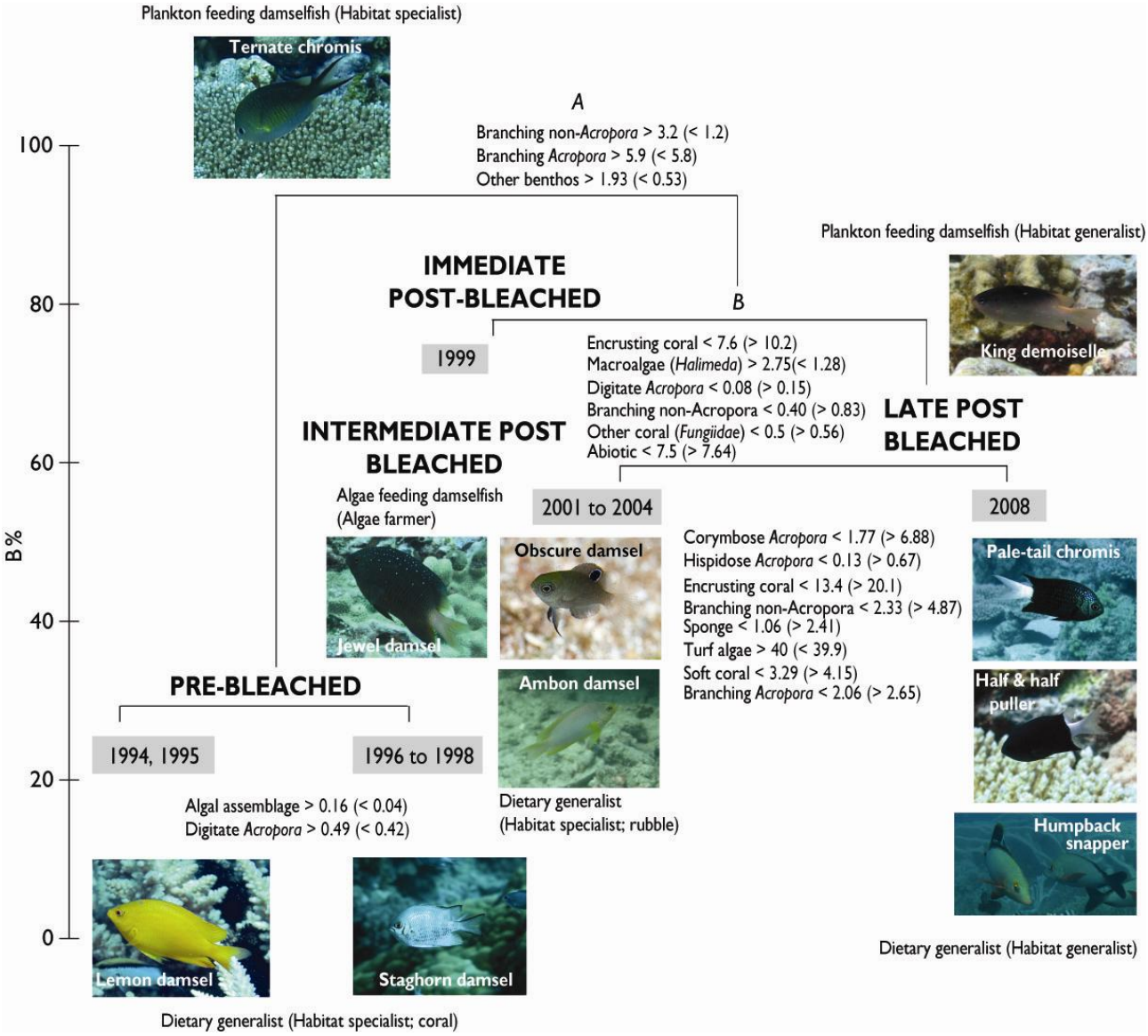


Fig. 3.2.11 Linkage tree showing the main fish species responsible for separating the various year groups at Scott Reef through time and the benthic groups responsible for the correlation between the fish and benthic communities. Unbracketed and bracketed thresholds given at each node indicate that a left and right path, respectively, should be followed through the tree.

Comparisons of fish faunas among locations

The dendrogram derived from cluster analysis of the mean densities of each fish species at each location between 1994 and 2008 is shown in Fig. 3.2.12. The first subdivision of the dendrogram separated the points representing the samples from the most protected location (SL2, a) from those in all other locations, with the division on the dendrogram occurring at 52.7%. Within the latter group (b), all of the samples from SL1, SL3 and SL4 were then split to form a separate group (c) that SIMPROF demonstrated was significantly different (Pi = 1.7, *p*

= 0.1%) from either of the two clusters comprising the samples from the more exposed locations, *i.e.* SS2 and SS3 (d) and SS1 (e). Within the subdivision (c) on the dendrogram, the samples formed three clusters (f-g) that comprised exclusively the samples from SL4, SL3 and SL1, respectively (Fig. 3.2.12). Within the clusters for each location, the points were further subdivided according to the pre-bleach, immediate post-bleach and late post-bleach communities identified in the above CLUSTER analysis. SIMPROF indicated that each of these groups were significantly different (data not shown).

RELATE analysis demonstrated that the similarity matrix derived from the densities of fish species at the various locations (and used to produce the dendrogram shown in Fig. 3.2.12 was correlated at higher taxonomic levels including genus (ρ = 0.82, P < 0.001) and family (ρ = 0.33, P < 0.001) and with two functional classifications (class 1 ρ = 0.61 and P < 0.001; class 2 ρ = 0.67, and P < 0.001). The low correlation at family level suggests that the trends shown in the previous dendrogram deteriorate at this level and highlights the wide degree of variation in functional requirements within families of fishes and the need for data to be collected at species and/or functional group level.

Ordination analysis of the data showed that the samples formed discrete groups according to location (Fig. 3.2.13A). Samples from the most protected location (SL2) formed a group on the far left of the plot, whereas those from the more exposed locations (SS1, SS2, SS3) formed a group at the right with those from other locations lying in between. When these samples were coded according to time-period, those from the pre-bleaching period lay at the top of the plot and those from the post-bleaching period lay in the middle and those from 2008 formed a group on the right (Fig. 3.2.13B).

It is clear from the CAP analysis that certain species occurred in greater numbers at particular locations (Fig. 3.2.13A). For example, *Stegastes nigricans*, *Plectropomus leopardus, Pomacentrus amboinensis, Dascyllus aruanus* and *Neoglyphidodon nigroris* made greater contributions to the fauna at SL2 whereas species such as *Chromis atripes*, *Pomacentrus vaiuli* and *Pomacentrus phillipinus* were more abundant at SL1 and SL3. At the more exposed outer reef slope locations (SS1, SS2 and SS3) the species compositions were characterised by greater numbers of *Forcipiger flavissimus*, *Chromis margaritifer* and *Chrysiptera rex*. Different suites of species were shown to characterise the different year groups identified previously by SIMPROF (Fig. 3.2.13B). Thus species heavily reliant on coral for food or shelter were more abundant in the 1994 to 1998 counts, e.g. *Chromis ternatensis*, *Amblyglyphidodon curacao*, *Plectroglyphidodon johnstonianus* and *Chaetodon punctofasciatus*. Alternatively, algae feeding/farming, detritivorous or omnivorous species such as *Scarus psittacus*, *Chrysiptera rex* and *Acanthurus nigricauda* characterised the fauna in post-bleaching periods (Fig. 3.2.13B).

Ordination analysis of count data for each location showed that there was a consistent separation of samples into a group containing all those from 1994-1999 on the left and all those from subsequent years on the right (Fig. 3.2.14). The lines overlain on each plot indicate that the fish species composition from 2001 onwards is different to that occurring prior to 2001, irrespective of location. Cyclone Fay affected the benthic community at SL2, SS1 and

SS2 in early 2004, more than other localities (see previous section), and this is reflected in the sharp shift in trajectory for 2004 on the ordinations for these locations (Fig. 3.2.14). While there are clearly distinct post-bleaching communities at each location, there is evidence of a shift in community composition towards pre-bleaching structure at some locations, *i.e.* SL1, SL4, SS2 and SS3.

Three-way PERMANOVA showed that the compositions of the fish faunas at Scott Reef were influenced significantly by location, and year and that there was a significant interaction between these factors (all $P < 0.001$). The component of variation was far greater for location (39.1) than for either year group (6.2) or the interaction (1.3).

Two-way crossed ANOSIM demonstrated that the species compositions of reef fish assemblages at Scott Reef differed significantly among locations and year groups (both $P < 0.001$) and that the *R*-statistic was greater for location (0.84) than year group (0.53). Pair-wise ANOSIM comparisons showed that the species compositions of the fish faunas at each location differed significantly from that at each of the other locations (all $P < 0.001$). The *R*-statistic values for pair-wise comparisons between the samples at the different locations were greatest for those between SL2 and each other location (all 1.000), and lowest for the comparisons between SS2 and either SS3 (0.410) or SL4 (0.565) (Table 3.2.3).

Table 3.2.3 Pairwise R-statistic values for location derived from 2-way crossed ANOSIM (Location x Year category) of the fish communities at Scott Reef between 1994 and 2008. All comparisons were significant at $P < 0.001$.

Location	SL1	SL2	SL3	SL4	SS1	SS2
SL2	0.998	-	-	-	-	-
SL3	0.763	1.000	-	-	-	-
SL4	0.594	1.000	0.820	-	-	-
SS1	0.749	1.000	0.928	0.723	-	-
SS2	0.889	1.000	0.864	0.565	0.706	-
SS3	0.874	1.000	0.876	0.688	0.744	0.410

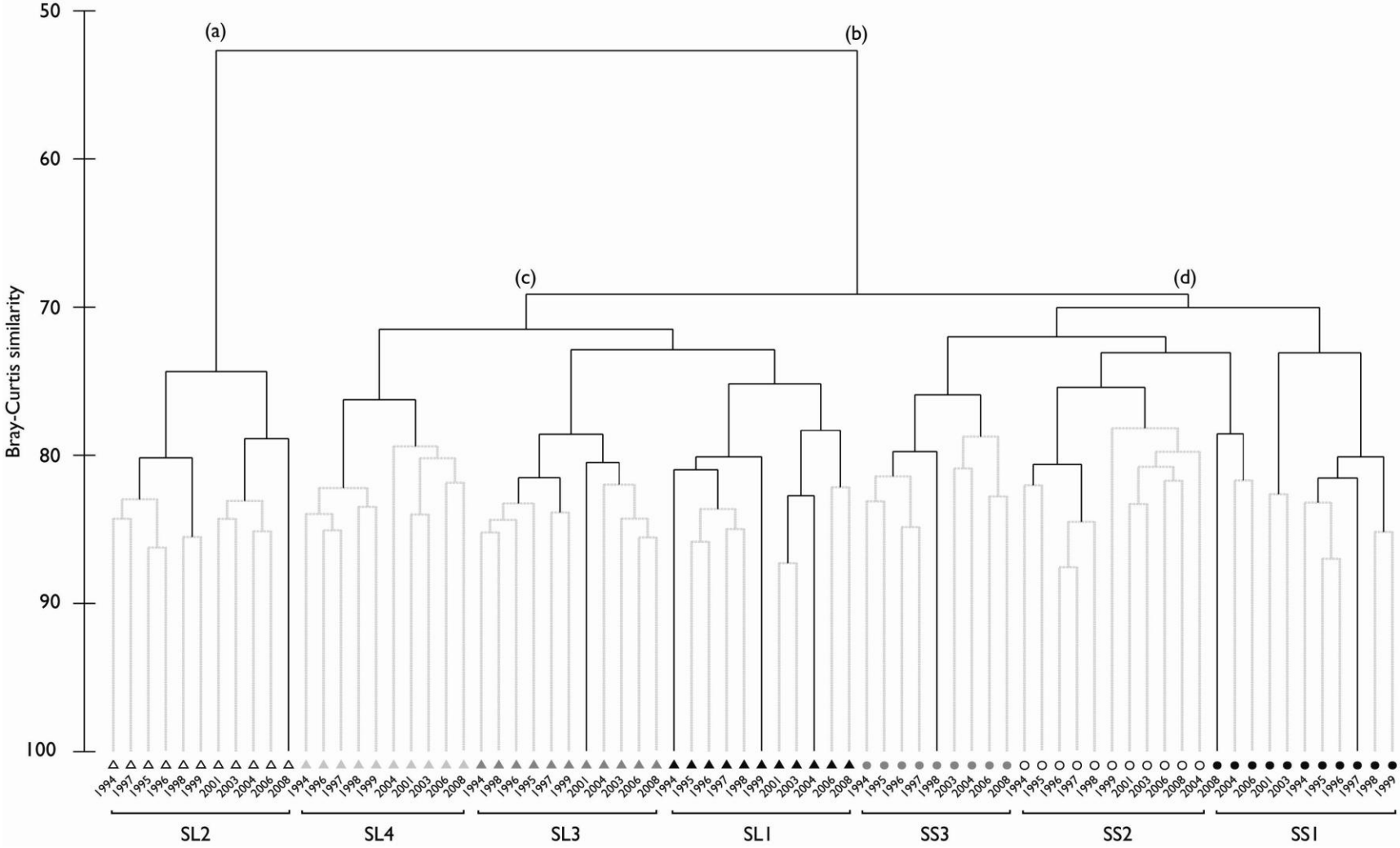


Fig. 3.2.12 CLUSTER analysis dendrogram of the mean densities of each fish species at seven locations at Scott Reef between 1994 and 2008. Solid lines indicate groups that the SIMPROF procedure determined were significantly different from each other

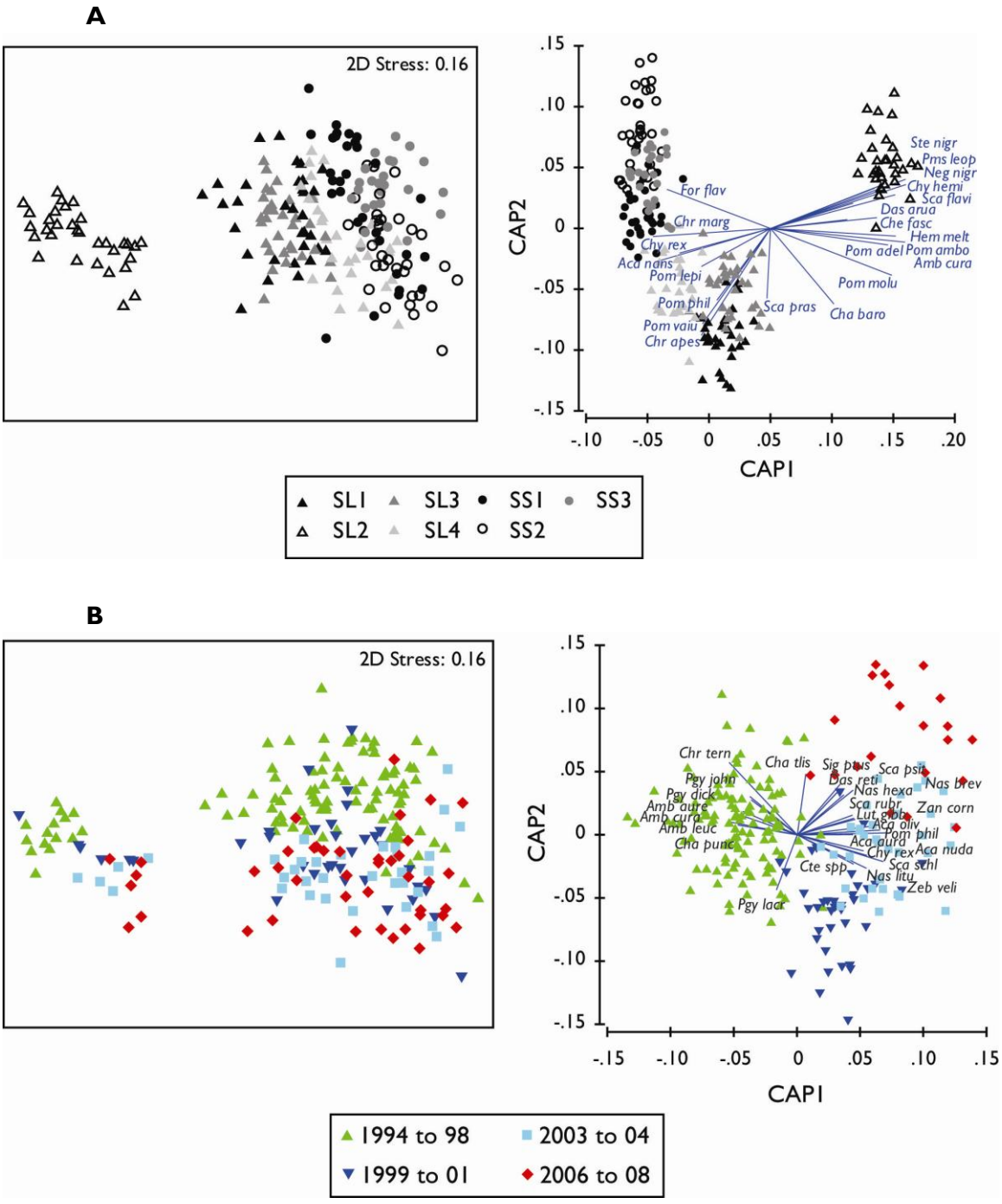


Fig. 3.2.13 Non-metric MDS ordination and canonical analysis of principal coordinates (CAP) plots of the species composition of fish assemblages at Scott Reef according to location (A) and year group (B).

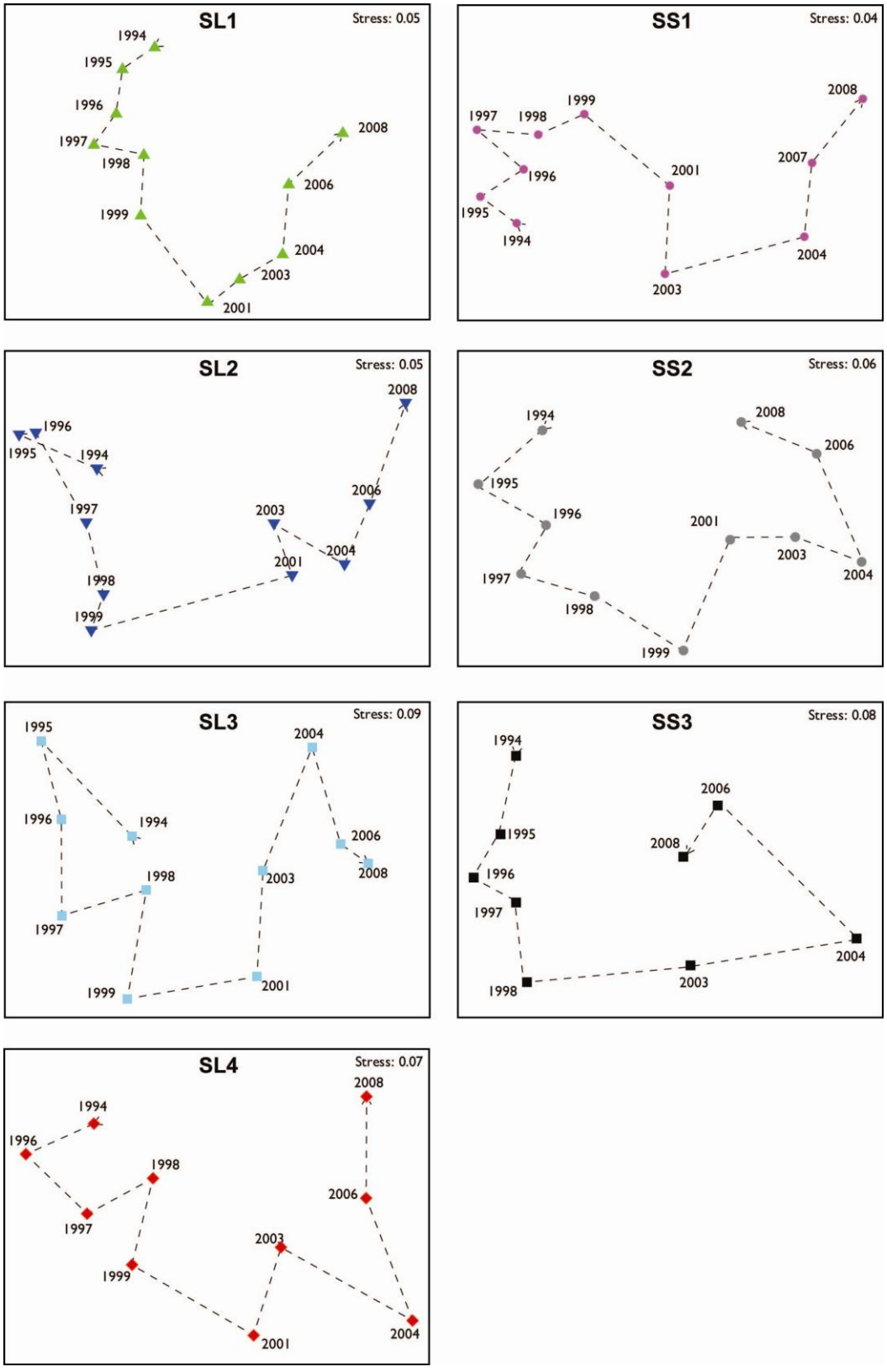


Fig. 3.2.14 Non-metric multidimensional scaling (nMDS) ordinations of the species compositions of fish assemblages at seven locations at Scott Reef between 1994 and 2008.

Discussion

Community trends in response to disturbance

Fish communities at Scott Reef have undergone significant change in composition through a 15 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% (Gilmour et al. 2009). The failure of the fish communities to return to a pre-bleaching state contrasts with benthic communities in the same system, which are now almost indistinguishable from those resident on the reef prior to bleaching (Gilmour et al. 2009). 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 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 damselfishes (Wilson et al. 2008). Following death of the coral and overgrowth by algae, abundances of herbivores increased, as did numbers of detritivores, which 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.

In highly connected reef systems, such the Great Barrier Reef, 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 coral reef systems 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 fish species to move among habitats in response to disturbance. However, a study of cryptobenthic fish communities on the Great Barrier Reef has also identified a shift from a pre-bleach to a post-bleach fish community (Bellwood et al. 2006a) that persisted for more than five years after the disturbance event (Bellwood *et al*. 2006). Both the present study and that of Bellowod et al. (2006a) recorded a significant increase in the number of trophic and habitat generalist species in post-bleaching fish assemblages. The late post-bleach fish community at Scott Reef is probably a transitional rather than a stable state, and continued monitoring at Scott Reef is required to determine if a return to pre-bleaching conditions will occur in future years.

Characteristics of bleached and non-bleached communities

A review of the effects of climate induced coral bleaching on coral 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. Our novel use of multivariate linkage trees (LINKTREE) has clearly demonstrated that the pre-bleach fish community at Scott Reef was correlated with greater contributions of branching *Acropora* and branching non-*Acropora* corals, each of which suffered massive mortality in the subsequent coral bleaching. The pre-bleached fish community at Scott Reef was characterized by the presence of coral dwelling fish species that feed mainly on coral or plankton such as *Chromis ternatensis*, *Pomacentrus amboinensis* and *Amblyglyphidodon curacao*. The intermediate post-bleach fish community between 2001 and 2004 was distinguished from that in 2008 by reduced contributions of corymbose and hispidose *Acropora*, encrusting corals, sponges and a greater contribution of turfing algae. It is not surprising that the fish species that distinguished this community (e.g. *Plectroglyphidodon lacrymatus* and *Pomacentrus amboinensis*) are not as reliant on live coral and feed predominantly on algae that they farm aggressively (Ceccarelli et al. 2001). 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) have stressed the importance of identifying and protecting groups of fishes involved in the resilience and regeneration of disturbed reef systems, thus the success of herbivorous fish species during the intermediate post-bleaching phase at Scott Reef, subsequent recovery of benthic communities and the significant relationship between the abundance of herbivores and percent cover of algae over a 15 year period, clearly indicates that herbivorous fish species have played an important role in the longer term resilience of Scott Reef (Nystrom and Folke 2001; Bellwood et al. 2004).

The increase of *Pomacentrus amboinensis* during the intermediate post-bleaching period is likely to be related to their preference for the rubble habitat (Wilson et al. 2008) that became more common at Scott Reef following the erosion and collapse of bleached coral skeletons during this period (Halford and Caley 2009). Dead coral or rubble-associated fishes also increased in numbers following disturbance at reefs in Papua New Guinea (Jones et al. 2004). 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). While the decline of coral dependent fish species following the bleaching was not surprising, as individuals must either move away to find the nutrition or protection from predators that corals provide or experience higher mortality (Pratchett et al. 2006; Pratchett et al. 2008), there were still unexpected and interesting

contrasts, particularly regarding variable rates of recovery at certain locations or for particular species. Thus, the recovery of coral associated plankton feeders was greatest at SL3 where the cooler tidal intrusions that characterise this location may lead to greater concentrations of plankton for these fish to feed on. In contrast, the abundance of plankton feeders remained low and stable at SL1 throughout the study period and may be related to the nutrient dynamics of this location that is subjected to a persistent oceanic eddy that may restrict productivity in this area (Brinkman 2007).

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 Great Barrier Reef, our results contrast, to some degree, with theirs for traditional abundance and diversity metrics. On the Great Barrier Reef, 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 and Nakazono 2001; Booth and 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.

Other changes in reef fish communities

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 15 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. This increase in abundance was accompanied by an increase in the numbers of 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 target 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 and Pacala 2005; DeMartini et al. 2008) have shown that 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 picivorous

and omnivorous 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.

References

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32-46

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E, Plymouth

Anderson MJ, Robinson J (2003) Generalized discriminant analysis based on distances. Australian & New Zealand Journal of Statistics 45: 301-318

Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. Ecology 84: 511-525

Bellwood DR, Fulton CJ (2008) Sediment-mediated suppression of herbivory on coral reefs: Decreasing resilience to rising sea levels and climate change? Limnology and Oceanography 53: 2695-2701

Bellwood DR, Hoey AS, Ackerman JL, Depczynski M (2006a) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Global Change Biology 12: 1587-1594

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

Bellwood DR, Hughes TP, Hoey AS (2006b) Sleeping functional group drives coral-reef recovery. Current Biology 16: 2434-2439

Bohnsack JA (1983) Species turnover and the order versus chaos controversy concerning reef fish community structure. Coral Reefs 1: 223-228

Booth DJ, Beretta GA (2002) Changes in a fish assemblage after a coral bleaching event. Marine Ecology-Progress Series 245: 205-212

Brinkman RM (2007) Physical oceanography and the corals of Scott Reef - patterns of disturbance and dynamics of recovery Australian Coral Reef Society Annual Symposium, Fremantle, Western Australia

Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90: 1478-1484

Cappo M, Meekan MR, Perry M, McCauley R, Harvey ES (2004) Traditional fishing puts the bite on sharks. Australasian Science 25: 29-32

Ceccarelli DM, Jones GP, McCook LJ (2001) Territorial damselfishes as determinants of the structure of benthic communities on coral reefs Oceanography and Marine Biology, Vol 39, pp 355-389

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) Nonparametric Multivariate Analyses of Changes in Community Structure. Australian Journal of Ecology 18: 117-143

Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92: 205-219

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 (1998) A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology 35: 523-531

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

Connell JH, Hughes TE, Wallace CC, Tanner JE, Harms KE, Kerr AM (2004) A long-term study of competition and diversity of corals. Ecological Monographs 74: 179-210

De'Ath G (2002) Multivariate regression trees: a new technique for modeling species-environment relationships. Ecology 83: 1105-1117

DeMartini EE, Friedlander AM, Sandin SA, Sala E (2008) Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. Marine Ecology-Progress Series 365: 199-215

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, McCormick MI, Jones GP (2007) Habitat choice, recruitment and the response of coral reef fishes to coral degradation. Oecologia 153: 727-737

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 1. 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

Guisan A, Edwards TC, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157: 89-100

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: in press

Halford AR, Thompson AA (1994) Visual Census Surveys of Reef Fish. Australian Institute of Marine Science Townsville, Australia

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, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318: 1737-1742

Holbrook SJ, Schmitt RJ, Brooks AJ (2008) Resistance and resilience of a coral reef fish community to changes in coral cover. Marine Ecology-Progress Series 371: 263-271

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, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: The link between benthic adults, fecundity, and larval recruits. Ecology 81: 2241-2249

Hughes TP, Connell JH (1999) Multiple stressors on coral reefs: A long-term perspective. Limnology and Oceanography 44: 932-940

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj 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

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 GP, Syms C (1998) Disturbance, habitat structure and the ecology of fishes on coral reefs. Australian Journal of Ecology 23: 287-297

Jones HA (1973) Marine geology of the northwest Australian continental shelf. Bureau of Mineral Resources. Geology and Geophysics Bulletin 136

Kokita T, Nakazono A (2001) Rapid response of an obligately corallivorous filefish Oxymonacanthas longirostris (Monacanthidae) to a mass coral bleaching event. Coral Reefs 20: 155-158

Kotze DJ, O'Hara RB (2003) Species decline - but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. Oecologia 135: 138-148

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: A comment on distance-based redundancy analysis. Ecology 82: 290-297

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

McKinney ML (1997) Extinction vulnerability and selectivity: Combining ecological and paleontological views. Annual Review of Ecology and Systematics 28: 495-516

Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. Ecological Economics 29: 215-233

Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. Fish and Fisheries 9: 261-285

Munday PL, Jones GP, Sheaves M, Williams AJ, Goby G (2007) Vulnerability of fishes on the Great Barrier Reef to climate change. In: Johnson J, Marshall P (eds) Climate Change and the Great Barrier Reef. Great Barrier Reef Marine Park Authority, Townsville, Australia, pp 357-391

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

Nystrom M, Folke C (2001) Spatial resilience of coral reefs. Ecosystems 4: 406-417

Pinheiro JC, Bates DM (2000) Mixed effects Models in S and S-PLUS. Springer

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

Pratchett MS, Wilson SK, Baird AH (2006) Declines in the abundance of Chaetodon butterflyfishes following extensive coral depletion. Journal of Fish Biology 69: 1269-1280

R Development Core Team (2007) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Sandin SA, Pacala SW (2005) Fish aggregation results in inversely density-dependent predation on continuous coral reefs. Ecology 86: 1520-1530

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

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

Sheppard CRC, Harris A, Sheppard ALS (2008) Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean. Marine Ecology-Progress Series 362: 109-117

Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. Ecology 81: 2714-2729

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 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, 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, Leno 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

Appendix

Appendix 3.2.1 List of fish species and their functional group classification

Species	Functional group level 1	Functional group level 2
Bolbometopon muricatum	corallivore	excavator
Chaetodon adiergastos	corallivore	facultative
Chaetodon auriga	corallivore	facultative
Chaetodon citrinellus	corallivore	facultative
Chaetodon ephippium	corallivore	facultative
Chaetodon flavirostris	corallivore	facultative
Chaetodon kleinii	corallivore	facultative
Chaetodon lineolatus	corallivore	facultative
Chaetodon lunula	corallivore	facultative
Chaetodon oxycephalus	corallivore	facultative
Chaetodon rafflesii	corallivore	facultative
Chaetodon semeion	corallivore	facultative
Chaetodon speculum	corallivore	facultative
Chaetodon vagabundus	corallivore	facultative
Chaetodon aureofasciatus	corallivore	obligate
Chaetodon baronessa	corallivore	obligate
Chaetodon bennetti	corallivore	obligate
Chaetodon meyeri	corallivore	obligate
Chaetodon octofasciatus	corallivore	obligate
Chaetodon ornatissimus	corallivore	obligate
Chaetodon pelewensis	corallivore	obligate
Chaetodon plebeius	corallivore	obligate
Chaetodon punctatofasciatus	corallivore	obligate
Chaetodon rainfordi	corallivore	obligate
Chaetodon reticulatus	corallivore	obligate
Chaetodon trifascialis	corallivore	obligate
Chaetodon trifasciatus	corallivore	obligate
Cheiloprion labiatus	corallivore	obligate
Plectroglyphidodon johnstonianus	corallivore	obligate
Chaetodon melannotus	corallivore	soft coral
Chaetodon ulietensis	corallivore	soft coral
Chaetodon unimaculatus	corallivore	soft coral
Ctenochaetus spp	detritivore	detritivore
Ctenochaetus striatus	detritivore	detritivore
Hemiglyphidodon plagiometopon	detritivore	detritivore
Acanthurus blochii	detritivore	EAM feeder
Acanthurus dussumieri	detritivore	EAM feeder
Acanthurus grammoptilus	detritivore	EAM feeder
Acanthurus leucocheilus	detritivore	EAM feeder
Acanthurus maculiceps	detritivore	EAM feeder
Acanthurus nigricauda	detritivore	EAM feeder
Acanthurus olivaceus	detritivore	EAM feeder

Appendix 1 continued. List of fish species and their functional group classification

Species	Functional group level 1	Functional group level 2
Acanthurus xanthopterus	detritivore	EAM feeder
Ctenochaetus binotatus	detritivore	EAM feeder
Ctenochaetus strigosus	detritivore	EAM feeder
Dischistodus perspicillatus	detritivore	EAM feeder
Stegastes nigricans	detritivore	EAM feeder
Calotomus carolinus	herbivore	algae feeder
Naso brachycentron	herbivore	algae feeder
Naso lituratus	herbivore	algae feeder
Naso spp	herbivore	algae feeder
Naso tuberosus	herbivore	algae feeder
Naso unicornis	herbivore	algae feeder
Acanthurus auranticavus	herbivore	algae feeder
Acanthurus bariene	herbivore	algae feeder
Acanthurus fowleri	herbivore	algae feeder
Acanthurus lineatus	herbivore	algae feeder
Acanthurus nigricans	herbivore	algae feeder
Acanthurus nigrofuscus	herbivore	algae feeder
Acanthurus pyroferus	herbivore	algae feeder
Acanthurus spp	herbivore	algae feeder
Acanthurus triostegus	herbivore	algae feeder
Chrysiptera biocellata	herbivore	algae feeder
Dischistodus melanotus	herbivore	algae feeder
Dischistodus prosopotaenia	herbivore	algae feeder
Dischistodus pseudochrysopoecilus	herbivore	algae feeder
Plectroglyphidodon lacrymatus	herbivore	algae feeder
Pomacentrus adelus	herbivore	algae feeder
Pomacentrus chrysurus	herbivore	algae feeder
Pomacentrus grammorhynchus	herbivore	algae feeder
Pomacentrus tripunctatus	herbivore	algae feeder
Pomacentrus wardi	herbivore	algae feeder
Siganus argenteus	herbivore	algae feeder
Siganus corallinus	herbivore	algae feeder
Siganus doliatus	herbivore	algae feeder
Siganus lineatus	herbivore	algae feeder
Siganus puellus	herbivore	algae feeder
Siganus punctatissimus	herbivore	algae feeder
Siganus punctatus	herbivore	algae feeder
Siganus spinus	herbivore	algae feeder
Siganus vulpinus	herbivore	algae feeder
Stegastes apicalis	herbivore	algae feeder
Stegastes fasciolatus	herbivore	algae feeder
Stegastes gascoynei	herbivore	algae feeder
Stegastes lividus	herbivore	algae feeder
Zebrasoma scopas	herbivore	algae feeder

Appendix 1 continued. List of fish species and their functional group classification

Species	Functional group level 1	Functional group level 2
Zebrasoma veliferum	herbivore	algae feeder
Cetoscarus bicolor	herbivore	excavator
Chlorurus bleekeri	herbivore	excavator
Chlorurus japanensis	herbivore	excavator
Chlorurus microrhinos	herbivore	excavator
Chlorurus sordidus	herbivore	excavator
Hipposcarus longiceps	herbivore	scrapers
Scarus altipinnis	herbivore	scrapers
Scarus chameleon	herbivore	scrapers
Scarus dimidiatus	herbivore	scrapers
Scarus flavipectoralis	herbivore	scrapers
Scarus forsteni	herbivore	scrapers
Scarus frenatus	herbivore	scrapers
Scarus ghobban	herbivore	scrapers
Scarus globiceps	herbivore	scrapers
Scarus niger	herbivore	scrapers
Scarus oviceps	herbivore	scrapers
Scarus prasiognathos	herbivore	scrapers
Scarus psittacus	herbivore	scrapers
Scarus rivulatus	herbivore	scrapers
Scarus rubroviolaceus	herbivore	scrapers
Scarus schlegeli	herbivore	scrapers
Scarus spinus	herbivore	scrapers
Cheilinus chlorourus	invertivore	invertivore
Cheilinus fasciatus	invertivore	invertivore
Cheilinus trilobatus	invertivore	invertivore
Cheilinus undulatus	invertivore	invertivore
Choerodon fasciatus	invertivore	invertivore
Coris aygula	invertivore	invertivore
Coris gaimard	invertivore	invertivore
Epibulus insidiator	invertivore	invertivore
Forcipiger flavissimus	invertivore	invertivore
Forcipiger longirostris	invertivore	invertivore
Gomphosus varius	invertivore	invertivore
Halichoeres biocellatus	invertivore	invertivore
Halichoeres hortulanus	invertivore	invertivore
Hemigymnus fasciatus	invertivore	invertivore
Hemigymnus melapterus	invertivore	invertivore
Lethrinus harak	invertivore	invertivore
Monotaxis grandoculis	invertivore	invertivore
Zanclus cornutus	invertivore	invertivore
Chaetodon mertensii	omnivore	non coral
Acanthochromis polyacanthus	omnivore	omnivore
Amblyglyphidodon curacao	omnivore	omnivore

Appendix 1 continued. List of fish species and their functional group classification

Species	Functional group level 1	Functional group level 2
Amblyglyphidodon leucogaster	omnivore	omnivore
Amphiprion akindynos	omnivore	omnivore
Amphiprion chrysopterus	omnivore	omnivore
Amphiprion clarkii	omnivore	omnivore
Amphiprion melanopus	omnivore	omnivore
Amphiprion ocellaris	omnivore	omnivore
Amphiprion percula	omnivore	omnivore
Amphiprion perideraion	omnivore	omnivore
Amphiprion sandaracinos	omnivore	omnivore
Amphiprion spp	omnivore	omnivore
Chelmon rostratus	omnivore	omnivore
Chrysiptera rex	omnivore	omnivore
Gnathodentex aureolineatus	omnivore	omnivore
Lethrinus atkinsoni	omnivore	omnivore
Lethrinus erythracanthus	omnivore	omnivore
Lethrinus erythropterus	omnivore	omnivore
Lethrinus miniatus	omnivore	omnivore
Lethrinus nebulosus	omnivore	omnivore
Lethrinus obsoletus	omnivore	omnivore
Lethrinus olivaceus	omnivore	omnivore
Lethrinus ornatus	omnivore	omnivore
Lethrinus rubrioperculatus	omnivore	omnivore
Lethrinus xanthochilus	omnivore	omnivore
Lutjanus adetii	omnivore	omnivore
Lutjanus argentimaculatus	omnivore	omnivore
Lutjanus biguttatus	omnivore	omnivore
Lutjanus bohar	omnivore	omnivore
Lutjanus carponotatus	omnivore	omnivore
Lutjanus decussatus	omnivore	omnivore
Lutjanus erythropterus	omnivore	omnivore
Lutjanus fulviflammus	omnivore	omnivore
Lutjanus fulvus	omnivore	omnivore
Lutjanus gibbus	omnivore	omnivore
Lutjanus kasmira	omnivore	omnivore
Lutjanus lemniscatus	omnivore	omnivore
Lutjanus lutjanus	omnivore	omnivore
Lutjanus monostigma	omnivore	omnivore
Lutjanus quinquelineatus	omnivore	omnivore
Lutjanus rivulatus	omnivore	omnivore
Lutjanus russellii	omnivore	omnivore
Lutjanus sebae	omnivore	omnivore
Lutjanus semicinctus	omnivore	omnivore
Lutjanus vitta	omnivore	omnivore
Macolor spp	omnivore	omnivore

Appendix 1 continued. List of fish species and their functional group classification

Species	Functional group level 1	Functional group level 2
Neoglyphidodon melas	omnivore	omnivore
Neoglyphidodon nigroris	omnivore	omnivore
Oxycheilinus celebicus	omnivore	omnivore
Oxycheilinus digrammus	omnivore	omnivore
Oxycheilinus orientalis	omnivore	omnivore
Oxycheilinus unifasciatus	omnivore	omnivore
Plectroglyphidodon dickii	omnivore	omnivore
Pomacentrus amboinensis	omnivore	omnivore
Pomacentrus australis	omnivore	omnivore
Pomacentrus bankanensis	omnivore	omnivore
Pomacentrus brachialis	omnivore	omnivore
Pomacentrus moluccensis	omnivore	omnivore
Pomacentrus nagasakiensis	omnivore	omnivore
Pomacentrus nigromarginatus	omnivore	omnivore
Pomacentrus pavo	omnivore	omnivore
Pomacentrus vaiuli	omnivore	omnivore
Premnas biaculeatus	omnivore	omnivore
Gracila albomarginata	piscivore	piscivore
Plectropomus areolatus	piscivore	piscivore
Plectropomus laevis	piscivore	piscivore
Plectropomus leopardus	piscivore	piscivore
Plectropomus maculatus	piscivore	piscivore
Plectropomus oligacanthus	piscivore	piscivore
Variola albimarginata	piscivore	piscivore
Variola louti	piscivore	piscivore
Acanthurus albipectoralis	planktivore	planktivore
Acanthurus mata	planktivore	planktivore
Acanthurus thompsoni	planktivore	planktivore
Amblyglyphidodon aureus	planktivore	planktivore
Chromis acares	planktivore	planktivore
Chromis agilis	planktivore	planktivore
Chromis amboinensis	planktivore	planktivore
Chromis atripectoralis	planktivore	planktivore
Chromis atripes	planktivore	planktivore
Chromis chrysura	planktivore	planktivore
Chromis iomelas	planktivore	planktivore
Chromis lepidolepis	planktivore	planktivore
Chromis lineata	planktivore	planktivore
Chromis margaritifer	planktivore	planktivore
Chromis nitida	planktivore	planktivore
Chromis retrofasciata	planktivore	planktivore
Chromis ternatensis	planktivore	planktivore
Chromis vanderbilti	planktivore	planktivore
Chromis viridis	planktivore	planktivore

Appendix 1 continued. List of fish species and their functional group classification

Species	Functional group level 1	Functional group level 2
Chromis weberi	planktivore	planktivore
Chromis xanthochira	planktivore	planktivore
Chromis xanthura	planktivore	planktivore
Chrysiptera flavipinnis	planktivore	planktivore
Chrysiptera hemicyanea	planktivore	planktivore
Chrysiptera rollandi	planktivore	planktivore
Chrysiptera talboti	planktivore	planktivore
Dascyllus aruanus	planktivore	planktivore
Dascyllus melanurus	planktivore	planktivore
Dascyllus reticulatus	planktivore	planktivore
Dascyllus trimaculatus	planktivore	planktivore
Hemitaurichthys polylepis	planktivore	planktivore
Macropharyngodon spp	planktivore	planktivore
Naso brevirostris	planktivore	planktivore
Naso vlamingii	planktivore	planktivore
Neoglyphidodon polyacanthus	planktivore	planktivore
Neopomacentrus azysron	planktivore	planktivore
Neopomacentrus bankieri	planktivore	planktivore
Neopomacentrus cyanomos	planktivore	planktivore
Paracanthurus hepatus	planktivore	planktivore
Pomacentrus coelestis	planktivore	planktivore
Pomacentrus lepidogenys	planktivore	planktivore
Pomacentrus philippinus	planktivore	planktivore
Pomachromis richardsoni	planktivore	planktivore
Naso hexacanthus	planktivore	planktivore

3.3. Demographic analysis of coral populations: contrasting life histories, stage classes and disturbance regimes

Introduction

A primary aim of coral ecology is to understand the causes and consequences of patterns of change of communities under varying environmental conditions. To this end, monitoring programs have documented the impact of natural disturbances and the subsequent recovery of communities over periods of years to decades. Today, however, monitoring programs must also quantify the impacts of anthropogenic disturbances, which are jeopardising the condition of coral reefs globally (Downs et al. 2005). Evidence of the combined effect of natural and man-made disturbance is provided by many accounts of a changing community structure and/or reduced coral cover on reefs around the world, of which the worst cases involve a phase-shift to a system dominated by algae (Hughes 1994; Shulman and Robertson 1996; Ostrander et al. 2000; Aronson et al. 2002). In these instances, there is often a complex combination of social and economic causes underlying the degradation. In order to prevent and remedy these problems we need to 1) fully understand *why* the degradation had occurred and 2) quantify the consequences for communities if the stressors are not mitigated.

Traditionally, monitoring programs of coral communities have quantified changes in percentage cover of various benthic categories (e.g. corals, algae, rubble). These data are then correlated with major changes in key biological (e.g. crown-of-thorns starfish, pathogens) or physical parameters (e.g. cyclones, sedimentation). Such studies have provided valuable information about the distribution of different coral communities on reefs around the world and their exposure and resilience to a range of natural and anthropogenic disturbances (e.g. Brown et al. 2002; DeVantier et al. 2006); when combined with the information obtained from manipulative experiments over smaller spatial and temporal scales (Knowlton and Jackson 2008), long-term monitoring studies underpin much of our current knowledge of coral reef ecology. However, coral reefs today are exposed to an increasing number, frequency and combination of disturbances and stressors (Jackson et al. 2001; Knowlton 2001; Pandolfi et al. 2003; Hughes et al. 2007; Wilkinson 2008). Understanding the effects of these multiple stressors requires more comprehensive studies, particularly if the consequences of anthropogenic disturbances are to be decoupled from background (natural) disturbances (Downs et al. 2005; Smith et al. 2005; Knowlton and Jackson 2008). Monitoring studies on many reefs around the world now require information not just about how but also *why* coral communities have changed, and some indication of the future consequences for these ecosystems under different scenarios. Collection of demographic data in combination with a monitoring program can address this need.

Demographic studies can help to explain why coral communities have changed and provide some indication of the future consequences of these changes, beyond what can be inferred from percentage cover data alone. For example, percentage cover data is strongly influenced by the largest corals within the community. The abundance of new recruits and small

individuals contribute little to percentage cover, yet it is these individuals that are among the most susceptible to common stressors (e.g. sedimentation, algal competition) and are required for future maintenance of populations (Hunte and Wittenberg 1992; Connell et al. 1997; Bak and Meesters 1999; Birrell et al. 2008). For example, under conditions of degraded water quality, in which rates of recruitment and survival of the smallest colonies are chronically reduced, percentage cover data will provide little warning of the long-term consequences for population maintenance. The consequences of this stressor will only become evident several years after their onset when loss of recruits finally flows through to adult populations. In addition to compromising population maintenance, loss of small recruits dramatically reduces resilience to further disturbances.

For these reasons, it is prudent that a long term monitoring study not only quantifies changes in percentage cover and community structure in response to disturbances and stressors, but also provides a demographic explanation for the changes, so that there is a causal link between the changes and the stressor(s), and some indication of the future consequences for communities. Quantifying changes in the rates of recruitment, growth and survival of classes of individuals of representative coral species, as the population's vital rates, provides a demographic explanation for observed changes in percentage cover (e.g. Caswell 1989; Hughes 1996; Lirman and Miller 2003). The application of these data to simple matrix models also yields a single measure of 'population health', the asymptotic growth rate (λ), which estimates the contribution of life history stages to population maintenance and can project the future consequences of disturbance (Caswell 1989; Ebert 1999). For example, in the previous scenario of degraded water quality, reductions in recruitment and survival of the smallest size classes would be detected in demographic data, as would the sub-lethal impacts (e.g. growth, injury, reproduction) on the larger colonies. The cumulative impact on these different life history stages and traits would be evident in the population's growth rate, providing a relative estimate of the likely decreases (or increases) in population size should the conditions persist. The associated changes in population structure could then be projected over time and linked to changes in percentage cover, to show the potential consequences for the population if the stressors are not mitigated. Inferences about the life history stages and traits (e.g. recruitment, juvenile survival) that are most important to population maintenance and are impacted by the disturbance can then be derived from the model output (elasticities) (Ebert 1999; Caswell 2000; Bruna and Oli 2005). Importantly, apparent links between life history stages/traits and stressor(s) can then be tested in experiments to confirm links between the disturbance and the demographic reason(s) for the degradation, which can inform management strategies (Downs et al. 2005). For these reasons, demographic data provides a valuable tool in the task of prevention of the degradation of coral communities.

Despite the benefits of a demographic approach, relatively few studies have collected and applied demographic data to coral populations, with some notable exceptions (e.g. Done 1987; Babcock 1991; McFadden 1991; Hughes 1996; Fong and Glynn 2000; Edmunds 2005; Done et al. 2007). The lack of studies is due partly to their being logistically difficult and the considerable variation that usually exists in parameter estimates, both of which increase bias in results and make the interpretation of the impacts of disturbances more difficult. Such

variability arises from both demographic and temporal (stochasticity) sources (Ebert 1999). The former occurs in corals as they are long-lived, clonal organisms that have a complex life cycle that includes pelagic larvae that are sexually produced, a variety of asexual recruits and juvenile and adult stages whose growth (size) can increase or decrease (partial-mortality) rapidly (Hughes et al. 1992). Associated with these changes in size are changes in other life history traits, such as fecundity and survival. Consequently, the appropriate choice of size/stage classes for demographic models is particularly important. In addition to this demographic variation, disturbance creates temporal variation in coral communities (Tanner et al. 1996; Connell 1997). Corals are characteristically found in shallow water in tropical regions, where they are exposed to disturbances of varying scale and severity; there are minor but frequent stressors such as high winds, sedimentation, predation, and less frequent but more severe disturbances such as cyclones or elevated water temperatures (e.g. Bythell et al. 1993b).

Here, we present the preliminary results of a demographic study of two common groups of corals at Scott Reef, a system of reef atolls off north-west Australia. We investigate the importance of demographic and temporal variation by comparing rates of growth and recruitment among life history stages, species and disturbance regimes. For one species, vital rates are incorporated into population matrix models and outputs compared among life history stages, locations and disturbance regimes.

Materials and Methods

Study species and life-cycle stage classes

The study species were replicate colonies of *Acropora spicifera* and *Goniastrea spp.*. The *Goniastrea spp.* group consisted of *G. retiformis* and *G. edwardsii*, because the density of any one species alone was not sufficient to provide the required replication for the study. *Goniastrea retiformis* and *G. edwardsii* are closely related, have the same growth form and are distinguished primarily by differences in corallite shape and structure. Thus, an important assumption is that the differences between these two species are too small to confound demographic analysis of their populations as a group.

The life cycle of both species groups was divided among size classes that roughly corresponded to stages of ecological relevance. In particular, new recruits were <5 cm in diameter, colonies matured at 15 cm in diameter, and colony area increased greatly above 25 cm diameter. Thus, the life cycle and transitions through the life cycle were defined by the following size/stage classes: recruits <5 cm; juveniles 5 to 15 cm; adults 15 to 25 cm; and large adults >25 cm (Fig. 3.3.1). The demographic data for recruits was limited to colonies ≥1cm in maximum diameter. Rates of recruitment, survival and growth of corals <1cm were not quantified, as reliable information at this cryptic stage could not be obtained. However, rates of recruitment, growth and survival of corals <1cm were accounted for, as the differences between the number of corals <5 cm, and the number of corals ≥1 cm to <5 cm.

Colony size and growth were defined by maximum colony diameter, rather than area. Both *Acropora spicifera* and *Goniastrea spp.* colonies have an elliptical growth form when viewed from above. Growth and changes in colony size were quantified from photographs taken each year directly above the colony and/or at right angles to the maximum colony length when first tagged. Colony images were digitised to provide estimates of colony perimeter, area and maximum diameter. The maximum diameter of colonies was strongly correlated with area (n = 4042; Adj. $R^2 = 0.97$; Area = 16.74 – 2.56 diameter + 0.56 diameter^2), and was a good predictor of colony area regardless of size. Consequently, maximum diameter was used to quantify annual rates of growth and decreases in colony size due to injury, as changes in length could be more easily interpreted than changes in area.

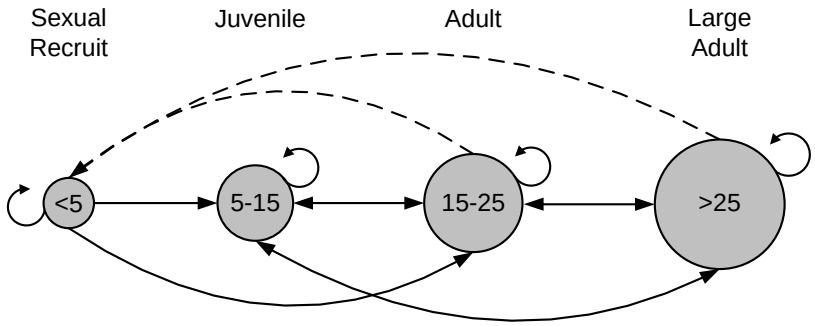
Defining locations and populations

This study was conducted at 4 locations across Scott Reef. None of the locations were on the outside of the reef at the reef slope habitat, because working the reef slope habitat is weather dependent and demographic study required guaranteed access to study sites at this remote atoll system. Although all study locations were characterised as lagoonal habitat, they were exposed to different physical conditions, particularly current speeds (Smith et al. 2008). In general, SL4 was situated at the bottom of North Reef on the edge of the deep channel and

was the location most exposed to high currents; SL1 and SL3 were at the east and west hook of South Reef, respectively, and exposed to moderate currents; SL2 was at the bottom of the South Reef lagoon and was most sheltered from currents and waves.

At each location, two study sites were separated by approximately 300m in water depths of between 3 and 6 m. Each study site was approximately 50 m x 25 m in area. In each, colonies of *A. spicifera* were first tagged in 2006, while colonies of *Goniastrea spp.* were first tagged in 2008, to provide a comparison between species of coral with contrasting life histories. Analysis of survival data indicated no differences between sites within locations (Appendix 1), so sites were pooled and data analysed and presented at the scale of the location.

A)



B)

	FROM	1 Sexual Recruits	2 Juveniles	3 Adult	4 Large Adult
	TO	(<5cm)	(5-15cm)	(15-25cm)	(>25cm)
1	Sexual recruits (<5cm)	1,1 r_{SR}		1,3 f_{SR}	1,4 f_{SR}
2	Juveniles (5-15cm)	2,1 g_J	2,2 r_J	2,3 g_J	2,4 g_J
3	Adult (15-25cm)	3,1 g_A	3,2 g_A	3,3 r_A	3,4 r_A
4	Large Adult (>25cm)		4,2 g_{LA}	4,3 g_{LA}	4,4 r_{LA}

Fig. 3.3.1 Life cycle diagram and transition matrix for *Acropora spicifera* at Scott Reef.
A) Life cycle diagram. Colonies may remain within a size/stage class (↻) or make the transition to another size class (→) between censuses. Size classes (cm) correspond to life history stages; sexual recruits, juveniles, adults and large adults. B) Size-structured transition matrix. Colonies may remain (r_x) within a size class, or go (g_x) to another size class within a year. Sexual recruits are produced by adult and large adult colonies (f_x) each year. Not all transitions are possible and element notation corresponds to the output for each matrix projection. For example, 1,4 f_{SR} is the contribution of sexual recruits by large adult colonies, and 3,2 g_{Fj} is the transition of juvenile colonies to adult colonies.

The size-frequency distribution of each study species was quantified along permanent transects in 2008 and 2009. At each of the two sites at each location, three permanent transects (30 m) were established. Along each transect, the maximum diameter of colonies was measured to the nearest centimetre within a width of 0.25m from the transect centre line for colonies <10 cm, and within a width of 2 m for colonies >10 cm. At a few sites or for a few years, transect width was increased to account for variation in density and ensure sufficient replication. Given negligible differences in demography of colonies between replicate sites at each location, the size-frequency data were pooled at the scale of the location. The population at each location was defined by the sum of the size-frequency distributions of six transects; three at each of two sites. The size-frequency distributions for colonies ≤10cm and >10cm along each transect were standardised to an area of 30 m x 2 m (60m^2), and then summed across all six transects. Thus, the population at each location was defined as the number and size of colonies within an area of 360m^2. The number of recruits (< 5cm), juveniles (5 to 15cm), adults (15 to 25cm) and large adults (>25 cm) was calculated from the size-frequency distribution of colonies within the 360m^2 that defines each population/location.

Population vital rates and matrix models: Acropora spicifera

Rates of recruitment were adjusted to account for the number of adult colonies (≥15 cm). The number of recruits per adult colony was then adjusted to account for the different contribution of adults and large adults. The contribution of adults and large adults to recruitment was assumed to vary proportionately to the area of colonies within each of these size classes, since fecundity and reproductive output in corals are known to increase exponentially with colony area, given the corresponding increase in the number of polyps ((Hall and Hughes 1996). The strong correlation (n = 4042; Adj. R^2 = 0.97; Area = 16.74 – 2.56 diameter + 0.56 diameter^2) between maximum diameter and area was used to calculate the mean area of each colony within the adult and large adult stages, at each location. The total area and number of colonies was then used to calculate the mean colony area. The mean colony area of small and large adults was then divided by the sum of both to calculate the proportional contribution to colony area; this proportion was then multiplied by the mean number of recruits per adult to estimate the contribution of small and large adults to recruitment, adjusted for differences in colony area (see Table 3.3.1).

The annual rates of growth and survival determine the mean rates of transition of individuals through their life cycle within the population, such as the probability of a juvenile coral surviving and growing to adult size, or a large adult being injured and shrinking. Collectively, these mean rates of transition are the population's vital rates (Table 3.3.2). The transitions between life history stages at each census were divided into the proportion of polyps remaining (R_x) in their current stage, or going (G_x) to another stage, and multiplied by their yearly rates of survival to give yearly rates of remaining (r_x), or going (g_x) (Ebert 1999). All transition probabilities were investigated to determine whether they were realistic, and adjustments made to the rates if appropriate (Ebert 1999). For example, a mean rate of survival for all individuals within a stage class can not be 100% yr^{-1}, which is an artefact of insufficient replication; if 20 large adults were tagged then all may survive the year by chance,

but if 2000 were tagged some mortality would be inevitable. For projection models that run over many iterations (years) of the vital rates to the point of convergence, mean rates of survival of 100% must be reduced to a more accurate estimate. For the large adults, the maximum rate of remaining as large adults was reduced to 0.86 where necessary, which was based on their rates of growth, maximum sizes within populations, and an inferred maximum time they could remain in this stage (32 years).

The transition matrices (vital rates) for each population and annual survey period (Table 3.3.2) were applied to stage-structured matrix models (Caswell 1989). Transition matrices were analysed using the program MATRIX.BAS to give the finite population growth rate (Lambda; λ), stable-stage distribution and elasticities (Ebert 1999). A population is increasing in size if $\lambda > 1$, and decreasing in size if $\lambda < 1$. The stable-stage distribution is the relative abundance (c_x) of each stage once the matrix has converged, and the rate of convergence is indicated by the dampening ratio (ρ) (Ebert 1999). Populations that are slow to converge will have a small dampening ratio. Elasticities (e_i) are the proportional contribution of life history stages and their transitions to the population growth rate (λ).

Results

Growth and Survival: Acropora spicifera *and* Goniastrea spp.

The rates of growth and survival of *A. spicifera* colonies during the first two years of the study (2006-2008; 2007-2008) were strongly influenced by the passing of Cyclone George in March 2007. However, the impacts of the cyclone varied among locations and colony size classes. For locations and size classes that were worst affected, the reductions in growth and survival were evident over two survey periods because the cyclone occurred within approximately two months of the end of the first period and the start of the second (May 2007). Location SL3 was most exposed to the cyclone, and the reductions in colony growth and particularly survival were evident during the first survey period; location SL4 was less exposed and the impacts were slower to manifest, with survival during the first survey period being higher than at SL3 (Fig. 3.3.2; 3.3.3). However, by the end of the second period, the colonies at SL4 that had been injured by the cyclone continued to lose their tissue and many eventually died, causing a mean negative rate of growth for the largest colonies, and rates of survival similar to those at the SL3 (Fig. 3.3.2; 3.3.3). In comparison, there was limited evidence of cyclone impact at location SL1 and no apparent impact at SL2 (Fig. 3.3.2; 3.3.3).

Rates of survival of all size classes at locations SL1 and SL2 were > 80% yr^{-1} during the first two survey periods (2006-2008) (Fig. 3.3.2). The rates of colony growth varied more among these sheltered locations than did survival, and were consistently slower at SL1 than SL2 for all size classes (Fig. 3.3.3). Mean rates of growth at SL1 ranged between 2.3 and 5.5 cm yr^{-1} over the two year period, compared with 4.5 and 9.2 cm yr^{-1} at SL2. The lower rates of survival and growth at SL1 suggest minor impact from Cyclone George, which was supported by a higher rate of injury (16%) to the larger colonies (>15cm), compared with SL2 (2%).

Although greater than at SL2, any impact from Cyclone George at SL1 was far less than at the exposed locations. For example, the rate of injury to colonies over the two year period was 40% at SL4, while at SL3 a low rate of injury of 8% was an artefact of few colonies surviving long enough to be recorded with an injury, due to their high rates of mortality following the cyclone.

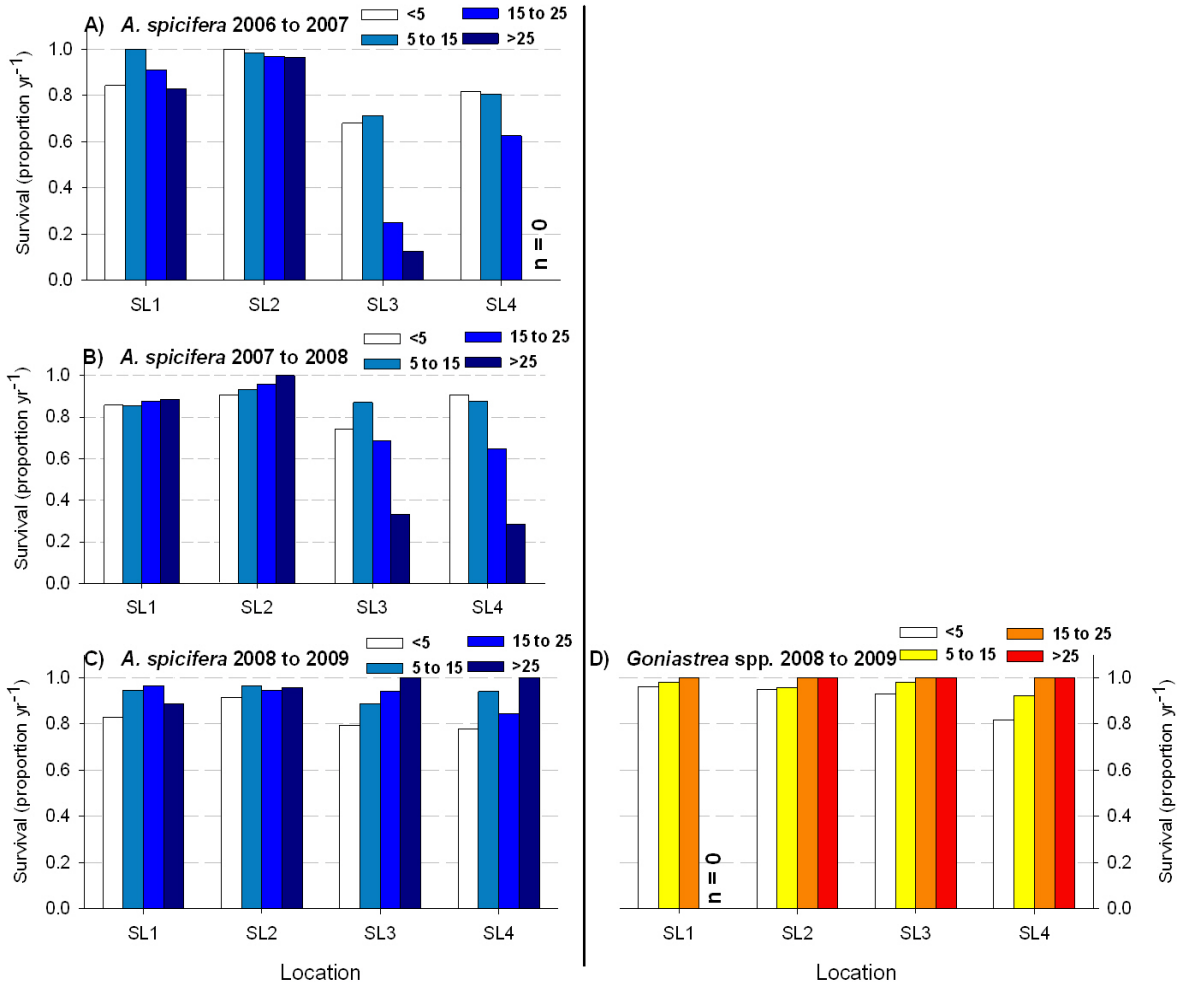


Fig. 3.3.2 Rates of survival for colonies in different size classes and locations. Annual surveys were conducted in May each year; *Acropora spicifera* was first tagged in 2006 and *Goniastrea spp.* first tagged in 2008. Survey periods were 1) 2006 to 2007; 2) 2007 to 2008 and 3) 2008 to 2009. Cyclone George impacted communities in March 2007.

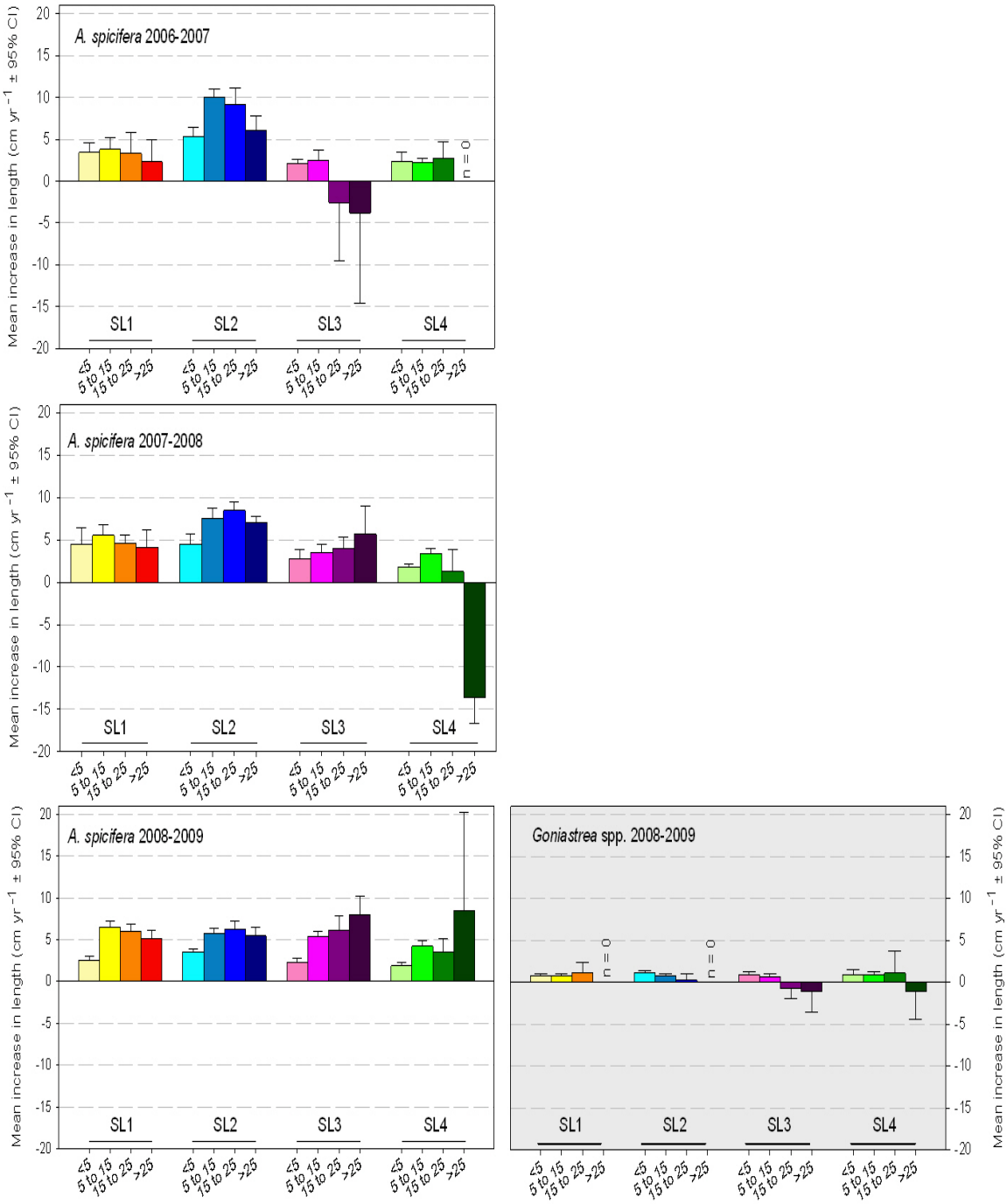


Fig. 3.3.3 Mean rates of growth for colonies in different size classes and locations. Growth is the change maximum colony diameter (cm). Injured colonies can decrease in size due to the loss of live tissue, which can result in mean negative rates of growth for the size class. Annual surveys were conducted in May each year; *Acropora spicifera* was first tagged in 2006 and *Goniastrea spp.* first tagged in 2008. Survey periods were 1) 2006 to 2007; 2) 2007 to 2008 and 3) 2008 to 2009. Cyclone George impacted communities in March 2007.

The impact of Cyclone George on the growth and survival of colonies at locations SL3 and SL4 varied differently among the colony size classes over the first two survey periods. The first survey period ended approximately two months after Cyclone George. At this time, survival of all size classes was lowest at SL3, then SL4, and rates of survival were inversely related to colony size class, being lowest for the largest colonies (although colonies in the largest colonies were not found at SL4 and could not be tagged). The rates of survival of the smaller (<15cm) size classes at SL3 (>67%) and particularly SL4 (>80%) were closer to those (> 80%) at the locations (SL1, SL2) sheltered from the cyclone, whereas rates of survival of the larger size classes (> 15cm) were much lower (<63%) at SL4 and particularly SL3 (<25%) than at the sheltered locations (Fig. 3.3.2).

A similar pattern of variation in rates of survival among locations and size classes existed for rates of growth. The severe and immediate impact of the cyclone on the larger (>15 cm) colonies at SL3 was evident in their rates of growth during the first survey period (Fig. 3.3.3). The incidence of injury to these larger size classes was much higher (40%) than at the other locations (<25%), resulting in mean negative rates of growth (Fig. 3.3.3). By comparison, the mean rate of growth (2.7 cm yr^{-1}) of the larger size class (15 to 25 cm) at SL4 was more similar to that at location SL1 (3.3. cm yr^{-1}).

During the second survey period (2007 to 2008), the impacts of the cyclone continued to be evident at locations SL3 and SL4 and were still mostly restricted to the larger (>15cm) size classes, although rates of survival for all size classes at SL3 were higher than in the previous year (Fig. 3.3.2). At SL4, the rate of survival (65%) of adult colonies (15 to 25 cm) was similar to the previous year (63%), and lower than at SL3 (69%) (Fig. 3.3.2). Additionally, the rate of survival of large adults was also lower (29%) at SL4 than at SL3 (33%) during the previous year. The low survival of the largest size class at SL4 during this period was related to the high (100%) incidence of injury and the negative mean rate of growth (Fig. 3.3.3), although these rates were also an artefact of low colony replication, given that 5 of 8 tagged colonies died and the remainder were injured and decreased in size.

There was no evidence of impacts from Cyclone George persisting through the third survey period (2008 to 2009) and no evidence of any other major disturbance. The third survey period was the first in which colonies of the massive *Goniastrea spp.* were tagged. Across all locations, there were consistent differences between the rates of growth and survival of *Goniastrea spp.* and *Acropora spicifera*. In particular, the survival of all size classes of *Goniastrea spp.* was higher than for *A. spicifera* (Fig. 3.3.2), and the rates of growth much slower (Fig. 3.3.3). The rates of survival of *Goniastrea spp.* were >93% for all size classes and locations, with the exception of 82% for the smallest size class at one (SL4) location, compared with > 75% for *A. spicifera*. Conversely, mean rates of growth for *Goniastrea spp.* were much slower (< 1cm yr^{-1}) and less variable than for *A. spicifera* (2 to 9 cm yr^{-1}).

During the calm conditions of the third survey period, the rates of growth and survival of *A. spicifera* were generally higher than in previous years, and with less variation among locations and size classes. Additionally, there was no clear pattern to the variation in growth and survival among the locations and size classes. The rates of survival among size classes varied differently at each location, apart from lower survival of the smallest size class. However, the difference in survival between the smallest size class and the next lowest rate was at most 6% (range 3-6%) at any location.

Rates of recruitment and transition: Acropora spicifera *(2006 to 2009)*

Population structures differed among the locations, and these differences were consistent over two years (Fig. 3.3.4). In particular, the numbers of recruits were consistently highest at location SL1, as were the numbers of all other stages. Additionally, there were consistently fewer large adults at SL3 and SL4 than at the other locations. The most notable difference between the years was the much higher number of recruits and juveniles in 2009 at all locations, and smaller increases in the number of adults and large adults at most locations (Fig. 3.3.4).

Based on the assumption that the populations were most likely to be self-seeded at the scale of locations, estimates of the number of recruits produced per adult and large adult colony were calculated for use in the population models. In particular, the numbers of recruits at each location were adjusted for the number and area of adult and large adult colonies (Table 3.3.1). Following this adjustment, the number of recruits produced per large adult colony were between 2 and 4 times more than for the adults at all locations; among locations, rates were consistently 2 or more times higher at SL4. At locations SL1, SL2 and SL3, the number of recruits per adult or large adult colony were similar during both years, despite the differences in population structure (Table 3.3.1).

The rates of recruitment, growth and survival of colony stage classes determined the mean rates of transition through their life cycle, or their population's vital rates. Thus, differences in growth and survival among the colony stage classes, locations, and disturbance regimes, were evident in the vital rates of the population (Table 3.3.2). For example, during the years (2006 to 2008) of impact from Cyclone George, there was a high rate of transition of the adults and large adults to smaller stages following their injury; conversely, the probabilities of remaining in the same stage or transitioning to a larger stage were highest during the comparatively good conditions in the third survey period (2008 to 2009). These vital rates were incorporated into population models to provide estimates of population growth (lambda; λ), the relative importance of the different transitions to population growth (elasticity), and the population structure should conditions persist indefinitely (stable stage structure).

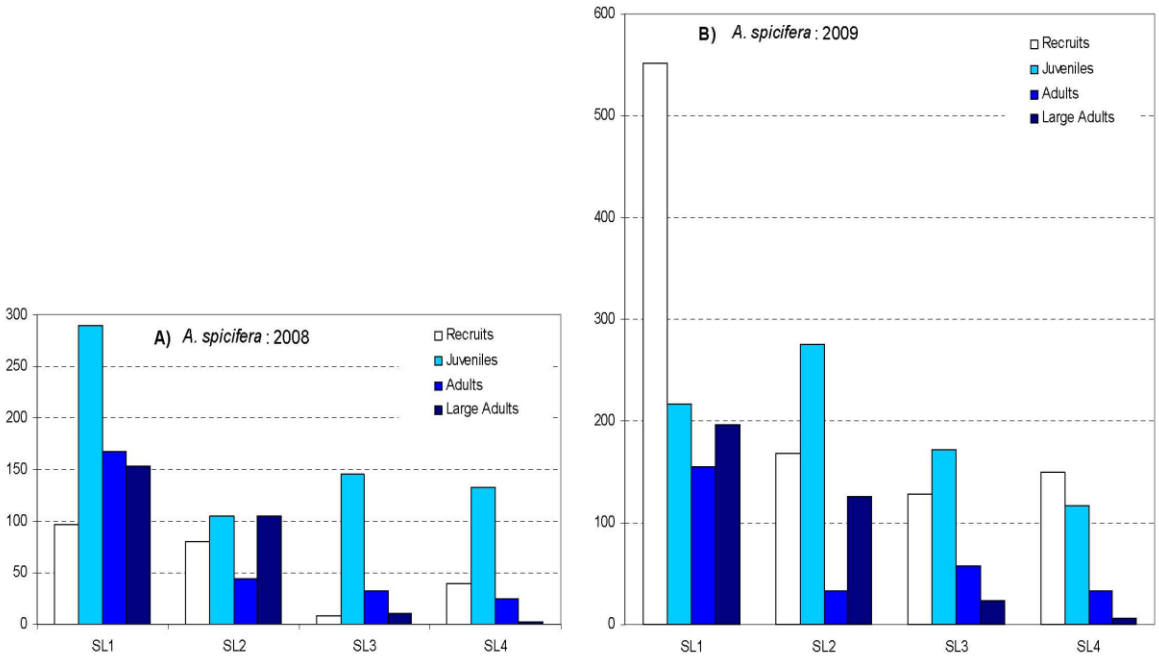


Fig. 3.3.4 Population structure of *Acropora spicifera* during two survey periods (2007-2008; 2008-2009). Population structures were derived from the colony size-frequency distributions according to the following categories: recruits < 5 cm; juveniles 5 to 15 cm; adults 15 to 25 cm and; large adults >25 cm.

Table 3.3.1 Rates of recruitment for populations of *Acropora spicifera*. The numbers of recruits and adult colonies were derived from population size-frequency distributions. The number of recruits per adult and large adult colony, proportionally adjusted for colony area, was calculated for use in matrix models.

Year	Location	Population				Small Adults					Large Adults				
		Number recruits	Number adults	Recruits per adult	Sum mean adult area per colony (cm^2)	Number colonies	Total colony area (cm^2)	Mean area per colony (cm^2)	Proportion adult colony area	Recruits per colony	Number colonies	Total colony area (cm^2)	Mean area per colony (cm^2)	Proportion adult colony area	Recruits per colony
2007-2008	SL1	96	321	0.30	740.79	167	29877.79	178.91	0.24	0.07	154	86529.74	561.88	0.76	0.23
	SL2	80	149	0.54	862.57	44	8586.23	195.14	0.23	0.12	105	70079.52	667.42	0.77	0.42
	SL3	8	43	0.19	629.69	32	5447.33	170.23	0.27	0.05	11	5054.04	459.46	0.73	0.14
	SL4	40	27	1.48	506.03	25	3961.12	158.44	0.31	0.46	2	695.18	347.59	0.69	1.02
2008-2009	SL1	552	352	1.57	774.42	155	29620.39	191.10	0.25	0.39	197	114915.12	583.33	0.75	1.18
	SL2	168	159	1.06	938.26	33	6064.54	183.77	0.20	0.21	126	95065.10	754.48	0.80	0.85
	SL3	128	82	1.56	624.84	58	9893.57	170.58	0.27	0.43	24	10902.39	454.27	0.73	1.13
	SL4	150	39	3.85	527.65	33	5754.63	174.38	0.33	1.27	6	2119.60	353.27	0.67	2.58

Table 3.3.2 Vital rates for populations of *Acropora spicifera* populations in different locations and survey years. Vital rates include the proportion of recruits produced per adult and large adult colony, and the proportion of recruits, juvenile and large adult colonies remaining in that stage or going to another stage, within the annual survey period. Not all transitions occur each year and not all transitions are possible. Transitions are *from* columns *to* rows.

2006 to 2007 Location	From / To	<5 #	<5 prop.	5 to 15 #	5 to 15 prop.	15 to 25 #	15 to 25 prop.	>25 #	>25 prop.	Grand Total
SL1	<5	3	0.09				0.07		0.23	3
	5 to 15	23	0.72	37	0.76	4	0.12			64
	15 to 25	1	0.03	11	0.22	13	0.38	5	0.17	30
	>25			1	0.02	14	0.41	19	0.66	34
SL2	<5	5	0.20				0.12		0.42	5
	5 to 15	20	0.80	13	0.20	1	0.03			34
	15 to 25			41	0.62	4	0.13			45
	>25			11	0.17	26	0.81	28	0.86	65
SL3	<5	2	0.08				0.05		0.14	5
	5 to 15	15	0.60	35	0.59	2	0.07	1	0.03	50
	15 to 25			7	0.12	4	0.14	1	0.03	12
	>25					1	0.04	3	0.08	4
SL4	<5	7	0.21				0.46		1.02	9
	5 to 15	19	0.58	71	0.70	2	0.06	2	0.05	90
	15 to 25	1	0.03	11	0.11	12	0.38	4	0.10	24
	>25					6	0.19	10	0.25	6
Grand Total		96		238		89		57		480

2007 to 2008 Location	From / To	<5 #	<5 prop.	5 to 15 #	5 to 15 prop.	15 to 25 #	15 to 25 prop.	>25 #	>25 prop.	Grand Total
SL1	<5	2	0.10				0.07		0.23	5
	5 to 15	14	0.71	35	0.51					46
	15 to 25	1	0.05	22	0.32	13	0.41	1	0.03	37
	>25			2	0.03	15	0.47	30	0.86	47
SL2	<5	8	0.25				0.12		0.42	8
	5 to 15	20	0.63	12	0.27	1	0.02			33
	15 to 25	1	0.03	25	0.57	7	0.14			33
	>25			4	0.09	39	0.80	65	0.86	108
SL3	<5	4	0.13				0.05		0.14	6
	5 to 15	18	0.58	50	0.65					66
	15 to 25	1	0.03	16	0.21	7	0.44			24
	>25			1	0.01	4	0.25	4	0.33	9
SL4	<5	17	0.40				0.46		1.02	21
	5 to 15	22	0.51	83	0.68	4	0.12	1	0.10	106
	15 to 25			23	0.19	13	0.38	1	0.10	37
	>25			1	0.01	5	0.15	1	0.10	6
Grand Total		108		274		108		102		592

2008 to 2009 Location	From / To	<5	<5	5 to 15	5 to 15	15 to 25	15 to 25	>25	>25	Grand Total
SL1	<5	49	0.47	0	0					50
	5 to 15	36	0.35	50	0.40			1	0.01	86
	15 to 25	1	0.01	64	0.51	41	0.47	5	0.05	111
	>25			5	0.04	43	0.49	79	0.82	127
SL2	<5	20	0.21							20
	5 to 15	65	0.69	53	0.62			2	0.02	120
	15 to 25	1	0.01	30	0.35	20	0.36	2	0.02	53
	>25					33	0.59	108	0.86	141
SL3	<5	23	0.37	0	0.00					24
	5 to 15	27	0.43	67	0.54	2	0.06			95
	15 to 25			44	0.35	15	0.43	3	0.17	62
	>25					16	0.46	15	0.83	31
SL4	<5	26	0.39					0	0.00	27
	5 to 15	26	0.39	76	0.56	4	0.09	5	0.45	110
	15 to 25			51	0.38	25	0.56	2	0.18	78
	>25			1	0.01	9	0.20	4	0.36	14
Grand Total		274		441		208		226		1149

Population matrix models: Acropora spicifera *(2006 to 2009)*

The population growth rates (λ) of *Acropora spicifera* varied among the locations and survey periods according to their exposure to cyclone disturbance (Fig. 3.3.5). Location SL3 was most affected by Cyclone George and had the lowest population growth rate during the first (λ = 0.63) and second (λ = 0.70) survey periods, representing relative decreases in population size of >30% within a year. The impact of the cyclone was less severe at location SL4, but the population growth rates over both survey periods (λ = 0.89; 0.90) were less than 1 (stable) despite the highest adjusted rates of recruitment (Table 3.3.1), reflecting relative decreases in population size of around 10% within the year. Additionally, the changes in population growth rates at these exposed locations reflected the more severe and immediate impact at SL3 during the first survey period, and the less severe but more persistent impact at SL4 (Fig. 3.3.5). Similarly, small impacts from Cyclone George at location SL1 were evident in a stable population growth rate (λ = 1.00), but also related to the low adjusted rates of recruitment (Table 3.3.1). Population growth rates over the first two survey periods were highest (λ = 1.18; 1.10) at location SL2, reflecting relative increases in population size of between 10% and 20% each year.

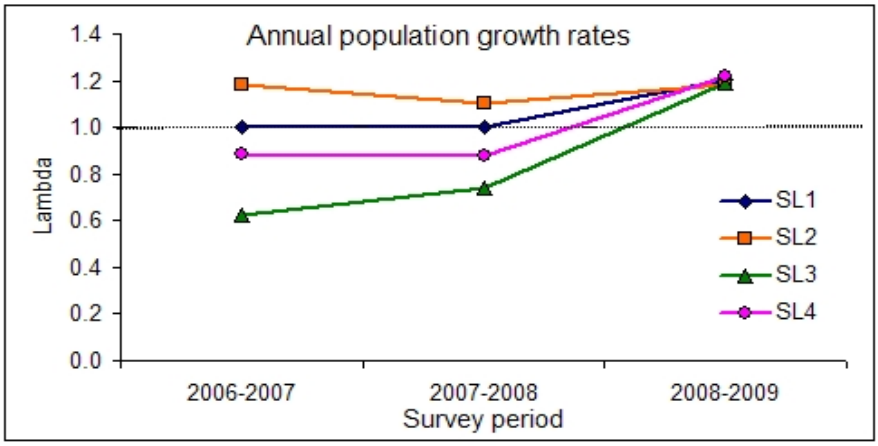


Fig. 3.3.5 Finite population growth rates (λ yr-1) for *Acropora spicifera* populations in different locations and survey periods. Population growth rates summarise the rates of recruitment growth and survival of individuals within the population, and are derived from repeated iteration of the vital rates to the point of convergence. Cyclone George impacted populations during the first (2006 to 2007) and second (2007 to 2008) survey periods. Populations are stable when λ = 1.

Table 3.3.3 Transition elasticises for *Acropora spicifera* populations in different locations and survey periods. Transition elasticises are derived from matrix population models and represent the relative contribution of each transition to the population growth rate. The largest three elasticises are highlighted with a grey box and bold text, the forth and fifth largest elasticises are in bold text. Cyclone George impacted populations during the first (2006-2007) and second (2007-2008) survey periods.

Transition	2006-2007				2007-2008				2008-2009			
	SL1	SL2	SL3	SL4	SL1	SL2	SL3	SL4	SL1	SL2	SL3	SL4
Recruit to Recruit	0.007	0.020	0.003	0.035	0.009	0.038	0.017	0.035	0.083	0.026	0.046	0.068
Recruit from Adults	0.014	0.010	**0.020**	**0.062**	0.007	0.009	0.029	**0.067**	0.024	0.014	0.024	**0.097**
Recruit from Large Adult	0.056	**0.087**	0.003	0.050	**0.073**	**0.119**	**0.051**	0.044	**0.105**	0.107	0.081	0.049
Recruit to Juvenile	0.067	**0.097**	**0.023**	**0.102**	**0.073**	**0.120**	**0.078**	**0.102**	**0.124**	**0.118**	**0.104**	**0.146**
Juvenile to Juvenile	**0.292**	0.020	**0.856**	**0.408**	**0.075**	0.040	**0.547**	**0.436**	0.062	**0.131**	**0.090**	**0.151**
Adult to Juvenile	0.027	0.003	**0.025**	0.009	--	0.002	--	0.010	--	--	0.006	0.014
Large Adult to Juvenile	--	--	0.001	0.001	--	--	--	0.002	0.002	0.003	--	0.018
Recruit to Adult	0.003	--	--	0.010	0.007	0.007	0.002	0.009	0.005	0.003	--	--
Juvenile to Adult	**0.086**	**0.101**	**0.049**	0.113	**0.066**	**0.104**	**0.074**	**0.114**	**0.115**	**0.121**	**0.111**	**0.174**
Adult to Adult	**0.087**	0.020	0.014	**0.096**	0.060	0.017	**0.110**	**0.097**	0.086	0.055	0.086	**0.156**
Large Adult to Adult	0.051	0.068	0.000	0.009	0.015	--	--	0.008	0.014	0.005	0.043	0.013
Juvenile to Large Adult	0.008	--	--	--	0.007	0.018	0.004	--	0.011	--	--	0.005
Adult to Large Adult	**0.099**	**0.155**	0.004	**0.060**	0.081	**0.101**	0.047	0.054	**0.109**	**0.114**	**0.123**	0.075
Large Adult to Large Adult	**0.204**	**0.418**	0.001	0.044	**0.527**	**0.425**	0.042	0.022	**0.261**	**0.302**	**0.286**	0.034

During the calm conditions of the third survey period (2008 to 2009), the population growth rates were very similar (($\lambda \approx 1.2$) at all locations (Fig. 3.3.5), reflecting the convergence of rates of growth and survival among locations and colony size classes. Of all the transition rates, the adjusted rates of recruitment varied the most among the locations during the calm conditions (Table 3.3.1), but their contribution to population growth was less than for other transitions (Table 3.3.3).

The relative contribution of the different transitions to population growth was estimated by their elasticities (Table 3). Transition elasticities for the different locations and colony stages varied according their exposure to disturbances. Consequently, during the first two survey periods, transition elasticities were most similar at the locations that were exposed to (SL3, SL4) or sheltered from (SL1, SL2) the impacts of cyclone George, whereas in the third survey period there was a greater degree of similarity across all locations (Table 3.3.3). For example, in the first two survey periods at locations SL1 and SL2, by far the highest (40% to 55%) contribution to population growth was made by the survival of the large adult colonies, with the exception of a 20% contribution at SL1 during the first year (Table 3.3.3). The large adult colonies made a high contribution to population maintenance at these locations because colonies remained in this largest size class for many years, given high rates of survival, and they made by far the greatest cumulative contribution to recruitment. Conversely, at the

locations exposed to cyclone George, the relative contribution of large adults to population maintenance was < 5%, because under these conditions many were either killed or shrank to adult size following their injury (Table 3.3.3). Under conditions of cyclone disturbance, it was the survival of the juvenile colonies that made by far the largest (40% to 85%) contribution to population maintenance because of their higher survival rate and subsequent growth to the adult stage (Table 3.3.3). Indicative of the moderate impact of cyclone George at location SL1 was the similar contribution by the survival of large adults (20%) and juveniles (29%) to population maintenance (Table 3.3.3).

During the calm conditions in the third survey period, the contribution of different transitions to population maintenance was more similar among the locations than in previous years (Table 3.3.3). Additionally, within each location the elasticity values were more evenly spread among several stages and transitions. For example, elasticities were highest for the survival of the large adults at all locations but SL4, ranging between 25% and 30%. Additionally, the transition of juveniles to adults, recruits to juveniles, and/or the survival of juveniles, also made relatively large but similar (10 to 20%) contributions to population growth at all locations. The most obvious difference among the locations was the low elasticity value (3%) for the survival of large adults at SL4, and the higher elasticity (16%) for the survival of adult colonies (Table 3.3.3); this was due to the injury of large adults and their shrinkage to smaller stage classes, but this high rate of transition to smaller stages could also be biased by low replication (n = 11).

Discussion

Life history strategies of A. spicifera *and* Goniastrea spp.

During the year of relatively calm conditions, there were clear differences in the rates of growth and survival between the two study species. The differences between the species groups corresponded to predicted differences in life history strategies between corals with a fragile plate-like growth form and a robust massive growth form. *Acropora spicifera* colonies have a plate-like growth form that is similar to many of the most common species on Indo-Pacific reefs. In contrast, the *Goniastrea spp.* colonies have a robust and massive growth form, or a more encrusting growth form, that is also common to many abundant species. Life history theory and previous studies show that the *Acropora* corals grow quickly and have high reproductive output and recruitment, but are susceptible to many small-scale (e.g. direct competitive interactions, predation) or large-scale disturbances (e.g. high water temperatures, high wave energy); conversely, *Goniastrea* grow slowly, have moderate reproductive output and recruitment, and are less susceptible to common disturbances (Harrison and Booth 207; Babcock 1991; Hall and Hughes 1996; Connell 1997; Connell et al. 2004; Wakeford et al. 2008). The results of this study support this theory, with the rates of growth of *A. spicifera* being at least 2 times, and up to 9 times, faster than for *Goniastrea spp.*, whereas the rates of survival of all size classes of *Goniastrea* were equal to or higher than for *A. spicifera*.

Colonies of *Goniastrea spp.* had not yet been tagged when Cyclone George passed Scott Reef, so the impact on this more robust coral is not known. However, this massive coral is predicted to be less affected by wave energy than the more fragile *Acropora spicifera*, particularly for the large colony size classes (Madin et al. 2006; Madin et al. 2008). Similarly, changes in percentage cover at Scott Reef indicate that massive corals such as the *Goniastrea* were less impacted by the bleaching event than were *Acropora* (Smith et al. 2006; Smith et al. 2008). Although the models have not yet been run for the *Goniastrea spp.* at Scott Reef, the differences in growth and survival are also likely to be evident in the population growth rates. During the calm conditions in the third survey period, the population growth rates for *A. spicifera* were approximately 1.2, indicating a rapid relative increase in population size of around 20% each year. Conversely, the slower growth and possibly lower recruitment rates for the *Goniastrea spp.* are more likely to result in a population growth rates closer to 1 (stable). However, given the differences in susceptibility to disturbances, it would also be expected that environmental stochasticity arising from cycles of natural disturbance over periods of approximately a decade (Connell 1997) will cause population growth of *Acropora spicifera* to vary above ($\lambda > 1$) and below ($\lambda < 1$) stability; that is, periods of relatively severe impact followed by relatively rapid recovery. Conversely, population growth rates for *Goniastrea spp.* would be predicted to vary less within a cycle of natural disturbance and would consistently be closer to stable ($\lambda = 1$). However, to test the impacts of disturbance on the vital rates of populations, or density dependent effects following periods of calm conditions, studies must continue through at least one natural cycle of disturbance and recovery (approximately 10 years).

Impacts of Cyclone George on Acropora spicifera *populations*

Populations of *Acropora spicifera* were surveyed over three annual periods, during which Cyclone George impacted populations two months before the end of the first survey period. Not all populations were impacted by the cyclone, but for those worst affected (SL3, SL4), the associated reductions in growth and survival were evident over several months. How these impacts were manifest, however, varied among the populations according to their level of exposure. For example, at the location most exposed (SL3) to the cyclone there were large and immediate impacts, causing the rates of growth and survival to be lowest during the first survey period; during the second period, survival and growth were higher. By comparison, the population at SL4 was less exposed to the cyclone and there were smaller decreases in growth and survival in the first survey period; however, because many colonies that been injured continued to lose live tissue and/or die over several months, the rates of growth and survival during the second survey were lower that in the previous period. Similarly, there was some evidence of cyclone impacts at SL1, and the small associated reductions in growth and survival resulting from colony injuries were more evident in the second survey. Consequently, the impacts of cyclone disturbance varied differently among locations and through time, and were not evident for more than a year (Knowlton et al. 1981).

Regardless of the degree to which populations were exposed to the impacts of Cyclone George, there were consistent patterns of susceptibility among size-classes at all locations.

The largest colonies (>15 cm) were far more likely to have been injured, fragmented and killed by the wave energy produced by the cyclone, and the smaller size classes were far less affected. Given their fragile growth form, larger *Acropora* colonies are generally more affected by waves than small colonies (Knowlton et al. 1981; Highsmith 1982; Madin et al. 2008). Additionally, the larger colonies were more likely to have survived with an injury between surveys, and therefore, to have decreased in size (Hughes and Jackson 1980). By comparison, the rates of survival of small colonies at the exposed locations were similar to that at the locations sheltered from the cyclone and the following year in calm conditions.

The variation in the vital rates of the *Acropora spicifera* populations, according to their exposure to Cyclone George, was evident in the output of the population models. At the exposed locations, annual growth rates (λ) were <1 during the first two survey periods, reflecting decrease in population size resulting from the cyclone. The population growth rate was lowest at SL3 during the first survey period, and increased during the second. The population growth rate was slightly higher at SL4, but similar over the two year period, reflecting the less severe but persistent impacts at this location. At SL1, small impacts from Cyclone George were evident in a stable population growth rate ($\lambda = 1$), but were also related to the low adjusted rates of recruitment. By comparison, population growth rates were highest at SL2 and were similar over all years, further supporting the lack of cyclone impact at this location. Indeed, by the third survey there was no evidence of ongoing impact from the cyclone, and during the calm conditions the population growth rates at all locations converged at around 1.2. A population growth rate of 1.2 suggests relative increases in population size of 20% per year, which is particularly rapid. Clearly, these populations of *Acropora* are capable of rapid increases in abundance during good conditions following disturbances (Harrison and Booth 207; Baird and Hughes 2000; Halford et al. 2004). Thus, recovery following even severe disturbances can occur within years if the effects are selective, impacting only some locations and life history stages. Cyclone disturbances are characteristically selective and spatially heterogeneous, and coral reefs have evolved resilience to periodic exposure (Woodley et al. 1981; Bythell et al. 1993a; Connell 1997). For example, at Scott Reef not all locations were impacted by Cyclone George and there was comparatively little reduction in the survival of the smaller size classes. Consequently, recovery of populations following cyclone disturbance can be aided by the supply of recruits from those populations least affected, and the juvenile colonies that survived the disturbance can replace the dead adults and contribute to reproductive output within years of favourable conditions (Fong and Lirman 1995; Lirman 2003). Coral communities at Scott Reef are far more resilient to periodic cyclone disturbance than to less selective and more widespread disturbances, such as the mass-bleaching. The elevated water temperatures and mass bleaching in 1998 had a severe impact at all locations across Scott Reef and on all colony size classes (Smith et al. 2006). The associated reductions in recruitment and the abundance of small size classes had long lasting implications for the recovery of communities, which has taken more than a decade (Smith et al. 2008). Understanding how these disturbances impact the vital rates of populations provides insights into why combinations of disturbances can have such dramatic consequences for the resilience of communities, precluding recovery and causing long-term degradation in the worst instances. For example, the vital rates of *Acropora*

spicifera populations at Scott Reef indicate that similar corals are resilient to cyclones disturbances that may occur roughly every ten years. However, if coupled with a mass-bleaching event that occurred every one or two decades, recovery to the previous community structure and coral cover is unlikely. Similarly, a reduction in water quality at Scott Reef, and its associated effects on population vital rates, would dramatically reduce the resilience of communities to periodic cyclone disturbance and/or infrequent bleaching events. Combinations of disturbances, particularly chronic stressors (e.g. degraded water quality, coral disease, overfishing) coupled with periodic acute disturbances (e.g cyclones, elevated water temperatures) are commonly responsible for the long-term degradation of coral reefs (Jackson et al. 2001; Knowlton 2001; Pandolfi et al. 2003; Hughes et al. 2007; Wilkinson 2008).

References

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

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

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

Bak RPM, Meesters EH (1999) Population structure as a response of coral communities to global change. American Zoologist 39: 56-65

Bierzychudek P (1999) Looking backwards: Assessing the projections of a transition matrix model. Ecological Applications 99: 1278

Birrell CL, McCook LM, Willis BL, Diaz-Pulido G (2008) Effects of benthic algae on the replenishment potential of corals and the implications for the resilience of coral reefs. Oceanography and Marine Biology: An Annual Review 46: 25-63

Brown BE, Clarke KR, Warwick RM (2002) Serial patterns of biodiversity change in corals across shallow reef flats in Ko Phuket, Thailand, due to the effects of local (sedimentation) and regional (climatic) perturbations. Marine Biology 141: 21-29

Bruna EM, Oli MK (2005) Demographic effects of habitat fragmentation on a tropical herb: life-table response experiments. Ecology 86 1816-1824

Bythell JC, Bythell M, Gladfelter EH (1993a) Initial results of a long-term coral reef monitoring program: Impact of Hurricane Hugo at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands. Journal of Experimental Marine Biology and Ecology 172: 171-183

Bythell JC, Gladfelter EH, Bythell M (1993b) Chronic and catastrophic natural mortality of three common Carribean coral reefs. Coral Reefs 12: 143-152

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

Connell JH (1997) Disturbance and recovery of coral assemblages. Coral Reefs 16 (Suppl): 101-113

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

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

DeVantier L, De'ath G, Turak E, Done T, Fabricius K (2006) Species richness and community structure of reef-building corals on the nearshore Great Barrier Reef. Coral Reefs 25: 329-340

Done T (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 T, 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: 489-805

Downs CA, Woodley CM, Richmond RH, Lanning LL, Owen R (2005) Shifting the paradigm of coral-reef 'health' assessment. Marine Pollution Bulletin 51: 486-494

Ebert TA (1999) Plant and Animal Populations. Methods in Demography. Academic Press, New York

Edmunds PJ (2005) The effect of sub-lethal increases in temperature on the growth and population trajectories of three scleractinian corals on the southern Great Barrier Reef. Population Ecology 146: 350-364

Fong P, Glynn PW (2000) A regional model to predict coral population dynamics in response to El Nino-Southern Oscillation. Ecological Applications 10: 842

Fong P, Lirman D (1995) Hurricanes cause population expansion of the branching coral Acropora palmata (Scleractinia): Wound healing and growth patterns of asexual recruits. Marine Ecology 16: 317-335

Halford A, Cheal A, Ryan D, Williams DM (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. Ecology 85: 1893-1905

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

Harrison PL, Booth D (207) Chapter 13 Coral Reefs: Naturally dnamic and increasingly disturbed ecosystems

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

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 & Evolution 7: 292-295

Hughes TP, Gunderson LH, Folke C, Baird AH, Bellwood D, Berkes F, Crona B, Helfgott A, Leslie H, Norberg J, Nystrom M, Olsson P, Osterblom H, Scheffer M, Schuttenberg H, Steneck RS, Tengoe M, Troll M, Walker B, Wilson J, Worm B (2007) Adaptive management of the great barrier reef and the Grand Canyon world heritage areas. Ambio 36: 586-592

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

Hunte W, Wittenberg M (1992) Effects of eutrophication and sedimentation on juvenile corals: II. settlement. Marine Biology 114

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629

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

Knowlton N, Jackson JBC (2008) Shifting baselines, local impacts, and global change on coral reefs. Plos Biology 6: 215-220

Knowlton N, Lang JC, Rooney MC, Clifford P (1981) Evidence for Delayed Mortality in Hurricane-Damaged Jamaican Staghorn Corals. Nature 294: 251-252

Lirman D (2003) A simulation model of the population dynamics of the branching coral *Acropora palmata*: Effects of storm intensity and frequency. Ecological Modelling 161: 169-182

Lirman D, Miller MW (2003) Modeling and Monitoring Tools to Assess Recovery Status and Convergence Rates between Restored and Undisturbed Coral Reef Habitats. Restoration Ecology 11: 448-456

Madin JS, Black KP, Connolly SR (2006) Scaling water motion on coral reefs: from regional to organismal scales. Coral Reefs 25: 635-644

Madin JS, O'Donnell MJ, Connolly SR (2008) Climate-mediated mechanical changes to post-disturbance coral assemblages. Biology Letters 4: 490-493

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

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

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

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

Smith L, Gilmour J, Heyward A, Rees M (2006) Mass-bleaching, mortality and slow recovery of three commongroups of scleractinian corals at an isolated reef. Proceedings of 10th International Coral Reef Symposium 2: 651-656

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

Smith LD, Gilmour JD, Heyward AJ (2008) Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. Coral Reefs 27: 197-205

Tanner JE, Hughes TP, Connell JH (1996) The role of history in community dynamics: A modelling approach. Ecology 77

Wakeford M, Done TJ, Johnson CR (2008) Decadal trends in a coral community and evidence of changed disturbance regime. Coral Reefs 27: 1-13

Wilkinson C (2004) Status of Coral Reefs of the World. Australian Institute of Marine Science, Townsville

Wilkinson C (2008) Status of Coral Reefs of the World. Australian Institute of Marine Science, Townsville

Woodley JD, Chornesky EA, Clifford PA, Jackson JC, 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

Appendix

Appendix 3.3.1 Annual rates of survival for tagged colonies in different size classes, locations and sites. Colony sizes are defined as maximum colony length in centimetres. Colonies were surveyed during May each year. *Acropora spicifera* was first tagged in 2006, *Goniastrea spp.* were first tagged in 2008.

Taxa	Year	Size (cm)	SL1-1	SL1-2	SL2-1	SL2-2	SL3-1	SL3-2	SL4-1	SL4-2	All Sites
A. spicifera	2006-2007	<5	0.73	0.94	1.00	1.00	1.00	0.50	0.91	0.60	0.83
		5 to 15	1.00	1.00	1.00	0.96	0.78	0.59	0.83	0.77	0.86
		15 to 25	0.88	0.94	1.00	0.93	0.44	0.16	0.73	0.53	0.71
		>25	0.75	0.92	1.00	0.92	0.15	0.07	--	--	0.57
	2007-2008	<5	0.85	0.88	1.00	0.89	0.71	0.80	0.91	0.90	0.86
		5 to 15	0.85	0.86	0.95	0.91	0.90	0.83	0.80	0.95	0.88
		15 to 25	0.94	0.80	0.91	1.00	0.70	0.67	0.76	0.46	0.82
		>25	0.92	0.87	1.00	1.00	0.33	0.33	0.33	0.00	0.85
	2008-2009	<5	0.81	0.84	0.88	0.94	0.75	0.85	0.82	0.74	0.84
		5 to 15	0.88	0.99	0.96	0.97	0.91	0.87	0.93	0.96	0.93
		15 to 25	0.96	0.97	0.96	0.93	0.94	1.00	0.83	0.88	0.93
		>25	0.84	0.92	0.98	0.92	1.00	1.00	1.00	1.00	0.93
Goniastrea spp.	2008-2009	<5	0.98	0.95	0.95	0.95	0.95	0.91	0.88	0.79	0.94
		5 to 15	0.96	1.00	0.96	0.95	0.98	0.98	1.00	0.87	0.97
		15 to 25	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
		>25	--	--	1.00	--	1.00	1.00	1.00	1.00	1.00

3.4. Fish Genetics

3.4.1. Restricted population connectivity amidst subtle genetic structure in a damselfish on remote coral atolls

Introduction

For most marine organisms with a sedentary adult phase, the open ocean environment provides the opportunity for larvae to disperse away from their natal area and thus contribute to the genetic composition and demography of distant populations. However, depending on the interplay between the biology of a particular organism and its physical environment, this *potential* may be radically different to *realised* connectivity; the actual numbers of individuals that firstly utilise these physical transport systems (the oceanic highways and local freeways) to disperse among distant populations, and then secondly, survive and eventually reproduce in those destination populations (Hamilton et al. 2008; Pineda et al. 2008). Although it is well-recognised that the degree to which this potential is realised underpins the basic maintenance, distribution and diversity of marine populations and species, describing realistic patterns of connectivity has thus far been particularly challenging (Cowen and Sponaugle 2009; Jones et al. 2009). However, recently researchers have developed the capacity to not only begin to describe these patterns, but also probe their causes and consequences (Cowen and Sponaugle 2009).

Despite this recent progress, a lack of spatially explicit knowledge of realised connectivity represents the most critical scientific gap in the understanding required for the effective management of marine systems (Cowen et al. 2007; Mumby and Steneck 2008; Waples et al. 2008; McCook et al. 2009). In particular, information on connectivity is necessary for the design of networks of marine protected areas (Gerber et al. 2003; Sale et al. 2005). If local replenishment is supplemented with recruits produced from afar, populations will be maintained every generation by endogenous recruits, while recovery from severe occasional disturbances may be augmented by exogenous recruits. However, the fundamental questions are; how close do populations need to be to supplement local recruitment after a disturbance, and over what time scales will recovery occur? Answering these questions at the community or ecosystem level is no simple task; not only will connectivity patterns vary among taxa with different life histories, they will also vary spatially and temporally within species due to a myriad of biophysical factors including the nature of the disturbance. However, particularly for coral reefs where the frequency, spatial scale and intensity of disturbances are increasing (Hoegh-Guldberg et al. 2007; Alvarez-Filip et al. 2009), addressing this question is crucial.

Population theory suggests that when the probability of pelagic larvae locating a favourable habitat is low, as is the situation at geographically isolated offshore systems, then locally derived recruits are likely to be crucial for maintaining populations (Strathmann et al. 2002). Empirical evidence supports this theory; genetic subdivision of populations often increases around offshore systems compared with mainland populations (Johnson et al. 1994; Parsons

1996; Bell 2008). This limited exchange with neighbouring populations means that local production will drive population maintenance and recovery after disturbance, and is also likely to be crucial to the development of unique community assemblages (McCook et al. 2009), endemism (Robertson 2001), inbreeding and reduced genetic diversity (Frankham 1998; Ayre and Hughes 2004; Pérez-Ruzafa et al. 2006), that are often observed at offshore systems. As a consequence, it is crucial that a significant proportion of the reproductive population is protected to ensure maintenance processes of populations and unique components of genetic diversity are preserved (Miller and Ayre 2008; Almany et al. 2009). In the East Indian Ocean off north-west Australia (NWA), the offshore coral reefs are very geographically isolated, occurring along the continental shelf margin and separated by several hundreds of kilometres of open water (Fig. 3.4.1.1). These reefs have a diverse array of flora and fauna (Bryce *et al.* in press), and the lack of human impact make them high priorities for conservation, particularly given a background of worldwide declines in coral reef health. Consequently, the development of knowledge about patterns of realised connectivity and the role it plays in population dynamics is crucial to inform marine conservation and planning in this region.

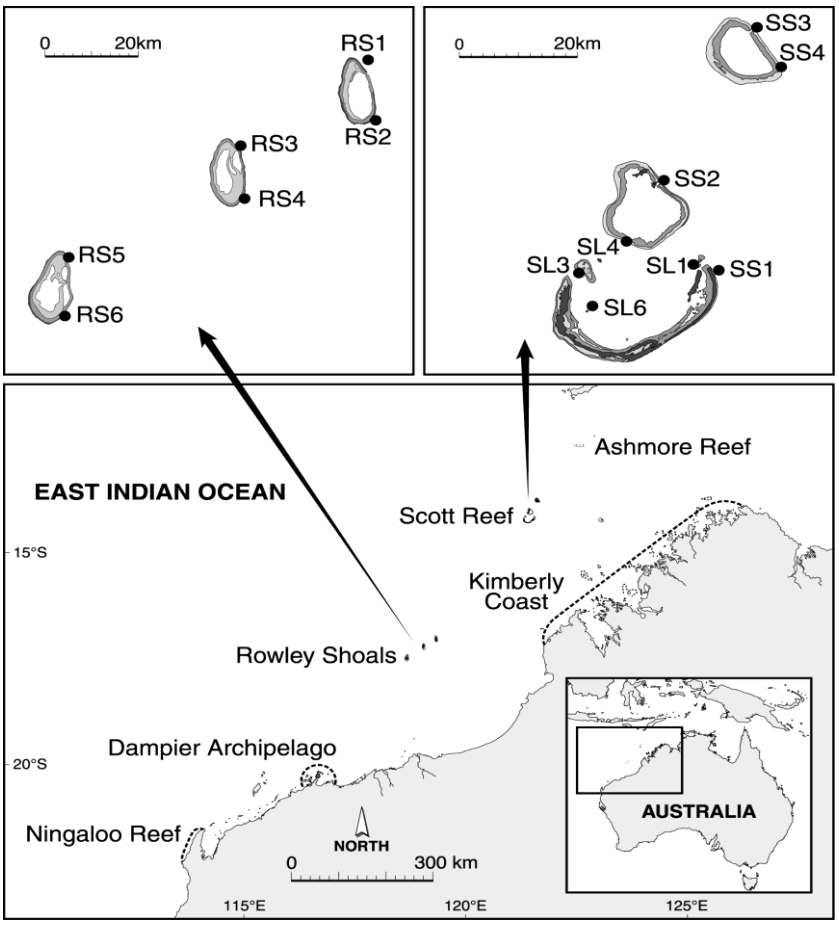


Fig. 3.4.1.1 Map of the major coral reef systems in north-west Australia showing sampling sites of *Chromis margaritifer* collected from Rowley Shoals and Scott Reef.

There are two broad surface currents that have the potential to transport larvae long distances in the region; in the austral autumn and winter, a slow moving current that originates in Indonesia and flows polewards along the continental shelf margin, while in the austral spring and summer, seasonal south-west winds induce a reversal of the current to the north-east (Cresswell et al. 1993; Holloway 1995). *In situ* satellite-tracked drifters suggest that transport of passive particles over the several hundred kilometres of open ocean between the reef systems of NWA will take between one and two months (Gilmour et al. 2009). These direct observations are supported by course calculations based mean current speeds ($0.2ms^{-1}$; Holloway 1995), which suggest that straight line movement over the several hundred kilometres between systems would take around one month.

These predictions based on simulated and empirical oceanographic data are supported by studies on hard corals at Scott Reef and the Rowley Shoals. Minimum competency periods of most coral larvae are less than a few days and few larvae can survive a pelagic existence for more than few weeks and still have the energy reserves to and undergo metamorphose (Nishikawa et al. 2003; Baird 2004; Nozawa et al. 2006). Genetic analyses of brooding and broadcast spawning species (Underwood et al. 2007; Underwood 2009; Underwood et al. 2009), and *in situ* observations (Gilmour et al. 2009), suggest that the majority of larvae in NWA not only settle immediately when competent, but also are retained close to their natal reef during this pre-competency period. However, differences in levels of genetic subdivision not only between the brooding and broadcast spawning species, but also within each system, suggested that reproductive mode and local hydrodynamics restrict or enhance routine dispersal distances within reefs (Underwood et al. 2009). Further, because genetic divergence was not large between Scott Reef and Rowley Shoals in the broadcast spawner, long-distance dispersal between these systems probably occurs sporadically over multiple generations or has been relatively strong at some time in the past (Underwood et al. 2009).

With the exception of these two coral species, little is known about the levels of connectivity in the offshore systems of NWA for other reef taxa. Some data suggests weak historical connections among populations of the coral trout, *Plectropomus leopardus*, over the 1700 km from Scott Reef to the Abrolhos Islands off the central west coast of Western Australia (Van Herwerden et al. 2009). However, *P. leopardus* does not occur at the Rowley Shoals, so this study is of little value at more limited spatial scales.

Here, we investigate for the first time the extent of genetic and ecological connections among offshore populations of a coral-associated reef fish, *Chromis margaritifer,* in NWA. Unlike corals, most fish larvae *must* spend at least several weeks in the plankton before they are able to settle. Moreover, fish larvae are by no means passive particles, with late stage larvae able to not only sustain swimming speeds that are faster than average current speeds, but have an ability to sense and swim towards reefs (Gerlach *et al.* 2007). Further, the occurrence and consequences of intraspecific variation in pelagic larval duration (PLD) is not well studied but likely to be greater than generally recognised (Bay et al. 2006). In particular, the ability of

planktotrophic larvae to feed reduces the energetic costs of delaying metamorphosis, and therefore may increase their chances of finding and successfully recruiting to suitable habitat from the open ocean (Leis 2002). Thus, depending on the interplay between the ontogenetic development of these behaviours and their oceanographic environment, either self-recruitment or successful long-distance dispersal will be facilitated.

The primary aim of this study is to determine the frequency and spatial scale of planktonic dispersal of larvae of a common coral-associated damselfish, *Chromis margaritifer,* among and within the atoll systems of the Rowley Shoals and Scott Reef in NWA. We focus on discriminating contemporary patterns of connectivity which are likely to be relevant to the demography of these populations from historical connections. In so doing, we not only identify some of the biological and physical factors that influence connectivity, but also explore the consequences of these patterns for the dynamics and genetics of these populations. *C. margaritifer* is a widely distributed pomacentrid occurring from the Line and Tuamoto islands in the central Pacific Ocean to Christmas Island in the eastern Indian Ocean (Allen 1991). In Western Australia, *C. margaritifer* is not only highly abundant on the slopes of the offshore reefs of NWA, but also occurs across a variety of reef habitats (including inshore reefs and lagoons) as far south as Shark Bay (26° 08') on the west coast of Australia (Hoese et al. 2006). In addition to these biogeographic and ecological characteristics that suggest a high potential for dispersal, this damselfish has a long PLD relative to most pomacentrids with a mean PLD of 30 days on the Great Barrier Reef (Thresher et al. 1989) and 33 days in Palau (Wellington and Victor 1989). Further, considerable numbers of recruits can be observed throughout the year at the offshore reefs of NWA (Mike Travers *pers. obs.*), suggesting that C. *margaritifer* lays its benthic eggs over several months of the year and larvae are likely to hatch across a wide variety of environmental conditions. Therefore, the expectation is that connections among reefs and systems in this damselfish will be strong relative to corals and probably representative of the upper limits of dispersal of many reef organisms in these systems.

To address this aim, we adopted a multidisciplinary approach. First, we analysed over 200 otoliths from *C. margaritifer* recruits to obtain accurate estimates of mean PLD and its variation among individuals and locations. Second, we used an oceanographic model to examine the potential for transport of propagules within and between systems. Third, we conducted a spatial analysis of sequence and microsatellite DNA variation to explore the genetic patterns and consequences of connectivity. Finally, we utilised adult and recruit census data to explore how timing of spawning and population size affected the genetic structure of this damselfish.

Methods

Otolith analysis

Over 200 juveniles (<15mm) of *Chromis margaritifer* were collected from Rowley Shoals and Scott Reef during March and October of 2008. Fish were measured to the nearest mm total

length (TL), fork length (FL) and standard length (SL), and weighed to 0.1 mg total weight (TW). The pair of sagittal otoliths were extracted, cleaned, and stored dry in envelopes prior to processing. One of the pair was weighed (to 0.1 mg) and mounted on a glass slide and ground following the method of Secor *et al*. (1991). The number of increments on each section was counted along the dorsoventral axis from the core to the edge and from the periphery to the core at ×400 or ×1000 magnification depending on microstructure clarity. The increments in all of the otoliths viewed were unambiguous. Settlement rings corresponded to the type Ia abrupt settlement marks of Wilson & McCormick (1999). This type of settlement mark is distinguished by an abrupt transition from widely spaced (pre-settlement) increments to narrower (post-settlement) increments (Fig. 3.4.1.2). Pre-settlement age, which is equivalent to pelagic larval duration (PLD), was determined by counting the number of increments (days) between hatching (first increment) and settlement. Hatch dates were back-calculated by subtracting the number of post- and pre-settlement increments from the date of capture, and hatch frequency plot was calculated by applying a instantaneous mortality rate of 0.1 d^{-1} (according to Stevenson and Campana 1992). Average PLD (± SD) was determined at Rowley Shoals and Scott Reef, and significant differences were tested with a two-tailed T test.

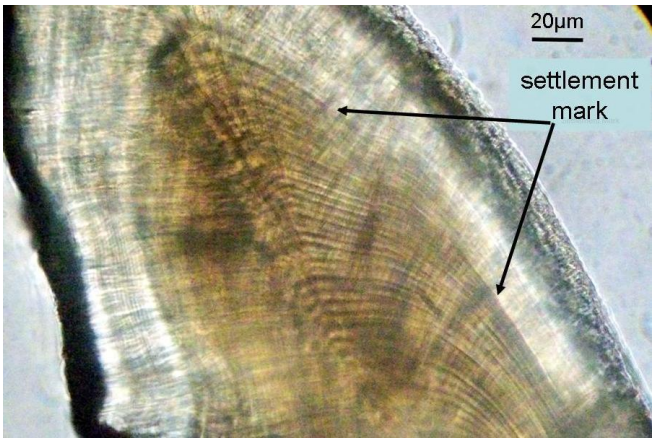


Fig. 3.4.1.2 Picture of sagittal otolith of *Chromis margaritifer* from Scott Reef showing the settlement mark.

Oceanographic model

To explore the potential for transport of passive particles by oceanic currents in this region, we utilised the interface, Connle, developed by CSIRO (Condie and Andrewartha 2008). This model measures circulation patterns from a three-dimensional non-linear hydrodynamic model referred to as MECO (Model of Estuaries and Coastal Oceans) and forced by realistic wind, temperature and salinity fields. A particle-tracking module is embedded within this model and allows estimation of connectivity through the individual tracking of large numbers (10^5) of neutrally buoyant particles seeded randomly through the water column across the north-west model domain. The circulation and particle movement calculations were conducted simultaneously, with particle positions being updated every 10 min by the interpolated model current velocities. The probability that any two regions within the model domain were connected was computed for a range of dispersion times on a 0.1° geographical grid. We present the statistical outputs for six different scenarios: particles released from Rowley Shoals in summer for 7 (1st quarter), 28 and 56 days when the north-easterly flow is

the strongest; and then particles released from Scott Reef in autumn for 7 (2nd quarter), 28 and 56 days when the south-westerly flow is the strongest. Particle distributions for all scenarios were estimated across the entire dispersion period (within lifetime option) and averaged across the six years (1994-1999).

DNA extraction, microsatellite characterisation and quality control

DNA for the development of the microsatellite library was extracted from several *C. margaritifer* individuals using the Qiagen DNeasy extraction kit for animal tissue according to the manufacturer's instructions and included the optional RNAse treatment. DNA concentrations were quantified on a spectrophotometer (Nanodrop 3300, Thermo Scientific), and extractions were pooled to provide 100 µL of DNA with a concentration of approximately 400 ng/µL. Genetic Identification Services used this genomic DNA to construct DNA libraries according to the protocol outlined in Jones et al. (2002). Briefly, 300 - 750 bp fragments were adapted and subjected to magnetic bead capture (CPG, Inc.) to produce four libraries enriched with AAC, CATC, TACA, TAGA motifs. More than 50% of clones were enriched for microsatellites in each library. Ninety-six clones were sequenced from these libraries and primers were designed for 20 loci using the software DesignerPCR v 1.03 (Research Genetics, Inc).

DNA for all genetic analysis subsequent to the microsatellite library preparation was extracted with the high throughput membrane-based DNA extraction protocol of Ivanova et al. (2006). Quality and quantity of genomic DNA was ascertained through gel electrophoresis using 1% standard agarose (Amresco) and final concentration was diluted by one third with millepore purified sterilised water to a final concentration of about 10-20 ng.

To mitigate and report scoring error of microsatellites, quality control procedures suggested by Bonin et al. (2004) and DeWoody et al. (2006) were implemented. First, a subset of the samples (48) from site SL1 at Scott Reef were screened (on a 3730 capillary sequencer; Applied Biosystems) to test quality of fluorescently labelled PCR products across a variety of multiplex reaction conditions. One µL of the diluted genomic DNA was used in 10 µL PCR reactions using Qiagen multiplex PCR kit in an eppendorf Mastercyler (epgradient S). The master mix contained 5µL 2XPCR MM, and primer concentrations were adjusted to yield consistent and relatively even fluorescence among loci. Fluorescently labelled forward primers were mixed with unlabelled forward primers at a ratio of 1:9 for all loci, except for Cm_A011, which was mixed at a ratio of 1:4. The PCR cycling parameters, which were identical for all three multiplex reactions, were as follows; 1x 95°C (15 min), 35x (30s at 95°C, 90s at 56°C, and 60 s at 72 °C) and 1x 60°C (30 min). For multiplex 1 and 2, 1.8 µL of product from each PCR were mixed with GeneScan-500 LIZ internal size standard, and analysed on an ABI 3730 Sequencer. For multiplex reaction 3, locus Cm_D103 could not be successfully amplified in the same reaction as the other 3 loci, and was therefore amplified separately in a singleplex reaction, and 1.8 µL of this singleplex reaction was added to 1.8 µL of the multiplex reaction (that included Cm_A011, Cm_B102 and Cm_d114) and mixed with 15 µL size standard/formamide mix. Electropherograms were visualised and scored using the

software GeneMarker v1.8 (SoftGenetics). Three of the 13 loci amplified non-specific product or failed to amplify any product in some individuals under the multiplex reaction conditions and were abandoned. Table 3.4.1.1 shows the primer sequences, fluorescent labels at the 5' end of forward primer, multiplex reaction conditions and PCR product characteristics of the final ten loci. An estimate of error rate (the ratio between the observed number of allelic differences and the total number of allelic comparisons) was measured by reanalysing a subset of blind samples according to Bonin et al. (2004). Independent genotyping of 24 individuals selected from three sites randomly spread across the sampling area was carried out from DNA extraction through to final allele scoring. A low error rate of 0.83% was detected, which unlikely to bias this study (Bonin et al. 2004). Finally, during genotyping of the full data set with the final 10 loci, all automated allele calls were visually inspected, individuals with suspect electropherograms were repeated, and negative controls utilised.

Observed and expected heterozygosity and the fixation index was calculated in GenAlEx v6, and the presence of null alleles were assessed with Micro-Checker v2.2.3 (van Oosterhout et al. 2004). Three loci, Cm_A115, Cm_B007 and Cm_D114 showed evidence of Hardy Weinberg disequilibrium due to presence of null alleles at frequencies of 0.16, 0.17 and 0.07 respectively.

Genetic sampling

In April 2008, 580 adult Chromis margaritifer individuals were collected on SCUBA using a combination of hand nets, barrier nets and clove oil from 13 sites at Scott Reef and Rowley Shoals (Fig. 3.4.1.1). Fish were collected from replicate sites on each reef and sample sizes ranged from 32 to 53 (Table 3.4.1.2) with an average of 45 individuals per site. Data on sex, reproductive status and size of each fish were also recorded. A dorsal fin clip was placed in 100% ethanol (analytical grade) pending DNA extraction, and whole samples were frozen for subsequent otolith extraction.

Table 3.4.1.1 Characteristics of 10 microsatellite loci for the damselfish *Chromis margaritifer* showing the locus name, Genbank accession number, repeat motif, forward (F) and reverse (R) primer sequences including fluorescent label, multiplex reaction, product size in base pairs, number of alleles (N_A), observed (H_O) and expected (H_E) heterozygosity and inbreeding coefficient (F_{IS}). Significant deviations from Hardy Weinberg equilibrium (F_{IS} values) detected with FSTAT v2.9.3 (at $p < 0.05$) are in bold. All reactions were performed with annealing temperature of 56° on a sample size of 48 fish.

Locus	Genbank Acc #	Repeat	primer sequence (5'-3')	multi-plex	primer conc (uM)	product size (bp)	N_A	H_O	H_E	F_{IS}
Cm_A011	GQ918260	$(GTT)_9$	F: FAM_CGCTGGTAACACTTG	3	0.60	175-199	10	0.82	0.81	0.002
			R: GGTCTGATGTCCGTAAATGA		0.60					
Cm_A110	GQ918261	$(AAC)_7$	F: VIC_CCTCAGCAGTTTGTCCTG	2	0.25	127-133	4	0.18	0.20	0.107
			R: TGTTGTTGTCCGTTGTTATG		0.25					
Cm_A115	GQ918262	$(GTT)_7$	F: NED_CTGGTTGTGGTTCTTCTGTGAC	2	0.37	269-332	12	0.47	0.76	**0.394**
			R: TCATGGAGTCATTCTGGATCAC		0.37					
Cm_A119	GQ918263	$(GTT)_{11}$	F: PET_TCTGGTGAAGGTCAGACTCC	1	0.40	196-241	13	0.88	0.85	-0.022
			R: ACGTGTCGGGTCACAGATTA		0.40					
Cm_B007	GQ918264	$(CATC)_{15}$	F: FAM_AGCACACTACGTTTCACTCCTG	1	0.25	176-328	21	0.59	0.93	**0.370**
			R: TTAGGGATATGGTGAGGGACTC		0.25					
Cm_B102	GQ918265	$(CCAT)_7$	F: FAM_GCCGATGATTCAGTTTGA	3	0.35	275-387	5	0.55	0.52	-0.047
			R: GCGACCCTACAGAGGATT		0.35					
Cm_B117	GQ918266	$(GGAT)_{19}$	F: NED_GGAGCAGCAGGTTATCAGG	1	0.40	200-300	31	0.96	0.95	0.003
			R: CGTCGTCTCATTGTGTTCG		0.40					
Cm_D006	GQ918267	$(CTAT)_{20}$	F: FAM_GCCTTACTGTGTTGTGTTGC	2	0.40	370-430	26	0.92	0.93	0.027
			R: GCCAGGGGAAACCTTTAC		0.40					
Cm_D103	GQ918268	$(TAGA)_9$	F: NED_CTTTCCTTAGAGGCACATTCCT	3[a]	0.40	268-352	21	0.90	0.93	0.047
			R: TCCAGTGTAACACATGGACAT		0.40					
Cm_D114	GQ918269	$(TAGA)_{24}$	F: PET_AGACAACAGGAGGGTAAGTCAC	3	0.35	175-323	31	0.82	0.95	**0.147**
			R: CGTTTAATATGCTGCTGGTTAC		0.35					

* Locus Cm_D103 was amplified separately in a singleplex reaction and then mixed with products from the multiplex 3 at a ratio of 1:1.

DNA sequencing and statistical analysis

To provide an evolutionary backdrop to the fine-scale microsatellite analysis of C. margaritifer, we targeted the Hypervariable Mitochondrial Control Region I (D-loop) in a subset of samples. The forward primer dLoopF developed by Bay et al. (2006) was used together with the universal reverse primer CR-E (Lee et al. 1995). Amplification using the polymerase chain reaction (PCR) was conducted in an eppendorf Mastercyler (epgradient S) as 25 µL reactions (0.2 units Fisher Biotech Tth DNA polymerase Taq, 2.5 µL of 10X PCR Buffer, 2.5 mM MgCl2, 2.5 µLof 10 uM dNTP's, 0.4 mM of each primer, 20 ng template DNA). The PCR cycling profile involved an initial 2 min denaturing step at 94°C, then 35 cycles of 30 s at 94°C, 45 s at 48°C and 60 s at 72°C followed by a 10 min terminal extension phase at 72°C. PCR products were cleaned with Axygen PCR cleanup kit and sequenced in the forward and reverse reaction. Using this procedure, a 292 basepair product was sequenced in four or five individuals from most sites. Forward and reverse sequences were aligned with the program Sequencher 4.8, and haplotype and nucleotide diversity were assessed using the program MEGA v4 (Tamura et al. 2007).

Both the universal primers and the modified primers appeared to amplify an unknown region in the genome that was not the hypervariable control region, and the sequences could not be aligned with D-loop sequences of sister species (including sequences amplified in our lab). A phylogenetic analysis was conducted with MEGA v4 using the Neighbour-Joining method and the evolutionary distances were computed using the Maximum Composite Likelihood method in the units of the number of base substitutions per site (Tamura et al. 2004). A bootstrap consensus tree was inferred from 500 replicates (Felsenstein 1985). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (500 replicates) are shown next to the branches (Felsenstein 1985). All positions containing gaps and missing data were eliminated from the dataset.

Microsatellite genotyping

All 580 individuals collected from 13 sites were genotyped according to the procedure above, and allelic patterns were calculated with GenAlEx v6 (Peakall and Smouse 2006) to estimate the unbiased expected heterozygosities under Hardy-Weinberg equilibrium, and the number of private alleles at the ten microsatellite loci (Table 3.4.1.2). Tests for Hardy-Weinberg and linkage disequilibrium were conducted with FSTAT v2.9.3 (Goudet 1995) and significance levels were based on 1000 permutations of alleles among individuals within sites and were adjusted with sequential Bonferroni correction for multiple tests when $P < 0.05$ using the inbreeding coefficient F_{IS}. Consistent with the initial screening, significant heterozygote deficits loci were detected at 12 out of the 13 sites for each of the loci Cm_A115, Cm_B007 and Cm_D114 (F_{IS} values and significance are given in Table 3.4.1.1). Analysis with Micro-Checker v2.2 (van Oosterhout et al. 2004) indicated that these homozygote excesses were most likely due to null alleles (with a null allele frequency of 0.09 – 0.17). Although there were very few null homozygotes at these three loci (as the frequency of individuals that did not amplify any product was less than 0.0029 at each of these loci), this conclusion is supported not only by the presence of Hardy-Weinberg equilibrium at all other loci at all sites, but also that no evidence for significant linkage disequilibrium was detected (see results). Thus, heterozygote deficits were unlikely to be caused by biological or sampling issues. Consequently, for all subsequent analysis that used allele frequencies at the population level (specifically, the Analysis of Molecular Variance, Fisher exact tests of population differentiation, genetic distance and genetic diversity calculations), we used an adjusted data set calculated with Micro-Checker v2.2.3 to account for null alleles with the Brookfield 1 equation. For analyses that utilise individual genotypes as data (specifically, Spatial Autocorrelation, Allelic Aggregation Index and Landscape Shape Interpolation analyses) we used only the seven loci that were in Hardy-Weinberg equilibrium. Qualitative comparisons among these latter individual based analyses using the seven loci with analyses using the unadjusted data set with all ten loci revealed highly similar patterns.

Microsatellite population-level statistics

To estimate levels of genetic diversity within each system, we calculated gene diversity with FSTAT v2.9.3 (Goudet 1995) as an unbiased estimate of gene diversity (H_{SK}) per locus and

site. This measure adjusts for unequal sample sizes. We present average gene diversity Scott Reef and Rowley Shoals calculated across all sites within each system, and significance was tested by 1000 permutations of a randomized data set.

The proportion of the genetic variation partitioned between systems (F_{RT}), among sites relative to variation within systems (F_{SR}), and among sites relative to overall variation (F_{ST}) was estimated with the Analysis of Molecular Variance (AMOVA) framework implemented by GenAlEx v6 (Peakall and Smouse 2006). Additionally, we calculated the variation partitioned among the sites within each system ($F_{SR\ scott}$ and $F_{SR\ rowleys}$). Tests for statistical significance for all estimates were based on 1000 random permutation tests, we also applied a Fisher exact test to assess significance of differentiation among sites within each system with Genepop v4.0 (Raymond and Rousset 1995) using the default Markov chain parameters. Exact tests are the most powerful for detecting low genetic differentiation among populations (Waples and Gaggiotti 2006), particularly when sample sizes are unbalanced (Goudet et al. 1996). Because the dispersal potential for this damselfish is high and the effect of migration is therefore likely to be strong relative to mutation, we based our AMOVA on differences in alleles that evolve under the infinite allele model (F_{ST}), rather than the sum of squared size differences between allele sizes that evolve under the stepwise mutation model (R_{ST}) (see Balloux and Lugon-Moulin 2002). To account not only for the high degree of variation within populations of microsatellite markers, but also for the effects that potential differences in effective population sizes might have on subdivision, we also calculated a standardized measure of all the F - statistics according to the method of Meirmans (2006).

To visualise the genetic relationships among sites, we took a multidimensional approach that utilised genetic distances between pairs of sites to perform a Principle Coordinates Analysis, PCoA (sensu Jombart et al. 2009). We employed two independent and complimentary estimates of genetic distance, D_{LR} (Paetkau et al. 1995) and D_S (Nei 1972), both of which performed well in studies that evaluated the effectiveness of different genetic distances (Takezaki and Nei 1996; Paetkau et al. 1997). D_{LR}, the mean genotype log likelihood ratio across individuals from each pair of populations, was calculated with the online calculator Doh (Brzustowski 2002) and also seems to be well suited to measuring fine-scale population structure (Paetkau et al. 1995; Underwood et al. 2009). D_S, Nei's standard genetic distance, was calculated in GenAlEx v6 (Peakall and Smouse 2006) together with the final PCoA.

To estimate the number of migrants per generation (N_em) between Scott Reef and Rowley Shoals, we employed the method of Barton and Slatkin (1986) that uses a quasi-equilibrium theory to calculate Nm from the number of private alleles. Because the AMOVA found no evidence for subdivision within systems (see results), we treated each system as a single population (or deme) for this analysis implemented in Genepop v 4.0 (Raymond and Rousset 1995). We present results of Nm based on the estimate corrected for sample size.

Microsatellite individual-level statistics

In addition to the above summary statistics based on allele frequencies, we utilised the genetic identity and geographic location of individual fish to explore subtle spatial patterns of genetic structure. These analyses, akin to "landscape genetics" approaches (sensu Manel et al. 2003), share the desirable properties that they do not rely on the potentially arbitrary groupings of individuals and assumptions of equilibrium between gene flow and genetic drift, and are therefore sensitive to recent dispersal patterns (see Manel et al. 2003; Hedgecock et al. 2007; Hellberg 2007; Selkoe et al. 2008).

First, we visually characterised patterns of spatial genetic structure relative to the specific site sampled across our seascape by generating a "genetic landscape shape" with Alleles In Space v1 (Miller 2005; Miller et al. 2006). First, a connectivity network of sampling areas was constructed and inter-individual genetic distances were assigned to midpoints of site coordinates of the connectivity network edges. Then, a simple interpolation procedure was used to infer genetic distances at site locations on a uniformly spaced grid overlaid over the entire sampling area. A variety of interpolation parameters were used that produced qualitatively similar results, so we present results using 100X100 grid and distance weighting parameter a = 0.5. Because there was a complete lack of isolation by distance signal in our data (r = 0.011; analysis conducted with Alleles In Space v1), we used raw genetic distances to calculate surfaces. Further, because of our limited number of sampling sites relative to the size of sampling area, surfaces were calculated from midpoints of pairwise distances. The output is a three-dimensional surface plot in which X and Y coordinates correspond to geographical locations of sites on the rectangular grid and surface plot heights (Z) reflect genetic distances.

Second, we explored the propensity of damselfish larvae to self-recruit back to their natal reef within each system by employing a spatial autocorrelation analysis to assess the extent of genetic affinity among geographically proximate fish. Specifically, this method computes a correlation coefficient between the genetic distance and geographic distance of all pairs of individuals that fall within a given distance class, and each autocorrelation coefficient r is then plotted with respect to its given distance class. This analysis was conducted in GenAlEx v6 (Peakall and Smouse 2006). When dispersal is restricted and neutral loci are utilized, the autocorrelation coefficient will be positive at short distance classes, and will subsequently decline through zero and become negative at larger distance classes (Epperson and Li 1996; Smouse and Peakall 1999; Peakall et al. 2003; Double et al. 2005). Epperson (2005) showed that spatial autocorrelation provides robust estimates under a wide range of conditions with high statistical power, particularly at the shortest distance classes even when considerably fewer numbers of individuals and alleles that were employed here are used. To test for statistical significance of r at each distance class, the upper and lower bounds of the 95% confidence interval were defined by 1000 random permutations, and if r was located within this confidence belt, the null hypothesis of no spatial genetic structure was accepted. Of the alternative statistical tests provided by GenAlEx, this permutational test has the most power to reject the null hypothesis (Double et al. 2005).

Visual census surveys

Between 1994 and 2008, permanently marked transects were surveyed 12 times at Scott Reef and five times at Rowley Shoals. Underwater visual census was used to count adult reef fishes from a list of 210 species from 10 families (for details, see Heyward et al. 1995), but here we present data from counts of C. margaritifer along 50 × 1 m belt transects. Mean densities across all sites and associated 95% confidence intervals were calculated at each system. To gain an estimate of total population size at each system, we estimated the reef area of suitable habitat at each system, and multiplied this by the density estimates.

Results

Otolith analysis

Results from the otolith study showed that the PLD of C. margaritifer ranges from 16 to 42 d, with a mean PLD (± SD) of 34.9 d (± 4.1). Furthermore, a significantly longer mean PLD was detected at Rowley Shoals (35.8 d ± 4.0) compared with Scott Reef (34.2 d ± 4.0) at $p < 0.01$. Back-calculations of hatch dates showed that, although peak spawning occurred in winter and spring, a substantial proportion of larvae hatched throughout the year (Fig. 3.4.1.3). However, there were small differences between the two systems; peak spawning at Rowley Shoals occurred a month or so later than at Scott Reef. Note that the extremely low numbers hatching in September is probably an artefact of our sampling; recruits would have been too small to catch in the October collection, and were too large to be included in the analysis of the March collection.

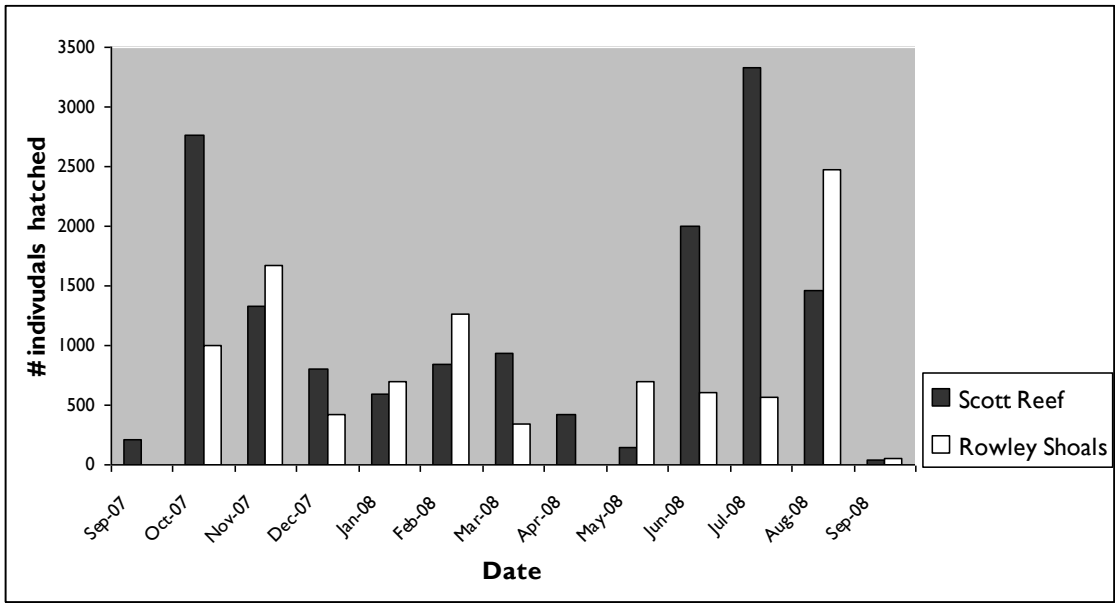


Fig. 3.4.1.3 Hatch frequency plot showing monthly birth dates of *Chromis margaritifer* from Scott Reef and Rowley Shoals back-calculated by subtracting the number of post- and pre-settlement increments from the date of capture, and standardised by applying a mortality rate of 0.1 d^{-1}.

Oceanographic model

In the region of Scott Reef and Rowley Shoals there was a clear reversal of dominant currents from north-east direction in austral summer (1st quarter) to the south-westerly direction in the austral autumn (2nd Quarter) (Fig. 3.4.1.4). Furthermore, irrespective of the time of year, during a dispersion period of one week, the probability that particles were retained close to the source reef was high with areas of low probability extending no more than a few tens of kilometres from source system (Fig. 3.4.1.4A and D). Even after a month, the general pattern was similar with high probabilities of retention of particles within the system, although the blue area of low probability expanded considerably (Fig. 3.4.1.4B and E). For particles with dispersion period of 56 days, the outer edge of the dispersal kernel of particles released from Rowley Shoals in summer encompassed the south section of Scott Reef, and similarly, particles released from Scott Reef in autumn encompassed the northern reef of Rowley Shoals (Fig. 3.4.1.4C and F). Thus, the model suggested that dispersal of larvae between Scott Reef and Rowley Shoals may be possible for larvae with PLD of greater than 28 days (assuming only passive dispersal). However, the likelihood of exchange between the systems was generally very low (< 1%), but simulations over different years showed a high degree of interannual variability. Of particular interest was that in the second quarter of 1998, a filament of relatively high probability (~ 5%) of particles released from Scott Reef extended southwest to within a few tens kilometres of Rowley Shoals after 56 days (insert in Fig. 3.4.1.4F). This filament was not only larger and stronger compared with probability averages across the six years in the same time period (main panel in Fig. 3.4.1.4F), but also contrasted markedly to probability distributions in 1994, 1996, 1997 and 1999 in which the blue area of low probability did not come within 100 kilometres of Rowley Shoals (data not shown).

Spatial structure of sequence variation

Because the targeted hypervariable control region of mtDNA was not amplified, and although the resulting haplotypes had a large amount of variation (60 out of 282 sites were variable; nucleotide diversity of 0.008), the distribution of variation was uninformative and none of the clusters in the phylogenetic tree had strong bootstrap support. Therefore, inferences from this phylogenetic analysis are tentative. However, the phylogenetic tree indicates little underlying geographic structure to genetic relationships among individuals from different sites at Scott Reef and Rowley Shoals (Fig. 3.4.1.5). Specifically, many individuals from each system share closely related or identical haplotypes.

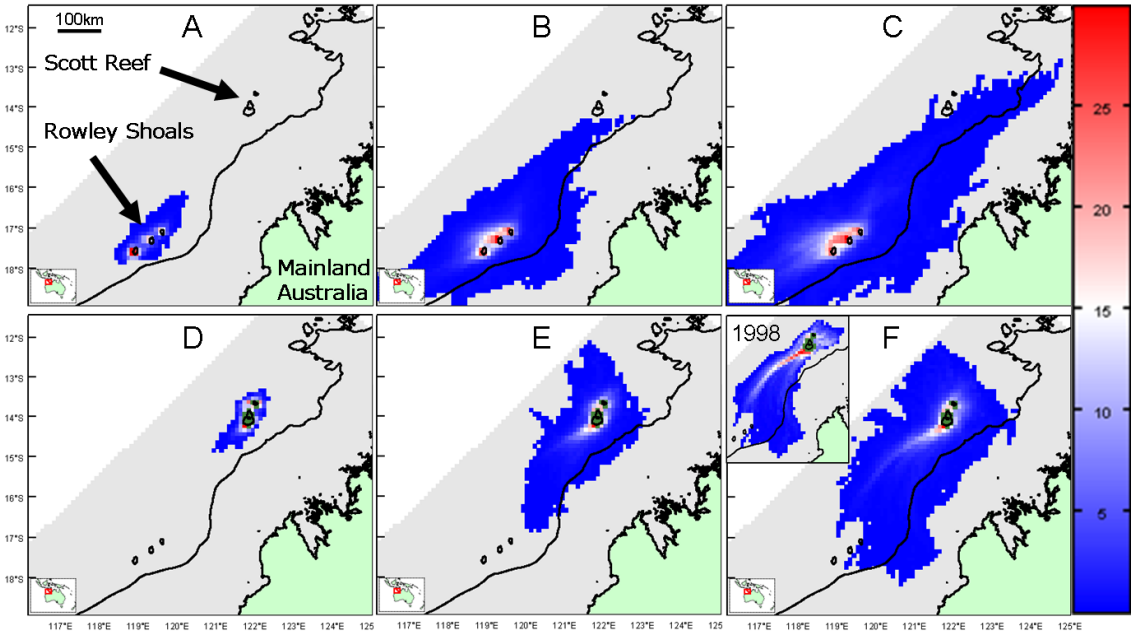


Fig. 3.4.1.4 Dispersal kernels from a three-dimensional non-linear hydrodynamic model forced by wind, temperature and salinity fields to estimate the probability of connectivity by passively dispersed particles within different time periods. Panes A, B and C show probability distributions of particles released from Rowley Shoals in the first quarter and run for 7, 28 and for 56 days respectively. Panes D, E and F illustrate probability distributions of particles released from Scott Reef in the second quarter and run for 7, 28 and for 56 days respectively. All results are based on particle distributions averaged across six years (1994-1999) apart from insert in panel F which was for 1998 only. The colour bar indicates probability of connectivity, and green colour is the release point of particles.

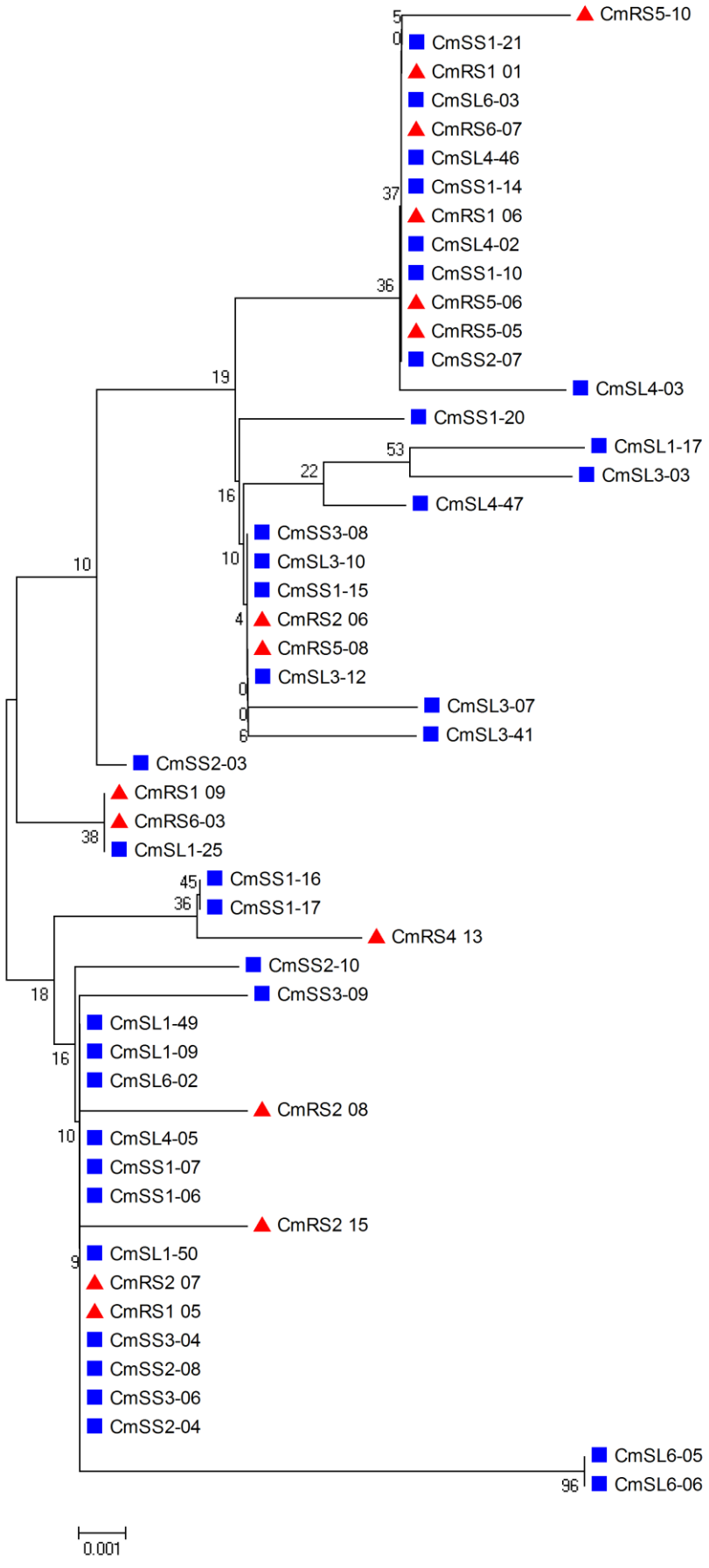


Fig. 3.4.1.5 A Neighbor-Joining bootstrap consensus tree showing genetic relationships among individuals of the damselfish *Chromis margaritifer*. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (500 replicates) is shown next to the branches. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Maximum Composite Likelihood method and are in the units of the number of base substitutions per site. The blue squares are Scott Reef sites, and the red triangles are Rowley Shoals sites.

Table 3.4.1.2 Details of the ten *Chromis margaritifer* microsatellite markers from Rowley Shoals and Scott Reef. Number of individuals genotyped at each site are given in brackets, along with the number of alleles (N_A), the unbiased proportion of expected (H_E) heterozygotes per locus and site, and F_{IS} calculated for each locus and each site (numbers in bold indicate significant deviations from Hardy-Weinberg Equilibrium because of heterozygote deficits). Also given are average number of alleles per locus (mean N_A), average unbiased expected heterozygosity (mean H_E), the average (mean F_{IS}) for each loci across all sites, and the number of private alleles (P_{VA}) at each site.

Site		Cm_A119	Cm_B007	Cm_B117	Cm_D006	Cm_A110	Cm_A115	Cm_A011	Cm_B102	Cm_D103	Cm_D114	P_{VA}
Rowley Shoals												
RS1 (52)	N_A	13	22	32	24	3	16	10	6	26	34	8
	H_E	0.87	0.94	0.97	0.94	0.27	0.83	0.82	0.64	0.94	0.95	
	F_{IS}	0.009	**0.203**	0.027	-0.006	-0.160	**0.398**	0.061	-0.051	0.063	**0.176**	
RS2 (43)	N_A	11	22	25	25	4	15	11	7	27	35	3
	H_E	0.82	0.94	0.95	0.94	0.27	0.76	0.82	0.68	0.95	0.96	
	F_{IS}	0.126	**0.212**	-0.026	-0.013	0.039	0.114	0.066	-0.067	0.024	0.057	
RS3 (53)	N_A	13	25	30	26	4	16	11	7	26	36	3
	H_E	0.86	0.94	0.96	0.94	0.13	0.83	0.80	0.67	0.94	0.96	
	F_{IS}	0.009	**0.283**	0.037	0.081	-0.044	**0.249**	-0.042	-0.092	0.121	**0.118**	
RS4 (37)	N_A	11	19	28	23	5	11	10	5	21	32	6
	H_E	0.86	0.93	0.96	0.94	0.25	0.76	0.84	0.64	0.94	0.96	
	F_{IS}	0.091	**0.245**	0.010	-0.040	0.018	**0.292**	0.227	-0.061	0.056	**0.098**	
RS5 (47)	N_A	12	18	29	27	2	13	10	6	25	33	2
	H_E	0.85	0.93	0.96	0.95	0.26	0.80	0.82	0.64	0.94	0.95	
	F_{IS}	-0.079	**0.201**	0.004	0.104	0.171	**0.211**	0.068	-0.061	0.050	**0.175**	
RS6 (44)	N_A	12	22	28	29	3	14	9	7	24	35	6
	H_E	0.83	0.94	0.96	0.95	0.21	0.73	0.83	0.64	0.95	0.95	
	F_{IS}	0.065	**0.304**	0.007	0.071	-0.097	**0.287**	0.015	-0.097	0.064	**0.165**	
Scott Reef												
SL1 (49)	N_A	13	21	31	26	4	12	10	5	21	31	4
	H_E	0.86	0.94	0.96	0.94	0.21	0.77	0.82	0.53	0.94	0.96	
	F_{IS}	-0.022	**0.370**	0.003	0.027	0.107	**0.394**	0.002	-0.047	0.047	**0.147**	
SL3 (41)	N_A	13	20	27	22	4	15	8	7	23	28	3
	H_E	0.86	0.94	0.96	0.93	0.20	0.80	0.82	0.62	0.94	0.94	
	F_{IS}	-0.016	**0.330**	0.014	0.067	-0.086	**0.333**	0.034	0.056	-0.035	**0.154**	
SL4 (50)	N_A	16	23	28	25	2	15	9	4	24	36	3
	H_E	0.87	0.95	0.96	0.95	0.17	0.82	0.79	0.60	0.94	0.96	
	F_{IS}	0.124	0.071	0.063	0.096	0.155	**0.297**	-0.010	-0.005	0.066	**0.101**	
SS1 (49)	N_A	11	22	30	25	5	16	9	7	23	33	5
	H_E	0.83	0.94	0.96	0.95	0.32	0.77	0.78	0.62	0.94	0.96	
	F_{IS}	0.067	**0.309**	0.065	0.099	0.297	**0.257**	0.004	-0.016	0.048	**0.131**	
SS2 (37)	N_A	12	16	26	24	2	14	9	7	26	29	4
	H_E	0.85	0.92	0.95	0.92	0.15	0.80	0.81	0.66	0.96	0.97	
	F_{IS}	0.084	**0.330**	0.035	0.004	-0.075	**0.157**	-0.073	0.096	0.102	**0.194**	
SS3 (32)	N_A	10	23	29	22	5	13	8	5	22	28	1
	H_E	0.86	0.95	0.96	0.95	0.36	0.76	0.78	0.64	0.94	0.96	
	F_{IS}	0.021	**0.214**	0.152	0.046	0.034	**0.390**	-0.005	0.128	0.206	**0.251**	
SS4 (45)	N_A	12	21	27	25	2	17	8	6	23	29	2
	H_E	0.84	0.94	0.96	0.95	0.20	0.84	0.78	0.67	0.94	0.96	
	F_{IS}	-0.006	**0.283**	0.075	-0.008	-0.111	**0.223**	0.021	0.059	0.147	**0.320**	
mean	N_A	12	21	28	25	3	14	9	6	24	32	
mean	H_E	0.85	0.94	0.96	0.94	0.23	0.79	0.81	0.63	0.94	0.96	
mean	F_{IS}	0.036	0.258	0.036	0.041	0.019	0.277	0.028	-0.012	0.074	0.161	

Spatial structure of microsatellite variation

Unbiased proportion of expected heterozygosities at each site are shown in Table 3.4.1.2. Average gene diversity at Scott Reef (mean H_{SK} = 0.809) and Rowley Shoals (mean H_{SK} = 0.811) was high and did not differ significantly (p = 0.254). The AMOVA detected very low and non-significant levels of subdivision among sites across the scale of the study with F_{ST} =

0.002 (P = 0.305). However, all of this geographic variation in the data was due to differences between systems (F_{RT} = 0.002, while $F_{SR\ all}$= 0.000), and when subdivision at this hierarchical level was considered, the differences were significant (P = 0.023). Variation due to differences among sites within each system of Scott Reef ($F_{SR\ scott}$ = 0.000) and Rowley Shoals ($F_{SR\ Rowleys}$ = 0.000) was zero and non-significant in both systems. The Fisher Exact test for differentiation among sites within each system also revealed significant differences among sites within Scott Reef significant (P = < 0.001), but not at Rowley Shoals (P = 0.236). When these estimates were standardised to the amount of within population diversity (according to Meirmans 2006), the subdivision levels increased considerably but relative distribution of variation remained the same; F'_{RT} and F'_{ST} = 0.011, while variation among sites within systems ($F_{SR\ all}$) remained zero. However, when variation among sites within Scott Reef was standardised, $F_{SR\ scott}$ increased to 0.002, while $F_{SR\ rowleys}$ remained zero. The private allele method estimated 25 migrants per generation between Scott Reef and Rowley Shoals.

The Principal Coordinates Analysis (PCoA) of pairwise genetic distances between sites supported these patterns of genetic structure. Both PCoA plots produced very similar results, and highlighted the differences in degree of differentiation within each system; the sites at Rowley Shoals clustered tightly together, in contrast to the broader spread of the Scott Reef sites (Fig. 3.4.1.6). Furthermore, although there was no major separation among sites within systems, there was no overlap of sites between systems, supporting the differences detected by the AMOVA and confirmed with the exact test.

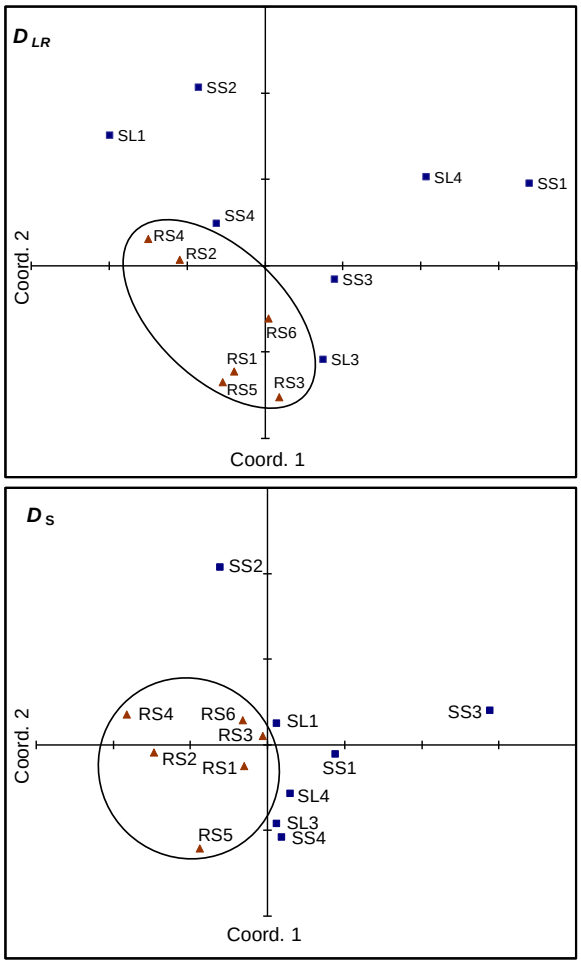


Fig. 3.4.1.6 Principal Coordinate Analysis (PCoA) showing the genetic similarity of *Chromis margaritifer* sampled at sites from Scott Reef and Rowley Shoals. Estimates of pairwise genetic distances were derived from the genotype likelihood ratio distance, D_{LR}, and Nei's standard genetic distance, D_S. The first two axes explained 56% and 60% of the variation for D_{LR} and D_S respectively.

The Genetic Landscape Shape interpolation analysis revealed some subtle patterns of genetic structure that were consistent with the AMOVA and genetic distance analyses (Fig. 3.4.1.7). The most obvious feature of the plot was the three spikes emerging from a ridge of relatively large genetic distances in the middle of the grid, depicting a substantial genetic discontinuity between Scott Reef and Rowley Shoals. Additionally, in this same general region of the grid but further south and west of these spikes, there was a strong dip in genetic distance, depicting high genetic similarities between individuals collected from particular sites from each system. Another feature of this surface plot is a general reduction in genetic distance within Rowley Shoals that was associated with several valleys indicating relatively high genetic similarity between individuals. Lastly, there were two features within Scott Reef that were noteworthy; first, there was a region of relatively low genetic distance in the south and west of the reef system, and second, a spike in genetic distance between individuals in the north and east of the system that correspond to sites located on the outer reef slopes.

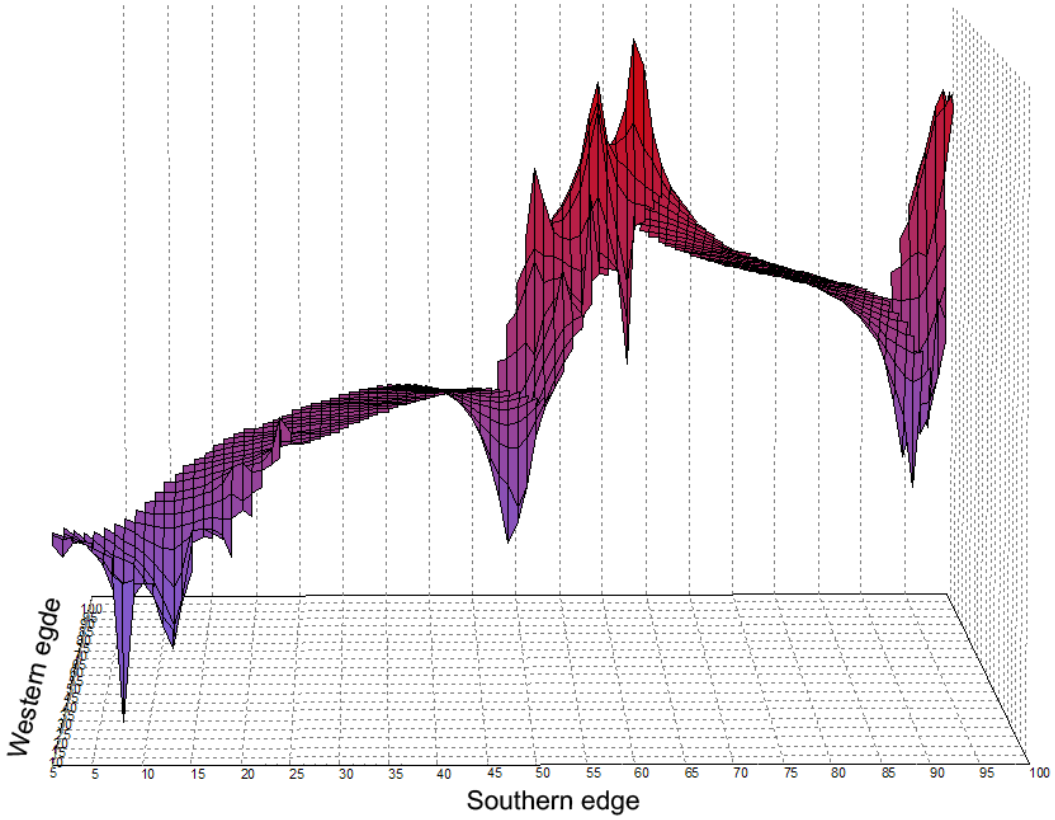


Fig. 3.4.1.7 Genetic landscape shape of *Chromis margaritifer* generated by 100 X 100 grid and a distance weighting of 0.5. Genetic distances correspond to heights of the surface plot (Z axis), and X and Y axes correspond to geographic locations within the overall physical seascape examined in this study (Fig. 3.4.1.1).

The spatial autocorrelation analysis tested whether the differences in genetic differentiation between Scott Reef and Rowleys Shoals was brought about by high levels of gene flow among geographically proximate groups of fish. This analysis was calculated from a large number pairwise comparisons at each distance class (minimum n = 1227, maximum n = 14748), and

the test for significance that we employed has been shown to be particularly powerful at testing significant fine-scale spatial structuring (Double et al. 2005). Despite this, the autocorrelation coefficient did not fall outside the 95% confidence belt at any distance class at either system, providing evidence that genetic relatedness between individual damselfish was not related to the geographic distance between those fish in these systems (Fig. 3.4.1.8).

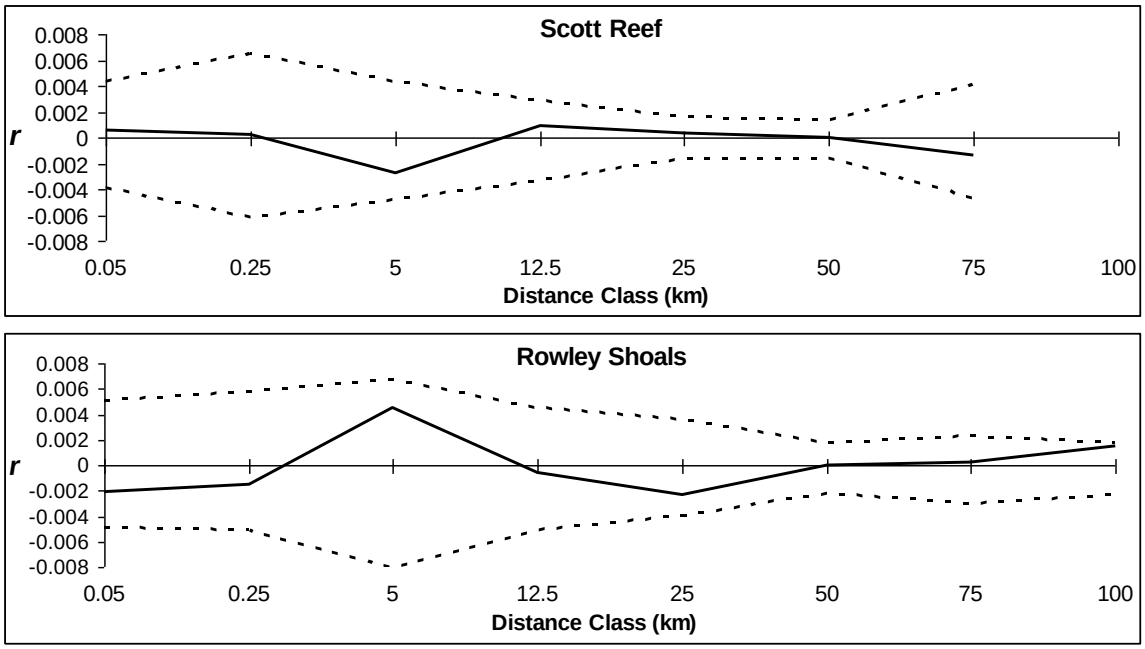


Fig. 3.4.1.8 Spatial autocorrelation analyses of the genetic correlation coefficient (r) as a function of distance for *Chromis margaritifer* at Scott Reef and Rowley Shoals calculated with GenAlEx v6. Dotted lines indicate the upper and lower bounds of the 95% confidence interval defined by 1000 random permutations.

Population density data

Visual census showed that C. margaritifer was on average over 3 times more abundant at Rowley Shoals (116 fish/250m^2 ± 7.4) than at Scott Reef (35 fish/250m^2 ± 8.8). When adjusted for total reef area, (270 km^2 at Rowley Shoals and 305 km^2 at Scott Reef) these differences remained (Rowley Shoals population size = 31,320,000 fish, Scott Reef population size = 10,675,000).

Discussion

Mayr (1963) stated that dispersal in most species involves many individuals that stay close to their origin and a few animals that move farther a field. The results of our study of the damselfish *Chromis margaritifer* support this insight. We utilised a seascape genetics approach to estimate the typical spatial scales of dispersal this species. Results from the otolith and oceanographic analyses suggest that it is possible for propagules passively dispersed over time scales encompassed by the PLD of *C. margaritifer* larvae to move between the atoll systems of

Scott Reef and Rowley Shoals, albeit with a low likelihood. Infrequent connectivity between the two systems was supported by the weak genetic discontinuity detected at this spatial scale. Taken together, these independent lines of evidence suggest that long distance dispersal of these damselfish larvae between Scott Reef and Rowley Shoals is restricted on a generation by generation basis, but probably occurs sporadically during atypical biophysical conditions. Although Rowley Shoals is essentially one panmictic population, significant and spatially inconsistent genetic differentiation was detected within the Scott Reef system. This chaotic pattern of genetic subdivision suggests incomplete mixing of *C. margaritifer* larvae within this system. Differences in population size and larval duration between the two systems, together with evidence from previous genetic data on hard corals, are consistent with these results.

Genetic connections between systems

Genetic variation of ten microsatellite loci from 580 fish across 13 sites at Scott Reef and Rowley Shoals revealed low levels of subdivision at all spatial scales (F'_{ST} = 0.011). Sequence data from a subset of this collection exhibited a congruent lack of underlying geographic structure. Furthermore, there was no difference in gene diversity between Scott Reef and Rowley Shoals, demonstrating that migration of these damselfish larvae between systems is frequent enough in both directions to exchange most genes that arise through mutation and replace other genes that are lost through genetic drift. Therefore, despite the presence of 400 kilometres of deep open ocean habitat between these offshore systems, it appears that gene flow has been strong enough to mitigate the divergence of distinct genetic lineages in this species. However, before we accept this conclusion, we need to address the possibility that this genetic signal has been influenced by past connections and equilibrium between migration, mutation and drift has not yet been reached (see Benzie 1999).

Scott Reef and Rowley Shoals are long-lived reef atolls on which corals similar to present community structure have existed for over 400, 000 years (Lindsay Collins *unpublished data.*). Over this time, dramatic changes in sea levels have occurred (Lambeck and Chappell 2001). During low sea level stands, Rowley Shoals and Scott Reef would have been adjacent to the coast, and it is possible that fringing reefs existed along the continental shelf margin that would have provided stepping stone connections between them (Lindsay Collins *pers. comm.*). Such fringing reefs would have drowned 18,000 years ago when sea levels rose at the end of the last glaciation. Thus, although equilibrium between drift and migration may take hundreds of generations (Waples and Gaggiotti 2006), considering the relatively high dispersal potential of *C. margaritifer*, the short generation times of this species, the isolation of these systems and the high mutation rate of microsatellite markers, the genetic signature of these quaternary sea level changes is likely to have eroded substantially over this time frame. Furthermore, during these glacial periods, evidence suggests not only that water temperatures were at least six degrees cooler, but also that the south-westerly flow originating in the Indonesian Throughflow was much weaker, compared with present day conditions (Okada and Wells 1997). Because these temperatures are not conducive to rapid coral growth (Stirling et al. 1998), it seems unlikely that an extensive network of large and diverse coral reefs with strong physical connections between them existed during these periods. Thus, we conclude that

contemporary influences are the dominant drivers of the overall genetic structure of *C. margaritifer*.

In addition to low levels of genetic differentiation, our oceanographic modelling analysis also indicates that the potential exists for contemporary dispersal of *C. margaritifer* larvae between Rowley Shoals and Scott Reef. Importantly, the magnitude of this potential was not the same among years, and although the probability of exchange was low in five out of the six years (<1%), in the autumn of 1998, the potential for transport between systems was substantially greater; the probability that particles released from Scott Reef moved to within 30 kilometres of Rowley Shoals was over 3% (Fig. 3.4.1.4F). This contrasted to other years, in which the probability was either zero or 0.1% for particles to disperse to within a similar distance of the other system. If such physical connections coincided with a productive spawning season, it is possible that a significant pulse of recruits originating at Scott Reef would be delivered to Rowley Shoals. Furthermore, the extended period of reproductive activity of *C. margaritifer* is likely to increase the range of environmental conditions encountered during the larval pelagic stage, increasing the chances of them hitchhiking (both ways) between systems during particularly strong flow regimes, on physical anomalies such as cyclones, or even by rafting on floating mats of *Sargassum* macroalgae. Indeed, the pattern of the Genetic Landscape Shape (Fig. 3.4.1.7) – in which a reduced genetic distance between individuals from some locations in each system contrasted to the more general pattern of large genetic distances between systems – illustrated the genetic signature that one would expect from such a stochastic migration event. Thus, the above evidence points to a pattern in which sporadic dispersal events maintain moderate to strong genetic connections between populations of *C. margaritifer* at Scott Reef and Rowley Shoals over multiple generations.

Ecological connections between systems

Amidst the background of low level subdivision, we detected a small but significant genetic discontinuity between Scott Reef and Rowley Shoals that demonstrated an absence of strong and regular dispersal between them. Indeed, all of the genetic variation that was detected among geographic locations was due to differences between the two systems. Further, while there was no major separation of sites within each system on the PCoA plots, Rowley Shoals sites not only formed a relatively tight cluster, there was also no overlap with Scott Reef sites (Fig. 3.4.1.6). The Genetic Landscape Shape also showed that the greatest genetic distances occur between systems (Fig. 3.4.1.7). Additionally, our private allele estimate of effective number of migrants per generation (N_em = 25) highlights how few successful migrants are required to maintain the genetic patterns detected here. To place this result into the perspective of an ecologically meaningful parameter, m (migration rate; the proportion of individuals in a population with exogenous origins), simulations of Hastings (1993) suggested that populations that exchange less than 10% of individuals ($m \leq 0.1$) are likely to be demographically independent. This means that the effective population sizes of *C. margaritifer* at each system would need to be less than 250 fish for the number of migrants per generation detected here to be demographically important. Even if we consider that effective population size can be up to three orders of magnitude smaller than census size in marine fish (Frankham

1995; Turner *et al.* 2002), our estimates of total abundance (in the tens of millions) is clearly many orders of magnitude greater than 250, and highlights the difference between genetically important and ecologically important migration.

Considering this genetic data together with results from the oceanographic model that estimated an general low probability (< 1%) of exchange between systems in most years of propagules with a life span similar to *C. margaritifer* larvae, the evidence indicates clearly that dispersal between systems is rare and unlikely to facilitate the ecological maintenance of *C. margaritifer* populations on a generation by generation basis.

Genetic and ecological connections within systems

In addition to inferences about long-distance migration between systems, we also gained insights into dispersal of *C. margaritifer* within each system. When the data were standardised to the amount diversity within each site, a weak signal of geographic structure was detected at Scott Reef ($F_{SR\ scott}$ = 0.002) but not at the Rowley Shoals ($F_{SR\ rowleys}$ = 0.000). Although Meirmans (2006) method is not amenable to permutational testing, the exact test confirmed that this differentiation was significant at Scott Reef. Similarly, the Genetic Landscape Shape also supported these results; genetic distances within Rowley Shoals were generally low relative to other areas of the grid, while specific dips between some locations were the smallest detected on the plot (Fig. 3.4.1.7). Within Scott Reef, genetic distances were also low to the south and west area of the system, but were high in the north and east of the system. This pattern was supported by a Genetic landscape Shape analysis using data from Scott Reef only (results not shown), and illustrates the differences in genetic structure within Scott Reef compared with Rowley Shoals brought about by relatively large genetic distances between some, but not all, sites. These results explain why the spatial autocorrelation did not detect significant spatial structure whereby fish at a near site were no more genetically related to each other than to fish from farther afield. Differences in genetic structure between these two systems were also observed in two species of hard coral, whereby spatial genetic structure was detected at finer scales at Scott Reef than at Rowley Shoals in both species (Underwood et al. 2009). The authors suggested that the complex geography at Scott Reef complicates and restricts current flow, retaining larvae close to their natal reef patch and contributing to self-recruitment of coral larvae over smaller spatial scales compared with Rowley Shoals. Although the damselfish data indicate a chaotic pattern of genetic patchiness that is not associated with a signal of self-recruitment, hydrographic complexity at Scott Reef may provide an adequate explanation for these observed patterns; the much longer larval phase of damselfish provides a greater opportunity for dispersal of larvae away from their natal origin, but the complicated flow patterns are unlikely to mix larvae completely within the system, creating conditions conducive to fine-scale, and possibly ephemeral, genetic patchiness.

In addition to local hydrodynamics, differences in the population and larval ecology may also be driving the differences in genetic structure between Scott Reef and Rowley Shoals. Our estimates of population size indicate that the population at Rowley Shoals is three times as

great as Scott Reef. If we accept that certain percentage of the larval pool will successfully disperse a certain distance between reefs, then the initial numbers produced by adult stocks have the potential to have a major impact on the final numbers arriving, particularly if the distances are in the area of the dispersal kernel where percentage of successful recruits drops off rapidly (see Fig. 2 in Steneck *et al.* 2009 for more detail). Thus, the larger population size and hence reproductive output at Rowley Shoals is likely to increase migration between reefs, and thus homogenise genetic structure within this system. In contrast, the smaller reproductive output at Scott Reef may mean that significantly less larvae successfully disperse between reefs within this system, and therefore create the conditions necessary for the development of fines-scale genetic patchiness. Additionally, the longer PLD at Rowley Shoals (presumably due to low water temperatures there) may also provide greater opportunity for mixing of the larval pool throughout this system compared with Scott Reef. Fine-scale oceanographic models, integrated with realistic biological models, are required to discriminate whether local hydrodynamics, reproductive output or variation in PLD are driving the different genetic structures at Rowley Shoals and Scott Reef.

Management ramifications

The inherent biophysical characteristics of marine populations often limit the power of genetic studies to infer patterns of dispersal that are relevant to short-term ecological processes that are of interest to management (Waples et al. 2008). In particular, occasional long-distance dispersal between populations by a small number of individuals is often sufficient to homogenise genetic structure among populations (Allendorf and Phelps 1981; Slatkin 1987; Waples 1998; Palumbi 2003). However, because demographic replenishment of populations is generally unaffected by such rare events, the "tipping point" where populations become demographically independent usually occurs when the underlying genetic signal is weak (Waples and Gaggiotti 2006). Therefore, our approach of combining high resolution genetic tools with other multidisciplinary approaches is crucial in order to examine realised patterns of connectivity and assess the relative importance and scales of routine versus occasional dispersal (Kinlan and Gaines 2003; Selkoe et al. 2008). The geographical isolation of the reef systems of the Rowley Shoals and Scott Reef are well suited to locating this tipping point; because long-distance dispersers can come only from a limited number of sources, the genetic signal of such events is relatively uncomplicated by intricate and variable source and sink dynamics.

The data presented here for *C. margaritifer* adds to a growing list of fish (e.g. Doherty et al. 1995; Almany et al. 2007; Gerlach et al. 2007), invertebrate (e.g. Johnson and Black 2006a; van Oppen et al. 2008; Underwood 2009), oceanographic (e.g. Largier 2003; Cowen et al. 2006; Lambrechts et al. 2008) and population modelling (e.g. Hastings and Botsford 2006) work demonstrating that locally produced larvae provide a significant input to recruitment in marine species with a wide range of life histories. Importantly, our study also supports the emerging consensus that long-distance dispersal and self recruitment are not mutually exclusive (Cowen *et al.* 2007; Jones *et al.* 2009). For example, Planes et al. (2009) showed that despite over 40% of clownfish recruits returned to their natal reef, 10% of recruits

immigrated from as far as 35 km away and were deemed to be demographically significant. Considering that *C. margaritifer* has a PLD three times longer, and occupies a wider range of habitats in larger numbers, compared with the clownfish, our results compare favourably with that of Planes et al. (2009); *C. margaritifer* seems to be capable of dispersing regularly over tens of km between reefs, and given the right confluence of conditions, infrequently over the 400 km between systems.

In geographical context of the offshore systems of NWA, this study of a coral reef fish augments previous work on hard corals (Underwood *et al.* 2007; Underwood *et al.* 2009), indicating that dispersal is rare between the offshore reef systems of Scott Reef and Rowley Shoals. These data sets are beginning to build a community perspective on connectivity from species with different dispersal abilities that will allow us to greatly enhance our understanding of connectivity processes and consequences (Gaines *et al.* 2007). Although the scale of dispersal *within* these offshore systems differs among these taxa, populations of a brooding coral, a broadcast spawning coral and a benthic spawning damselfish are likely to be maintained by production within each system. Indeed, given the relatively long PLD and the generalist nature of *C. margaritifer,* it is likely that many other species of coral reef fish are regularly dispersing over shorter distances than those presented here. The implication is that geographical isolation of these offshore systems may well confer demographic independence for many other coral reef species. If this is the case, these coral reef communities and ecosystems, not just individual species, at Scott Reef and Rowley Shoals will respond independently to disturbances such as cyclones and coral bleaching events. Thus, successful conservation planning will depend upon the protection of a major portion of the breeding stocks within each system. This means that the challenge for future research (a challenge that is not just confined to this region) should focus on elucidating patterns of fine-scale connectivity of many different species between and within reefs within each system to understand further processes that facilitate local resilience.

References

Allen GR (1991) Damselfishes of the world. Mergus Publishers, Hongkong

Allendorf FW, Phelps SR (1981) Use of allelic frequencies to describe populations structure. Canadian Journal of Fisheries and Aquatic Sciences 38: 1507-1514

Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. Science 316: 742-744

Almany GR, Connolly SR, Heath DD, Hogan JD, Jones GP, McCook LJ, Mills M, Pressey RL, Williamson DH (2009) Connectivity, biodiversity conservation, and the design of marine reserve networks for coral reefs. Coral Reefs 28: 339-351

Alvarez-Filip L, Dulvy NK, Gill JA, Cote IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proceedings of the Royal Society B-Biological Sciences 276: 3019-3025

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

Baird AH (2004) The ecology of coral larvae: settlement patterns, habitat selection and the length of the larval phase. Journal & Proceedings of the Royal Society of New South Wales 137: 43

Balloux F, Lugon-Moulin N (2002) The estimation of population differentiation with microsatellite markers. Molecular Ecology 11: 155-165

Barton NH, Slatkin M (1986) A quasi-equilibrium theory of the distribution of rare alleles in a subdivided population. Heredity 56: 409-415

Bay LK, Crozier RH, Caley MJ (2006) The relationship between population genetic structure and pelagic larval duration in coral reef fishes on the Great Barrier Reef. Marine Biology 149: 1247-1256

Bell JJ (2008) Connectivity between island Marine Protected Areas and the mainland. Biological Conservation 141: 2807-2820

Benzie JAH (1999) Genetic structure of coral reef organisms: ghosts of dispersal past. American Zoologist 39: 131-145

Bonin A, Bellemain E, Bronken Eidesen P, Pompanon F, Brochmann C, Taberlet P (2004) How to track and assess genotyping errors in population genetics studies. Molecular Ecology 13: 3261-3273

Bryce C, Whisson C, Fromont J, Huisman J, McKinney D, Morrison S, Moore G, Titelius M, Hass C, Morrison P, Kernohan (in press) A marine biological survey of Mermaid Reef (Rowley Shoals), Scott and Seringapatam Reefs. Western Australian Museum, Perth, Western Australia

Brzustowski J (2002) Doh assignment test calculator. available online at http://www2.biology.ualberta.ca/jbrzusto/Doh.php

Condie SA, Andrewartha JR (2008) Circulation and connectivity on the Australian North West Shelf. Continental Shelf Research 28: 1724-1739

Cowen RK, Gawarkiewicz G, Pineda J, Thorrold SR, Werner FE (2007) Population connectivity in marine systems an overview. Oceanography 20: 3-21

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. Science 311: 522-527

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 98: 14379-14389

DeWoody J, Nason JD, Hipkins VD (2006) Mitigating scoring errors in microsatellite data from wild populations. Molecular Ecology Notes 6: 951-957

Doherty PJ, Planes S, Mather P (1995) Gene flow and larval duration in seven species of fish from the Great Barrier Reef. Ecology 76: 2373-2391

Double MC, Peakall R, Beck NR, Cockburn A (2005) Dispersal, philopatry, and infidelity: dissecting local genetic structure in superb fairy-wrens (*Malurus cyaneus*). Evolution 59: 625-635

Epperson BK (2005) Estimating dispersal from short distance spatial autocorrelation. Heredity 95: 7-15

Epperson BK, Li T (1996) Measurement of genetic structure within populations using Moran's spatial autocorrelation statistics. Proceedings of the National Academy of Sciences of the United States of America 93: 10528-10532

Felsenstein J (1985) Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783-791

Frankham R (1995) Effective population size/adult population size ratios in wildlife: a review. Genetics Research 66: 95-107

Frankham R (1998) Inbreeding and extinction: island populations. Conservation Biology 12: 665-675

Gaines SD, Gaylord B, Gerber LRG, Hastings A, Kinlan BP (2007) Connecting places: the ecological consequences of dispersal in the sea. Oceanography 20: 90-99

Gerber LRG, Botsford LW, Hastings A, Possingam HP, Gaines SD, Palumbi SR, Andelman S (2003) Population models for marine reserve design: a retrospective and prospective synthesis. Ecological Applications 13: S47-S64

Gerlach G, J A, Kingsford MJ, Black KP, Miller-Sims V (2007) Smelling home can prevent dispersal of reef fish larvae. Proceedings of the National Academy of Sciences of the United States of America 104: 858-863

Gilmour JP, Smith LD, Brinkman RM (2009) Biannual spawning, rapid larval development and evidence of self-seeding for corals on an isolated system of reefs. Marine Biology 156: 1297-1309

Goudet J (1995) Fstat (version 1.2): a computer program to calculate F-statistics. Journal of Heredity 86: 485-486

Goudet J, Raymond M, de Meeüs T, Rousset F (1996) Testing differentiation in diploid populations. Genetics 144: 1933-1940

Hamilton SL, Regetz J, Warner RR (2008) Postsettlement survival linked to larval life in a marine fish. Proceeding of National Academy of Science 105: 1561–1566

Hastings A (1993) Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. Ecology 74: 1362-1372

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

Hedgecock D, Barber P, Edmands S (2007) Genetic approaches to measuring connectivity. Oceanography 20: 70-79

Hellberg ME (2007) Footprints on water: the genetic wake of dispersal among reefs. Coral Reefs 26: 463-473

Heyward A, Halford A, Smith L (1995) Coral Reef Ecosystems of North West Australia: Long-term monitoring of corals and fish at North Reef, South Reef and Seringapatam Reefs. Australian Institute of Marine Science

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, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318: 1737-1742

Hoese DF, Bray DJ, Paxton JR, Allen GR (2006) Fishes. Zoological catalogue of Australia, Vol. 35. In: Beasley PL, Wells A (eds) Part 2. ABRS & CSIRO Publishing, Melbourne

Holloway PE (1995) Leeuwin current observations on the Australian North West Shelf, May–June 1993 Deep-Sea Research Part I Oceanographic Research Papers 42: 285-305

Ivanova NV, deWaard JR, Hebert PDN (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. Molecular Ecology Notes 6: 998-1002

Johnson MS, Black R (2006) Islands increase genetic subdivision and disrupt patterns of connectivity of intertidal snails in a complex archipelago. Evolution 60: 2498–2506

Johnson MS, Watts RJ, Black R (1994) High levels of genetic subdivision in the peripherally isolated populations of the atherinid fish *Craterocephalus capreoli* in the Houtman Abrolhos Islands, Western Australia. Marine Biology 119: 179-184

Jombart T, Pontier D, Dufour A-B (2009) Genetic markers in the playground of multivariate analysis. Heredity 102: 330-341

Jones GP, Russ GR, Sale PF, Steneck RS (2009) Theme section on "Larval connectivity, resilience and the future of coral reefs". Coral Reefs 28: 303-305

Jones KC, Levine KF, Banks JD (2002) Characterization of 11 polymorphic tetranucleotide microsatellites for forensic applications in California elk (*Cervus elaphus canadensis*). Molecular Ecology Notes 2:425-427

Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrrestrial environments: a community perspective. Ecology 84: 2007-2020

Lambeck K, Chappell J (2001) Sea level change through the last glacial cycle. Science 292: 679-686

Lambrechts J, Hanert E, Deleersnijder E, Bernard PE, Legat V, Remacle JF, Wolanski E (2008) A multi-scale model of the hydrodynamics of the whole Great Barrier Reef. Estuarine Coastal and Shelf Science 79: 143-151

Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. Ecological Applications 13: S71-S89

Lee W, Conroy J, Howell W, Kocher TD (1995) Structure and evolution of teleost mitochondrial control regions. Journal of Molecular Evolution 41: 54-66

Leis JM (2002) Pacific coral-reef fishes: the implications of behaviour and ecology of larvae for biodiversity and conservation, and a reassessment of the open population paradigm. Environmental Biology of Fishes 65: 199-208

Manel S, Schwartz MK, Luikart P, Taberlet P (2003) Landscapge genetics: combining landscape ecology and population genetics. Trends in Ecology & Evolution 18: 189-197

Mayr E (1963) Animal species and evolution. Harvard University Press, Cambridge, USA

McCook LJ, Almany GR, Berumen ML, Day JC, Green AL, Jones GP, Leis JM, Planes S, Russ GR, Sale PF, Thorrold SR (2009) Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. Coral Reefs 28: 353-366

Meirmans P (2006) Using the AMOVA framework to estimate a standardized genetic differentiation measure. Evolution 60: 2399-2402

Miller KJ, Ayre DJ (2008) Protection of genetic diversity and maintenance of connectivity among reef corals within marine proteced areas. Conservation Biology 22: 1245-1254

Miller MP (2005) Alleles In Space: Computer software for the joint analysis of interindividual spatial and genetic information. Journal of Heredity 96: 722-724

Miller MP, Bellinger MR, Forsman ED, Haig SM (2006) Effects of historical climate change, habitat connectivity, and vicariance on genetic structure and diversity across the range of the red tree vole (*Phenacomys longicaudus*) in the Pacific Northwestern United States. Molecular Ecology 15: 145-159

Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends in Ecology & Evolution 23: 55-563

Nei M (1972) Genetic distance between populations. American Naturalist 106: 283-292

Nishikawa A, Masaya K, Kazuhiko S (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

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

Okada H, Wells P (1997) Late Quaternary nannofossil indicators of climate change in two deep-sea cores associated with the Leeuwin Current off Western Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 131: 413 432

Paetkau D, Calvert W, Sterling I, Strobeck C (1995) Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4: 347-354

Paetkau D, Waits LP, Clarkson PL, Craighead L, Strobeck C (1997) An empirical evaluation of genetic distance statistics using microsatellite data from bear (Ursidae) populations. Genetics 147: 1943-1957

Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. Ecological Applications 13: S146-S158

Parsons KE (1996) The genetic effects of larval dispersal depend on spatial scale and habitat charactersitics. Marine Biology 126: 403-414

Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian Bush Rat, *Rattus fuscipes*. Evolution 57: 1182-1195

Peakall R, Smouse PE (2006) GenAlEx 6: Genetic Analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6: 288-295

Pérez-Ruzafa Á, González-Wangüemert M, Lenfant P, Marcos C, García-Charton JA (2006) Effects of fishing protection on the genetic structure of fish populations. Biological Conservation 129: 244-255

Pineda J, Hare JA, Sponaugle S (2008) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography 20: 22-39

Planes S, Jones GP, Thorrold SR (2009) Larval dispersal connects fish populations in a network of marine protected areas. Proceedings of the National Academy of Sciences of the United States of America 106: 5693-5697

Raymond M, Rousset F (1995) Genepop (version 1.2): Population genetics software for exact tests and ecumenicism. Journal of Heredity 86: 248-249

Robertson DR (2001) Population maintenance among tropical reef fishes: Inferences from small-island endemics. Proceedings of the National Academy of Sciences of the United States of America 98: 5667-5670

Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ, Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution 20: 74-80

Secor DH, Dean JM, Laban EH (1991) Manual for otolith removal and preparation for microstructural examination. Electric Power Institute and the Belle W. Baruch Institute for Marine Biology and Coastal Research

Selkoe KA, Henzler CM, Gaines SD (2008) Seascape genetics and the spatial ecology of marine populations. Fish and Fisheries 9: 363–377

Slatkin M (1987) Gene flow and geographic structure of natural populations. Science 230: 787-792

Smouse PE, Peakall R (1999) Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure Heredity 82: 561-573

Steneck RS, Paris CB, Arnold SN, Ablan-Lagman MC, Alcala AC, Butler MJ, McCook LJ, Russ GR, Sale PF (2009) Thinking and managing outside the box: coalescing connectivity networks to build region-wide resilience in coral reef ecosystems. Springer, pp 367-378

Stevenson DK, Campana SE (1992) Otolith microstructure examination and analysis. Department of Supply and Services, Ottowa, Canada

Stirling CH, Esat TM, Lambeck K, McCulloch MT (1998) Timing and duration of the last interglacial: evidence for a restricted interval of widespread coral reef growth. . Earth and Planetary Science Letters 160: 745-762

Strathmann RR, Hughes TP, Kuris AM, Lindeman KC, Morgan SG, Pandolfi JM, Warner RR (2002) Evolution of local rectuitment and its consequences for marine populations. Bulletin of Marine Science 70: 377-396

Takezaki N, Nei M (1996) Genetic distances and reconstruction of phylogenetic trees from microsatellite DNA. Genetics 144: 389-399

Tamura K, Dudley J, Nei M, Kumar S (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. Molecular Biology and Evolution 24: 1596-1599

Tamura K, Nei M, Kumar S (2004) Prospects for inferring very large phylogenies by using the neighbor-joining method. Proceedings of the National Academy of Sciences of the United States of America 101: 11030-11035

Thresher RE, Colin PL, Bell LJ (1989) Planktonic duration, distribution and population structure of Western and Central Pacific damselfishes (Pomacentridae). Copeia 2: 420-434

Turner TF, Wares JP, Gold JR (2002) Genetic effective size is three orders of magnitude smaller than adult census size in an abundant, estuarine-dependent marine fish (Sciaenops ocellatus). Genetics 162: 1329-1339

Underwood JN (2009) Genetic diversity and divergence among coastal and offshore reefs in a hard coral depend on geographic discontinuity and oceanic currents. Evolutionary Applications 2 222-233

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 (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 Herwerden L, Choat JH, Newman SJ, Leray M, Hillersøy G (2009) Complex patterns of population structure and recruitment of *Plectropomus leopardus* (Pisces: Epinephelidae) in the Indo-West Pacific: implications for fisheries management. Marine Biology 156: 1595-1607

van Oosterhout C, Hutchinson W, Wills D, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Molecular Ecology Notes 4: 535-538

van Oppen MJH, Lutz AH, De'ath G, Peplow L, Kininmonth S (2008) Genetic traces of recent long-distance dispersal in a predominantly self-recruiting coral. Plos one 3: 1-12

Waples RS (1998) Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. Journal of Heredity 89: 438-450

Waples RS, Gaggiotti OE (2006) What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Molecular Ecology 15: 1419-1439

Waples RS, Punt AE, Cope JM (2008) Integrating genetic data into management of marine resources: how can we do it better? Fish and Fisheries 9: 423-449

Wellington GM, Victor BC (1989) Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Marine Biology 101: 557-567

Wilson DT, McCormick MI (1999) Microstructure of settlement-marks in the otoliths of tropical reef fishes. Marine Biology 134: 29-41

3.4.2. mtDNA sequences reveal limited geographic structuring of cardinalfish populations on offshore atolls

Introduction

Lack of knowledge of patterns of population connectivity is the most critical scientific gap in the understanding required for the effective management of marine systems (Sale et al. 2005; Fogarty and Botsford 2007; McCook et al. 2009)f. The pelagic larval stage of many marine species provide the opportunity for widespread dispersal, but evidence from a range of studies indicates that a large proportion of larvae of some marine species can self-recruit back to their source populations (Swearer et al. 1999; Taylor and Hellberg 2003; Jones et al. 2005; Johnson and Black 2006b; Almany et al. 2007). However, for most taxa, the relative proportion of dispersive and natal-homing propagules remains unknown.

Recent research has begun to identify the mechanisms and consequences of dispersal in organisms inhabiting the offshore reef systems of northwest Australia (NWA). A genetic study of hard corals showed that recruitment to the atoll systems of Scott Reef and Rowley Shoals was predominantly local (Underwood *et al.* 2007; Underwood *et al.* 2009). For both a brooding and broadcast spawning coral, significant genetic subdivision occurred between systems (>100 km), and among (>10 km) or within reefs (<10 km), implying that many reefs or reef patches were demographically independent. Given that such patterns were consistent despite differing reproductive modes of the corals, these results are likely to be representative of many hard corals in the region.

The present study builds on this earlier work by exploring the strength of historical genetic connections between Scott Reef and Rowley Shoals in two species of coral reef cardinalfish (*Cheilodipterus artus* and *Cheilodipterus quinquelineatus*). In contrast to coral larvae, fish larvae have more developed swimming and sensory capabilities, and it is unknown how this will affect their scales of dispersal patterns. Thus far, no published work has explored patterns of connectivity in fish within the offshore reefs of NWA.

Cardinalfish feed off the reef at night, and may therefore provide a crucial ecological role in bringing nutrients from the pelagic environment back onto the reef. The adults have strong homing behaviour to their diurnal resting sites where they congregate in multi-specific schools under reef overhangs in sheltered water usually in lagoons (Marnane 2000). These specific habitat requirements result in a very patchy distribution. Further, cardinalfish brood their eggs in their mouth before releasing larvae into the water column for duration of about three weeks. On the Great Barrier Reef, Gerlach *et al.* (2007) showed that larvae of several species of cardinalfish could not only distinguish, but also preferred, the odour of water from their home reef over water from other reefs. In one species, there was substantial genetic differentiation among reefs despite a strong potential for mixing by ocean currents over the scales of the study (< 25km). These results suggest cardinalfish larvae have the ability to sense and return to their natal reef. If such a homing tendency is strong, reproductive isolation

among geographic locations may result in the evolution of distinct genetic lineages in cardinalfish, as is the case in some other species such as the cleaner goby (Taylor and Hellberg 2003). Here, we test this prediction by examining the genealogical relationships of mtDNA sequences to explore the historical (evolutionary) forces that have shaped the genetic structure of two cardinalfish species *Cheilodipterus artus* and *Cheilodipterus quinquelineatus* at Scott Reef and Rowley Shoals two geographically isolated atoll reef systems in northwest Australia.

Methods

There are great practical difficulties involved in tracing movements of small propagules with high mortality rates throughout the wide expanses of the pelagic environment. As a consequence, there is absence of direct, empirical data detailing patterns of larval dispersal or retention, and most dispersal studies have utilised a range of indirect, interpretative and aggregative methods (Swearer et al. 2002). Genetic studies on larval dispersal have important practical and theoretical advantages over other methods, and have been employed regularly to explore these questions since the advent of molecular markers. These methods utilise the inherent differences in the DNA sequences of individual genomes that accumulate through selection or drift when gene flow is restricted. In this study, we employ a mtDNA marker, which is particularly useful for delineating species and evolutionary significant units, as well as reconstructing past demographic processes (for example bottlenecks, population size expansions) that have shaped the genetic variation seen in today's living populations (Moritz 1994).

In April 2008, a total of 580 individuals of *Cheilodipterus artus* were collected from 12 sites at both Scott Reef and the Rowley Shoals (Table 4.3.2.1). Sample sizes per site ranged from between 30 and 60 individuals for each species. It was impossible to distinguish *Cheilodipterus artus* from *Cheilodipterus quinquelineatus* underwater and as a result some of the latter species were also collected. These were included in the genetic analyses (Table 3.4.2.1). At Scott Reef, the cardinalfish occurred in sheltered lagoon habitats and under bommies in semi-sheltered microhabitats on the reef slopes. In contrast, at Rowley Shoals, cardinalfish occurred only in the sheltered lagoons. As a result, samples at Scott Reef were collected in both these habitats, but only in lagoon habitat at Rowley Shoals. Lastly, at Scott Reef, site SL3 is not clearly either a lagoon or slope habitat as it is exposed to swell but is not a steep drop off. For the purposes of this study, we have called it a lagoon site.

Table 3.4.2.1 GPS locations, sample sizes and site habitat of *Cheilodipterus artus* and *Cheilodipterus quinquelineatus* at Rowley Shoals (site name begins with R) and Scott Reef (site name begins with S).

Site	Habitat	GPS	*Cheilodipterus artus*	*Cheilodipterus quinquelineatus*
SL1	lagoon	14º 04.917' S 121º 56.831' E	60	-
SL3	lagoon	14º 04.142' S 121º 46.601' E	47	9
SL4	slope	14º 01.459' S 121º 51.720' E	31	23
SL6	lagoon	17º 08.303' S 119º 39.620' E	31	20
SS1	slope	14º 04.576' S 121º 58.554' E	63	-
SS2	slope	13º 55.305' S 121º 54.864' E	50	-
RS1	lagoon	17º 04.201' S 119º 38.596' E	50	19
RS2	lagoon	17º 08.272' S 119º 39.216' E	57	-
RS3	lagoon	17º 17.405' S 119º 22.196' E	50	26
RS4	lagoon	17º 18.748' S 119º 22.074' E	39	3
RS5	lagoon	17º 32.568' S 118º 57.870' E	49	-
RS6	lagoon	17º 35.335'S 118º 58.155' E	60	-
Total			587	100

We targeted the Hypervariable Mitochondrial Control Region I (D-loop) in a subset of both species of *Cheilodipterus* with the universal primers CR-A and CR-E (Lee *et al.* 1995). Amplification using the polymerase chain reaction (PCR) was conducted in an eppendorf Mastercyler (epgradient S) as 25µL reactions (0.2 units Fisher Biotech Tth DNA polymerase Taq, 2.5µL of 10X PCR Buffer, 2.5 mM MgCl2, 2.5 µLof 10 uM dNTP's, 0.4 mM of each primer, 20 ng template DNA). The PCR cycling profile involved an initial 2 min denaturing step at 94°C, then 35 cycles of 30 s at 94°C, 45 s at 48°C and 60 s at 72°C followed by a 10 min terminal extension phase at72°C. PCR products were cleaned up with Axygen PCR cleanup kit and sequenced in the forward and reverse reaction. Using this procedure, a 387 bp product was amplified in 58 *C. artus* from all 12 sites (4 to 5 individuals per site) and a 435 bp product was amplified 20 *C. quinquelineatus* individuals from 4 sites (5 individuals per site). Forward and reverse sequences were aligned with the program Sequencher 4.8, and haplotype and nucleotide diversity were assessed using the program MEGA v4 (Tamura *et al.* 2007).

General haplotype diversity measures and population differentiation measured by G_{ST} (Nei 1973) between Scott Reef and Rowley Shoals were estimated with DnaSP v 4.5 software (Rozas *et al.* 2003). Significance of population differentiation was assessed with a chi-square test also in DnaSP v 4.5. A phylogenetic analysis for each species was implemented with MEGA v4 using the neighbour-joining method and the evolutionary distances were computed in the units of the number of base substitutions per site using the Maximum Composite Likelihood method (Tamura *et al.* 2004). A bootstrap consensus tree was inferred from 500 replicates according to the method of Felsenstein (1985). The percentage of replicate trees in

which the associated taxa clustered together in the bootstrap test is shown next to each branche. All positions containing gaps and missing data were eliminated from the dataset.

Results

The underlying variation of D-loop sequences in *Cheilodipterus artus* was very high; 134 out of 387 sites were variable, and nucleotide diversity was 0.122. The phylogenetic tree showed a deep genetic split (> 20% sequence divergence) into two clades that had strong bootstrap support. These clades corresponded closely to the different habitats sampled; one consisted mostly of individuals from slope sites at Scott Reef, and the other clade almost entirely of individuals from lagoon sites at Scott Reef and Rowley Shoals (Fig. 3.4.2.1). Despite this general relationship, four individuals from Rowley Shoals lagoon and three from site SL3 at Scott Reef were in the "slope" clade, while two individuals from Scott Reef slope were in the "lagoon" clade. The distribution of haplotype variation was not associated with location; G_{ST} = 0.003 and this differentiation was not significant (P = 0.296). To test whether the variation between clades was masking any spatial structure, we also measured differentiation between Scott Reef and Rowleys Shoals within the "lagoon" clade, but the general patterns remained the same (G_{ST} = 0.002, P = 0.378). Finally, within the "lagoon" clade, there was another split into two subclades. Although this split was also quite deep (8.89% sequence divergence) and had strong bootstrap support, there was no geographic structure to this part of the tree.

The D-loop sequences from *Cheilodipterus quinquelineatus* yielded much less underlying variation; only 22 of the 431 sites were variable and nucleotide diversity was 0.008. The resulting phylogenetic tree exhibited extremely shallow phylogenetic structure, and bootstrap values were not strong (Fig. 4.3.2.2). As with *C. artus*, there was no spatial structure to the tree, and measure of population differentiation between systems was low and not significant (G_{ST} = 0.005, P = 0.328).

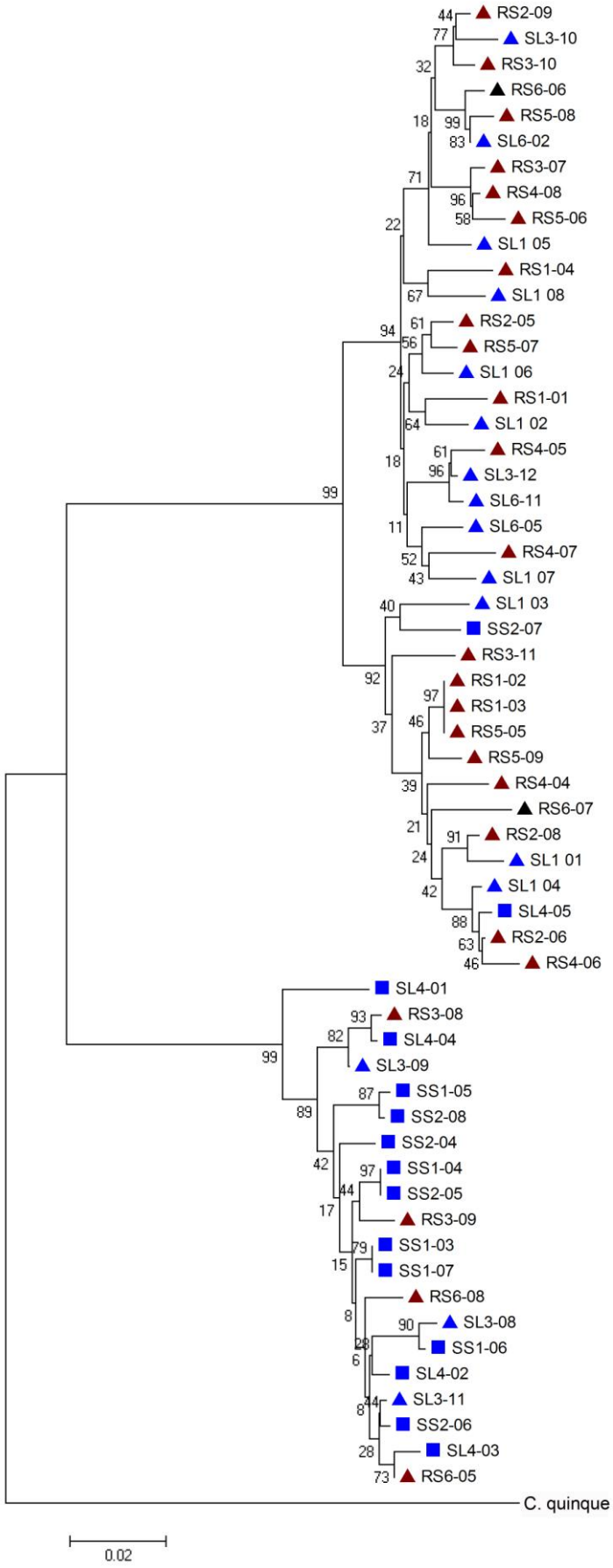


Fig. 3.4.2.1 A neighbour-joining bootstrap consensus tree showing genetic relationships among individual cardinal fish *Cheilodipterus artus*. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test is shown next to the branches. The blue squares - Scott Reef outer reef slope sites, the blue triangles - Scott Reef lagoon sites, red triangles - Rowley Shoals lagoon sites.

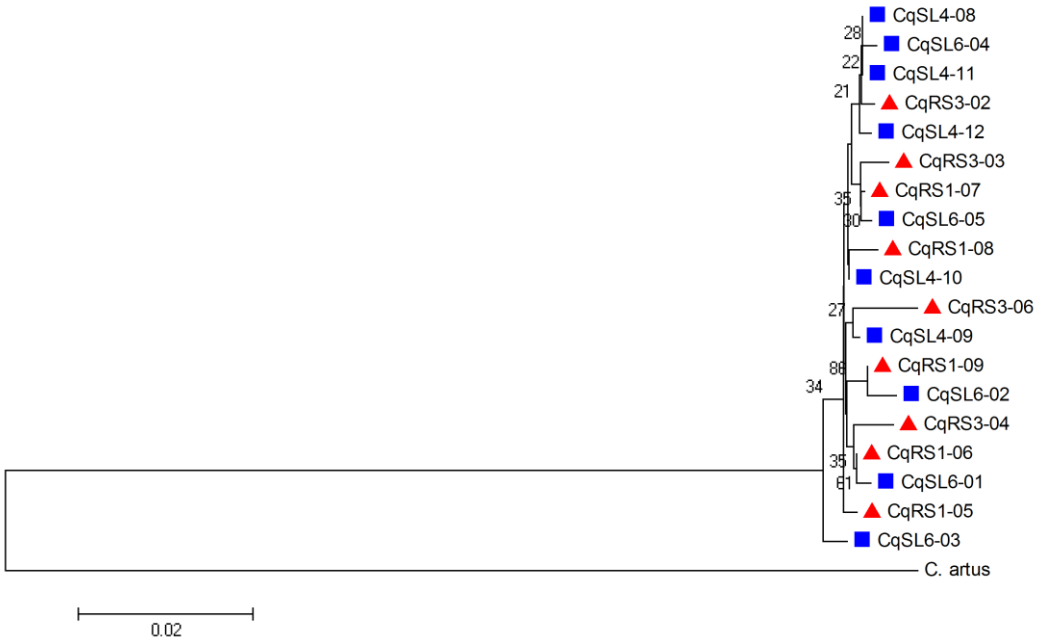


Fig. 3.4.2.2 A neighbour-joining bootstrap consensus tree showing genetic relationships among individual cardinal fish *Cheilodipterus quinquelineatus*. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test is shown next to the branches. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. Blue squares - Scott Reef sites, red triangles - Rowley Shoals lagoon sites.

Discussion

An unexpected finding of this study was the large genetic divergence into two clades in *Cheilodipterus artus* that corresponded closely, but not exclusively, to individuals collected in the lagoon habitat and the those collected on the reef slope. The most parsimonious explanation of this result is that the two clades comprise cryptic species that have been previously identified as *C. artus*. The alternative, but less plausible hypothesis is that these two clades are currently in the process of speciation, with behavioural characteristics limiting hybridization. A detailed morphological assessment of type specimens, together with an analysis with microsatellite markers, will be required to resolve this issue.

Irrespective of the taxonomic status of the two major clades, patterns of sequence variation at the mtDNA control region of both cardinalfish *Cheilodipterus artus* and *Cheilodipterus quinquelineatus* reveal an absence of geographical structuring among the reefs and between the systems of Scott Reef and Rowley Shoals. For *C. artus*, even within the "lagoon clade", there was clearly no geographic structure underlying these patterns; many individuals from Scott Reef and Rowley Shoals share closely related haplotypes. Further, the high levels of genetic variation within each clade (between 3% and 6% nucleotide divergence) suggests that these populations were not particularly isolated in evolutionary terms. The levels of variation

were much lower for *C. quinquelineatus*, but the pattern of no geographic structure was the same. In the context of population connectivity, these preliminary data suggest historical genetic mixing the scale of the study. Therefore, it appears that the larvae of these two cardinalfish either are capable of regularly dispersing the 400km between atoll systems, at least in evolutionary time scales (many generations), or have been well connected sometime in the recent past. Similar results were found by Underwood et al (CH3.1.4) for a damselfish (*Chromis margaritifer*) in these localities. Sequence data for this species also showed a lack of geographic patterns however, but microsatellite data revealed subtle genetic differentiation that was likely to be a result of restricted contemporary gene flow between systems. Therefore, it is not clear from sequence data presented here whether the self-recruitment of cardinalfish larvae to their natal reef drives replenishment over ecological time scales. Data from microsatellites are required to address this question.

References

Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. Science 316: 742-744

Felsenstein J (1985) Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783-791

Fogarty MJ, Botsford LW (2007) Population Connectivity and Spatial Management of Marine Fisheries. Oceanography 20: 112-123

Gerlach G, J A, Kingsford MJ, Black KP, Miller-Sims V (2007) Smelling home can prevent dispersal of reef fish larvae. Proceedings of the National Academy of Sciences of the United States of America 104: 858-863

Johnson MS, Black R (2006) Islands increase genetic subdivision and disrupt patterns of connectivity of intertidal snails in a complex archipelago. Evolution 60: 2498-2506

Jones GP, Planes S, Thorrold SR (2005) Coral reefs fish larvae settle close to home. Current Biology 15: 1314-1318

Lee W, Conroy J, Howell W, Kocher TD (1995) Structure and evolution of teleost mitochondrial control regions. Journal of Molecular Evolution 41: 54-66

Marnane MJ (2000) Site fidelity and homing behaviour in coral reef cardinal fishes. Journal of Fish Biology 57: 1590-1600

McCook LJ, Almany GR, Berumen ML, Day JC, Green AL, Jones GP, Leis JM, Planes S, Russ GR, Sale PF, Thorrold SR (2009) Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. Coral Reefs 28: 353-366

Moritz C (1994) Applications of mitochondrial DNA analysis on conservation: A critical review. Molecular Ecology 3: 401-411

Nei M (1973) Analysis of gene diversity in subdivided populations. Proceeding of National Academy of Science 70: 3321-3323

Rozas J, Sánchez-Delbarrio JC, Messeguer X, Rozas R (2003) DnaSP, DNA polymorphism analyses by the coalescent and other methods. Bioinformatics 19: 2496-2497

Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ, Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution 20: 74-80

Swearer SE, Caselle J, Lea D, Warner RR (1999) Larval retention and recruitment in an island population of coral-reef fish. Nature 402: 799-802

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

Tamura K, Dudley J, Nei M, Kumar S (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. Molecular Biology and Evolution 24: 1596-1599

Tamura K, Nei M, Kumar S (2004) Prospects for inferring very large phylogenies by using the neighbor-joining method. Proceedings of the National Academy of Sciences of the United States of America 101: 11030-11035

Taylor MK, Hellberg ME (2003) Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. Science 299: 107-109

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 (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

3.5. Patterns of reproduction and recruitment for coral communities at Scott Reef, an isolated atoll off north-west Australia

Introduction

Patterns of reproduction in spawning and brooding corals

Most corals on Indo-Pacific reefs reproduce by mass spawning (Harrison et al. 1984; Babcock et al. 1986; Harrison and Wallace 1990; Harrison and Booth 2007). Mass coral spawning is a spectacular event that involves the synchronous release of eggs and sperm by many corals in a single night each year. Mass spawning is particularly prevalent on reefs around Australia, and generally occurs a few nights after a full moon in spring (October / November) on the Great Barrier Reef, and autumn (March/April) on north-west Australian reefs (Harrison and Wallace 1990). On north-west Australian reefs, mass coral spawning in autumn has been documented as far south as the Abrolhos Islands (Babcock et al. 1994), through Ningaloo (Simpson 1991), and as far north as Scott Reef (Gilmour et al. 2009). More recently, however, a second spawning event has been discovered on the most northern reefs, occurring in spring at a similar time to that on the Great Barrier Reef. Although less prominent than that in autumn, spawning by multiple colonies and species during spring has been documented on reefs at Barrow Island, the Dampier Archipelago, the Rowley Shoals, and Scott Reef (Rosser and Gilmour 2008; Gilmour et al. 2009). The proportion of species and colonies participating in spawning events during spring and autumn each year is not known, nor is whether the phenomenon is a consequence of colonies within a species spawning at different times of the year, or some colonies spawning twice a year.

Although most corals on Indo-Pacific reefs mass spawn, some abundant and functionally important corals brood and release fully developed planulae larvae following internal fertilisation and embryogenesis (Harrison and Wallace 1990; Richmond and Hunter 1990). The larvae released by these brooding corals have the potential to settle quickly, within the natal community (Richmond 1988; Ayre and Hughes 2000; Harii et al. 2002; Nishikawa et al. 2003; Fan et al. 2006; Underwood et al. 2007). However, brooded larvae are also capable of surviving long periods before settling and may periodically disperse among distant reefs (Richmond 1988; Ayre and Hughes 2000; Harii et al. 2002). Compared with the spawning corals, the cycles of reproduction in brooding corals are less predictable and more complex. Brooding corals tend to have multiple cycles of gametogenesis, spawning, and planulation that culminate in the release of planulae larvae over many months or all year round (e.g. Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990; Tanner 1996; Zakai et al. 2006).

The ability of brooding corals to release planulae over several months in a year that are competent to settle means they can become an important component of local communities.

For example, a large number of brooded larvae can quickly occupy available space following a disturbance, potentially excluding other species (Harrison and Booth 2007). Indeed, some brooding corals are able to outcompete other species once they have settled and become established; although not good direct competitors, fast growing brooding corals such as *I. brueggemanni* and *Seriatopora hystrix* can outcompete other corals by overgrowing and overtopping (Lang 1973; Lang and Chornesky 1990; Tanner 1995). However, fast growing brooding corals with a fragile growth form are also susceptible to common disturbances, such as cyclones and elevated water temperatures (Knowlton et al. 1981; Highsmith 1982; Loya et al. 2001; Baird and Marshall 2002; Madin et al. 2008). The dominance of some brooding corals in the absence of disturbance, and their wide-spread mortality following disturbances, has been documented on many reefs, including Scott Reef (Smith et al. 2006b; Smith et al. 2008). Despite their importance in structuring coral communities, there remains little demographic information for brooding corals, including their patterns of reproduction. Knowing the patterns of gametogenesis, larval production and settlement for both brooding and spawning corals is necessary for management of human activities around critical periods of the life cycle. Estimates of 'reproductive significance' required by management agencies for different seasons and months within a year need information about both spawning and brooding corals.

Patterns of recruitment in spawning corals

The larvae produced during the different reproductive periods at Scott Reef maintain the coral communities and facilitate their recovery following disturbances. Moreover, the recovery of populations following major disturbances, which kill rather than injure colonies, relies heavily on sexual recruitment. This potential is, however, determined by the rates of recruitment and post-recruitment survival. For example, recovery of a community following a disturbance may be slow, even with high rates recruitment, if post-recruitment survival is low; conversely, recovery would also be slow under favourable conditions and high rates of post-recruitment survival, if the rates of recruitment are low. Quantifying rates of larval recruitment measures one key component of the resilience of coral communities (Knowlton and Jackson 2008); by also correlating changes in recruitment with changes in coral cover, some inferences also can be made about the degree of connectivity among locations within and among reefs and the importance of post-recruitment processes (Hughes et al. 2000b). If reefs are largely self-seeded and have only weak connections to others in the region, recovery from disturbances will be facilitated by the surviving broodstock, rather than the supply of larvae from reefs not impacted by the disturbance. Knowing the degree of connectivity among coral communities is particularly important for managing their exposure to an increasing array of disturbance (Ayre and Hughes 2004; Sale et al. 2005; Van Oppen and Gates 2006; Cowen et al. 2007).

In this study, the patterns of reproduction and the rates of recruitment were investigated at locations across Scott Reef. In particular, a variety of methods were used to infer the times of spawning and planulation by some of the most abundant shallow-water corals, around previously documented times of spawning in autumn and spring. Rates of recruitment were quantified following the primary mass spawning in autumn, and correlated with variation in

coral cover, to gain an insight into the degree of connectivity among locations and the resilience communities.

Methods

Study Sites

Scott Reef is an isolated reef system located 270km off mainland of north-west Australia (S14° 04', E121° 46') and consists of North and South Reef. Surveys of coral reproduction and recruitment were conducted at six locations across Scott Reef (SL1, SL2, SL3, SL4, SS1, SS2), which are 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 and recruitment surveys were conducted at the first site.

Reproductive surveys

Replicate colonies of the dominant spawning and brooding corals were sampled from all six locations several weeks (2 to 5 weeks) before the predicted dates of mass spawning in autumn (March/April) and spring (October/November), in 2008 and/or 2009. Additionally, some spawning corals and brooding corals were sampled several weeks after the mass spawning in autumn during each year. Colonies were sampled haphazardly from areas adjacent to, but away from, long-term monitoring transects. 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 the sterile colony margins.

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 2005, Baird et al 2002), according to the following criteria:

Score 1	Large pigmented (red or pink) eggs were clearly visible within polyps, indicating that colonies will spawn following the next full moon, and within one month;
Score 1/2	Unresolved egg state (between states 1 and 2) indicating that colonies will spawn following the next full moon or two full moons, and within one or two months;
Score 2	Large unpigmented (white or cream) eggs were clearly visible within polyps, indicating colonies will spawn following two full moons and 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.

Colony samples were stored in a solution of 10% formalin-seawater. Spawning corals were decalcified in10% 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 1985).

For the brooding corals *Isopora bruggemanni* and *Seriatopora hystrix*, and the massive *Porites spp.*, tissue samples were investigated using 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; Vargas-Angel et al. 2006).

Recruitment surveys

The rates of recruitment for corals at Scott Reef were quantified from 1996 to 1999, and in 2002, 2003, 2006 and 2008, at all six monitoring locations. At the first site at each location, six terracotta settlement plates (110mm x 110mm x 10mm) were deployed at the start of the first three monitoring transects, separated by approximately 50 m along reef slope (18 plates location^{-1} year^{-1}). The six plates were spaced haphazardly, approximately 1 m apart, and attached to the reef (see Mundy 2000) three weeks prior to the predicted mass coral spawning in autumn and collected eight weeks later. After collection, the settlement plates were bleached and the skeletons of coral recruits counted using a stereo-dissection microscope.

Results

Patterns of reproduction in spawning and brooding corals

The participation by corals in the mass spawning in autumn (2008, 2009) and spring (2008) was inferred from samples collected from several hundred colonies of 48 species at six

locations across Scott Reef. The stage of egg development was ranked for over 200 colonies *in situ* and in the lab, as was the size and number of more than 20 000 eggs of within polyps. These data confirm the pattern of a primary mass spawning in autumn, with a secondary multi-specific spawning event occurs in spring (Table 3.5.1).

Of 45 species sampled at Scott Reef during one or more periods, replicate colonies from 44 are known to spawn during autumn; 15 of these species spawn during spring and 14 spawn twice a year during each season (Table 3.5.1, Appendix 3.5.1). Of the species that spawn twice a year, most have a larger proportion of colonies spawning in autumn than in spring, providing further confirmation that the main reproductive period is during autumn (Appendix 3.5.1). However, there are some notable exceptions to this pattern. Of species sampled with sufficient replication (>10 colonies) that spawn during both autumn and spring, a significant percentage (30-70%) of four different *Acropora* spawned in spring (*A. cytherea, A. hyacinthus, A. samoensis* and *A. tenuis*). All recent evidence indicates that there is only one species, *A. millepora*, that spawns exclusively during spring, with 75% of colonies sampled during spring having mature gametes and none having mature gametes in autumn (N = 93). In addition to coral that spawn in spring, the results of histological analyses indicate colonies of the massive *Porites spp.* also spawn outside the primary reproductive period in autumn. Replicate colonies of the massive *Porties spp.* contained eggs and testes in various stages of development when sampled in spring and autumn. Although these stages of development did not suggest spawning during spring, they did indicate the potential for spawning during summer and/or autumn months (Table 3.5.2).

Table 3.5.1 Participation in mass spawning events during autumn (yellow), spring (blue) or both seasons (green). Participation was inferred from a combination of *in situ* egg scores and laboratory analysis of egg sizes.

Species	autumn	spring	autumn & spring
Acropora abrolhosensis			
Acropora aculeus			
Acropora anthocercis			
Acropora carduus			
Acropora cerealis			
Acropora clathrata			
Acropora cytherea			
Acropora digitifera			
Acropora echinata			
Acropora florida			
Acropora gemmifera			
Acropora grandis			
Acropora granulosa			
Acropora humilis			
Acropora hyacinthus			
Acropora indonesia			
Acropora intermedia			
Acropora latistella			
Acropora listeri			
Acropora microclados			
Acropora microphthalma			
Acropora millepora			
Acropora monticulosa			
Acropora muricata			
Acropora nasuta			
Acropora polystoma			
Acropora samoensis			
Acropora secale			
Acropora spicifera			
Acropora subglabra			
Acropora subulata			
Acropora tenuis			
Acropora valenciennesi			
Acropora valida			
Acropora vaughani			
Diploastrea heliopora			
Echinopora lamellosa			
Favia pallida			
Favia stelligera			
Galaxea fascicularis			
Lobophyllia hemprichii			
Montipora encrusting spp.			
Pavona venosa			

Of the brooding corals that have been sampled, histological analysis has been conducted on *Isopora brueggemanni* and *Seriatopora hystrix*. For both species and seasons, samples contained eggs and sperm in most developmental stages (Table 3.5.2). Planulae were present in both species during the autumn sampling, but only in *I. brueggemanni* in spring. 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 3.5.2 Stages of development of eggs and testes in massive *Porites spp*. and the brooding corals *Isopora brueggemanni* and *Seriatopora hystrix*. Development stages were derived from histological analysis.

Season	Species	Egg Stage					Teste Stage			
		I	II	III	IV	Planulae	I	II	III	IV
autumn	*Porites massive spp.*	8	2	0	0	---	1	1	0	0
	Isopora brueggemanni	14	24	13	11	13	18	22	9	4
	Seriatopora hystrix	12	16	17	5	5	3	4	7	0
spring	*Porites massive spp.*	5	5	2	0	---	0	1	1	0
	Isopora brueggemanni	1	2	4	2	4	0	3	1	0
	Seriatopora hystrix	5	5	4	5	0	2	0	2	0

Patterns of recruitment following mass spawning

The rates of recruitment at Scott Reef have continued to increase since the 1998 bleaching, with particularly large increases recent years (Fig. 3.5.1). The mean rate (± S.E.) of recruitment at Scott Reef has increased from <0.3 (± 0.2) recruits plate^{-1} yr^{-1} one year after the bleaching in 1999, to 2.3 (± 1.5) in 2003, and 60.2 (± 9.0) in 2009.

Mean rates (± S.E.) of recruitment in the last two years were higher than those before the bleaching, but decreased between 2008 (70.4 ± 5.7) and 2009. However, in 2008 there was considerable variation in rates of recruitment among locations (Fig. 1; CV = 198), and the mean rate was strongly skewed by 354 recruits plate^{-1} at one location (SL1); this was more than four times the pre-bleaching rates of recruitment or at any other of the locations in 2008. By comparison, the maximum recruitment at any one location in 2009 was less than half (157 recruits plate^{-1}) that in 2008, but recruitment had increased at all other locations and there was far less spatial variation (Fig. 3.5.1; CV = 83). By 2009, recruitment at all but one location was higher than that prior to the bleaching.

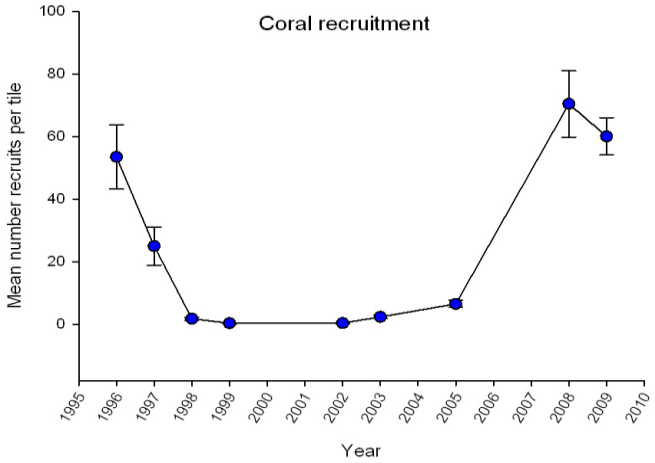


Fig. 3.5.1 Mean number of coral recruits on settlement tiles at locations across Scott Reef following the mass spawning in autumn. The coral bleaching occurred in 1998.

Rapid increases in coral recruitment in recent years reflect similar increases in coral cover across Scott Reef (Fig. 3.5.2A). Indeed, there is a strong (R^2 = 0.78) correlation between coral cover and recruitment at Scott Reef over the entire period of monitoring (Fig. 3.5.2B). Changes in coral cover through periods of disturbance and recovery yielded similar changes in the rates of recruitment at Scott Reef. However, increases in coral recruitment initially lagged behind those for coral cover, and increased more rapidly in recent years (Fig. 3.5.2A). For example, a there was relative increase in coral cover of 80% between 1999 and 2003, compared with 30% for recruitment; whereas, there was a similar (90%) relative increase in coral cover between 2003 and 2008, compared with a 2000% increase in recruitment. Nonetheless, the strength of the correlation between coral cover and recruitment at Scott Reef over the duration of the monitoring reflects strong stock-recruitment relationship at the scale of the reef atoll.

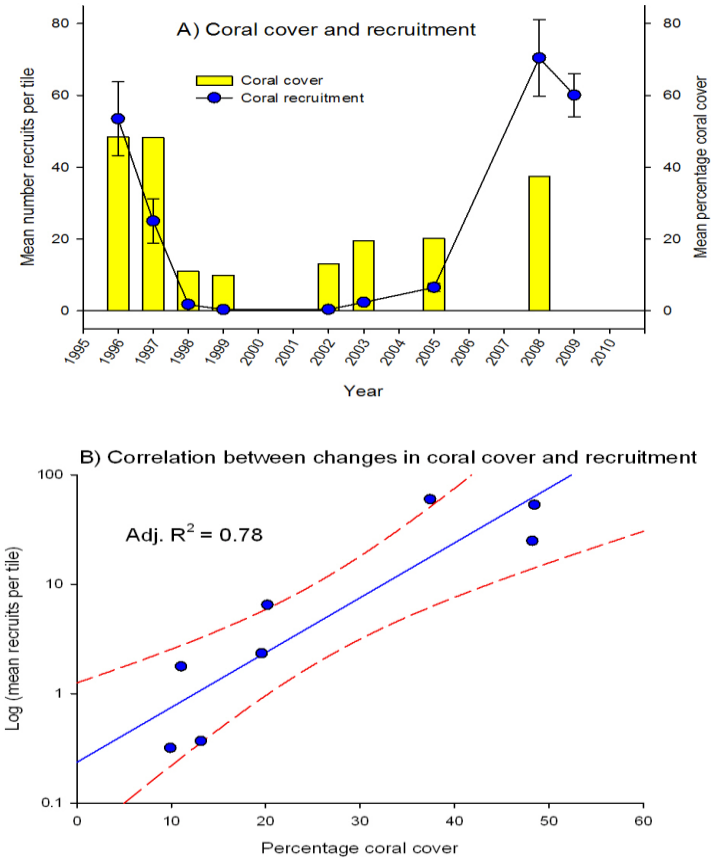


Fig. 3.5.2 Changes in coral recruitment and cover at Scott Reef. A) Mean changes in coral cover and recruitment at locations across Scott Reef over the period of monitoring. The mass bleaching occurred in 1998. B) Correlation between the mean percentage coral cover and number of recruits per tile over the period of monitoring; each point represents the data for percentage cover and recruitment from a single year, averaged across all locations.

Discussion

Multiple periods of reproduction by coral communities at Scott Reef

Ongoing research provides further support for the primary reproductive period for corals communities at Scott Reef being during autumn (March/April), although an increasing number of species and colonies have been found to reproduce at other times of the year. This mirrors observations elsewhere, such as on the Great Barrier Reef, where additional complexity in the patterns of spawning have been documented with increasing research effort. Most reproductive colonies from 45 species of broadcast spawning corals at Scott Reef spawned during autumn. In the last two years (2008/9), the participation in the autumn spawning has occurred after the full moon in March, with a relatively small proportion of some species spawning in autumn. The mass spawning in 2008 followed the full moon on 21 March, then an earlier full moon on 11 March in 2009. The early full moon in 2009 could have lead to a split spawning (Willis et al. 1985; Shimoike et al. 1992) or a primary spawning in April, yet there

was little evidence of either. 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 developmental activities should be halted during these periods. Indeed, a means by which to assess 'spawning significance' 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.

Although all evidence indicates the primary spawning at Scott Reef occurs during autumn, increasing numbers of corals are found to reproduce outside of this main period as more colonies, species and reproductive modes are sampled. Among the broadcast spawners, 31% (n = 14) of the species sampled also spawned during spring, in October 2008. For most (n = 10) of these species, a much lower proportion (<30%) of the colonies spawned during spring than in autumn. However, in four species, a relatively high proportion of colonies (>30%) spawned during spring, indicating that their reproductive output during this season is similar or higher than that in the primary mass spawning. Additionally, all evidence in recent years suggests that *Acropora millepora* spawns only during spring. Histological examination of reproduction in massive *Porites spp.* at Scott Reef also suggests a high proportion of colonies spawn outside the primary spawning period, potentially over several months throughout the year. Massive *Porites spp.* have been documented to spawn during the mass spawning period on other reefs around Australia, but also at other times of the year (Kojis and Quinn 1982; Harriott 1983; Willis et al. 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 (A. Baird unpublished data). In addition to these broadcast spawning corals, the brooding corals *Isopora brueggemanni* and *Seriatopora hystrix* also spawn and release planulae at times other than during primary mass spawning at Scott Reef, over several months between spring and autumn. 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 also tend to have multiple cycles of gametogenesis, spawning, and planulae release throughout the year (e.g. Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990; Tanner 1996; Zakai et al. 2006).

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). 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 2006; Mangubhai and Harrison 2008).

Patterns of biannual spawning by populations of the same species are either a consequence of individuals spawning at different times of the year, or some individuals spawning twice a year. Differences in the time of spawning among individuals can lead to reproductive isolation and genetic differentiation (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). If reproductive isolation arising from differences in the time of spawning is a permanent feature of the life histories of conspecific colonies, then it will lead to fixed genetic differences and sympatric speciation (Coyne 1992). Limited 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 at 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). Studies are currently underway at Scott Reef to determine whether biannual spawning by several species is a consequence of colonies having two gametogenic cycles, or their spawning at different times, within a year.

Coral recruitment and self-seeding at Scott Reef

Rates of coral recruitment at Scott Reef have increased rapidly in recent years and are now similar to that prior to the mass bleaching at all but one location. In the years after the bleaching, rates of coral recruitment were particularly low because many corals died and the reproductive output of the survivors was probably reduced by stress and injury (Michalek-Wagner and Willis 2001; Baird and Marshall 2002; Ward et al. 2002). Additionally, multiple lines of evidence (Gilmour et al. 2009; Underwood 2009; Underwood et al. 2009) indicate that other reef systems in the region (Ashmore Reef, Rowley Shoals) did not provide sufficient recruits to speed the recovery of communities at Scott Reef. Over subsequent years, the rates of recruitment increased gradually, and then more rapidly in recent years.

The rapid increases in recruitment in recent years reflect the maturation and subsequent growth of corals that had recolonised communities shortly after the bleaching (Smith et al. 2006a). Since the mass bleaching, there has been a shift at some locations across Scott Reef from an abundance of juvenile corals that do not reproduce, to adult corals with moderate reproductive output, and more recently, to large adult corals with much higher reproductive

output. It is the large adults that contribute disproportionately to reproductive output because the numbers of polyps in a colony increases exponentially with size (Hall and Hughes 1996). Rates of recruitment were highest at most locations in 2009, despite the decrease in the mean rate at Scott Reef since 2008. The mean rate in 2008 was skewed by a very strong pulse of recruitment at one location, which traditionally has higher recruitment that the other locations. Spatial variation in recruitment among the locations or groups of reefs is driven by the local abundance of adult colonies (Babcock 1988; Hughes et al. 2000a; Vermeij 2005), the distances of larval dispersal (Harrison and Booth 2007), and the oceanographic conditions during the dispersal period (Willis and Oliver 1988; Wolanski and Hammer 1988; Largier 2003). At Scott Reef, the local abundance of adult corals is particularly important in structuring spatial variation in patterns of recruitment, given evidence larvae may settle out of the water column within a week of spawning and may routinely disperse over distances of less than a few tens of kilometres (Gilmour et al. 2009; Underwood et al. 2009). However, oceanographic conditions during this dispersal period are also important, particularly at some locations. The consistently higher rates of recruitment at location SL1 are evidence of currents carrying larvae from other locations to the inner west hook at Scott Reef, where they become entrained in an eddy (Steinberg et al. 2006). Spatial variation in recruitment among the locations was less in 2009 than in 2008, due to a reduction in the maximum number of recruits at a single location and the increased number at all other locations. Consequently, recruitment rates in 2009 indicated that coral communities at Scott Reef are continuing to recover well from the mass bleaching in 1998 and that rapid increases in coral cover and recruitment should continue in the absence of additional disturbances.

Considerable changes in the coral cover and recruitment through periods of disturbance and recovery at Scott Reef were strongly correlated over the last fifteen years. This stock recruitment relationship, coupled with information about larval ecology, coral genetics and oceanography (Gilmour et al. 2009; Underwood 2009; Underwood et al. 2009) show that the recovery of coral communities at Scott Reef following disturbances will largely be facilitated by the survivors; the numbers of coral recruits originating from other reef systems in the region are unlikely to rapidly increase rates of recovery over ecological time scales. The scale of this stock-recruitment relationship is smaller than has been inferred in other studies coral reefs (e.g. Oliver and Willis 1987; Willis et al. 1988; Ayre and Hughes 2000; Hughes et al. 2000b), but this is not surprising given the isolation of Scott Reef. However, there is evidence of only limited exchange of larvae among even some locations within the Scott Reef system. These data are particularly important for the management of isolated reef systems (Ayre and Hughes 2004), such as those in north-west Australia, and further research at Scott Reef will investigate the scale of the stock-recruitment relationship and the degree of connectivity among locations.

References

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

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

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

Babcock RC (1988) Age-structure, survivorship and fecundity in populations of massive corals. In: Choat JH, Barnes D, Borowitzka MA, Coll JC, Davies PJ, Flood P, Hatcher BG, Hopley D (eds) Proceedings of the Sixth International Coral Reef Symposium, Townsville, Australia, pp 625-633

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

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

Dai CF, Fan TY, Yu JK (2000) Reproductive isolation and genetic differentiation of a scleractinian coral Mycedium elephantotus. Marine Ecology Progress Series 201: 179-187

Fadlallah YH (1983) Sexual reproduction, development and larval biology in Scleractinian corals. A review. Coral Reefs 2: 192-150

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

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 RM (2009) Biannual spawning, rapid larval development and evidence of self-seeding for scleractinian corals at an isolated system of reefs. Marine Biology 135: 451-462

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

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

Harii S, Kayanne H, Takigawa H, Hayashibara T, Yamamoto M (2002) Larval survivorship, competency periods and settlement of two brooding corals, *Heliopora coerulea* and *Pocillopora damicornis*. Marine Biology 141: 39-46

Harriott VJ (1983) Reproductive ecology of four scleractinian species at Lizard Island, Great Barrier Reef. Coral Reefs 2: 9-18

Harrison P, Babcock R, Bull GD, Oliver J, Wallace CC, Willis B (1984) Mass spawning in tropical reef corals. Science 223: 1186-1189

Harrison P, Booth DJ (2007) Coral reefs: naturally dynamic ecosystems and increasingly disturbed ecosystems. In: Connell SD, Gillanders BM (eds) Marine Ecology. Oxford University Press, Oxford, pp 316-377

Harrison P, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) Chapter 7 Coral Reefs. Elsevier Science Publishers, Amsterdam, pp 133-179

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

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

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

Knowlton N, Jackson JBC (2008) Shifting baselines, local impacts, and global change on coral reefs. PLoS Biology 6: 215-220

Knowlton N, Lang JC, Rooney MC, Clifford P (1981) Evidence for Delayed Mortality in Hurricane-Damaged Jamaican Staghorn Corals. Nature 294: 251-252

Kojis BL, Quinn NJ (1982) Reproductive strategies in four species of Porites (Scleractinia) Proc 4th Int Coral Reef Symp, pp 145-151

Lang J (1973) Interspecific Aggression by Scleractinian Corals. 2. Why the Rache is not Only to the Swift. Bulletin of Marine Science 23: 260-277

Lang JC, Chornesky EA (1990) Competition between sceractinian reef corals: A review of mechanisms and effects. In: Dubinsky Z (ed) Ecosystems of the world: coral reefs. Elsevier, Amsterdam, pp 209-252

Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. Ecological Applications 13: S71-S89

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

Mangubhai S, Harrison P (2006) Seasonal patterns of coral reproduction on equatorial reefs in Mombasa, Kenya. Proceedings of the Tenth International Coral Reef Syposium

Mangubhai S, Harrison PL (2008) Asynchronous coral spawning patterns on equatorial reefs in Kenya. Marine Ecology Progress Series 360: 85-96

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

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

Oliver JK, Babcock BC, Harrison PL, Willis BL (1988) Geographic extent of mass coral spawning: Clues to ultimate causal factors. Proceedings of the Sixth International Coral Reef Symposium, pp 803-810

Oliver JK, Willis B (1987) Coral-spawning slicks in the Great Barrier Reef: preliminary observations. Marine Biology 94: 521-529

Penland L, Kloulechad J, Idip D, van Woesik 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

Richmond R (1988) Competency and dispersal potential of planula larvae of a spawner versus a brooding coral. Proceedings of the 6th International Coral Reef Symposium, Townsville, pp 827-831

Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons amoung the Caibbean, 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. School of Biological Sciences and Biotechnology, Western Australia

Rosser NL, Gilmour JP (2008) New insights into patterns of coral spawning on Western Australian reefs. Coral Reefs 27: 1-5

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

Simpson CJ (1991) Mass spawning of corals on Western Australian reefs and comparisons with the Great Barrier Reef. Journal of the Royal Society of Western Australia 74: 85-91

Smith L, Gilmour J, Heyward A, Rees M (2006a) Mass-bleaching, mortality and slow recovery of three common groups of scleractinian corals at an isolated reef. Proceedings of the Tenth International Coral Reef Symposium, pp 651-656

Smith L, Gilmour J, Heyward A, Rees M (2006b) Mass-bleaching, mortality and slow recovery of three common groups of scleractinian corals at an isolated reef. Proceedings of 10th International Coral Reef Symposium 2: 651-656

Smith LD, Gilmour JD, 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

Stobart B, Babcock BC, Willis BL (1992) Biannual spawning of three species of Scleractinian coral from the Great Barrier Reef. Proceeding of the 7th International Coral Reef Symposium, Guam 1: 494-499

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 (1995) Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction Journal of Experimental Marine Biology and Ecology 190: 151-168

Tanner JE (1996) Seasonality and lunar periodicity in the reproduction of Pocilloporid corals. Coral Reefs 15: 59-66

Underwood JN (2009) Genetic diversity and divergence among coastal and offshore reefs in a hard coral depend on geographic discontinuity and oceanic currents. Evolutionary Applications 2 222-233

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 (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

Vermeij MJA (2005) Substrate composition and adult distribution determine recruitment patterns in a Caribbean brooding coral. Marine Ecology-Progress Series 295: 123-133

Ward S, Harrison P, Hoegh-Guldberg O (2002) Coral bleaching reduces reproduction of scleractinian corals and increases susceptibility to future stress Ninth International Coral Reef Symposium, Bali, pp 1123-1128

Willis BL, Babcock RC, Harrison PL, Oliver JK (1985) Patterns in the mass spawning of corals on the Great Barrier Reef from 1981 to 1984 Proceedings of the Fifth International Coral Reef Symposium, pp 343-348

Willis BL, Oliver J (1988) Inter-reef dispersal of coral larvae following the annual mass-spawning on the Great Barrier Reef Proceedings of the Sixth International Coral Reef Symposium, pp 853-859

Willis BL, Oliver JK, Choat JH, Barnes D, Borowitzka MA, Coll J, Davies PJ, Flood P, Hatcher BG (1988) Inter-reef dispersal of coral larvae following the annual mass spawning on the Great Barrier Reef. Proceedings of the Sixth International Coral Reef Symposium, Australia

Wolanski E, Hammer WM (1988) Topographically controlled fronts in the ocean and their biological influence. Science 241: 177-181

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

Zakai D, Dubinsky Z, Avishai A, Caaras T, Chadwick NE (2006) Lunar Periodicity of planula larvae release in the reef-building coral *Stylophora pistillata* Marine Ecology Progress Series 311: 93-102

Appendix

Appendix 3.5.1 Patterns of mass spawning by corals at locations across Scott Reef. Two methods were used to infer the season, and where possible the month, of spawning: 1) *in situ* egg scores based on size and pigmentation and 2) laboratory analysis of egg sizes within polyps. Depending on the method (*in situ*; laboratory), data are presented as either egg scores or the egg sizes (geometric mean; maximum and minimum).

Species	Inferred spawning time		Location	Method	Score / Egg size	Max. size	Min. size
	Season	Month					
Acropora abrolhosensis	autumn	March	SL2	*in situ*	2		
Acropora anthocercis	autumn	April	SL1, SL4	*in situ*	2		
	---	---	SS2-1	lab	139.75	397.1	68.7
Acropora carduus	autumn	March	SL2	*in situ*	1		
	autumn	March	SL2	lab	475.15	885.2	159.7
	autumn	March	SL2	lab	483.87	872.9	187.5
	autumn	March	SL2	lab	536.25	1285.6	194.6
	autumn	March	SL2	*in situ*	1		
	autumn	April	SL1	*in situ*	2		
	autumn	April	SL2	*in situ*	2		
	autumn	---	SL2	*in situ*	1/2		
Acropora cerealis	autumn	March	SL3, SL4, SS2	lab	532.56	1075.1	271.1
	autumn	March	SS2, SL4	lab	602.19	940.3	263.1
	autumn	April	SS2, SL4, SL2, SL3, SL1	*in situ*	2		
	autumn	April	SL4, SL3, SS2	*in situ*	2		
	autumn	---	SS2, SL4	*in situ*	1/2		
Acropora clathrata	autumn	March	SS2	lab	541.16	806.9	353.6
	autumn	April	SS2	*in situ*	2		
	autumn	---	SS2	*in situ*	1/2		
Acropora cytherea	autumn	April	SL1, SL2, SL3, SL4, SS2	*in situ*	2		
	autumn	April	SL2	*in situ*	2		
	---	---	SL4, SL2	lab	153.36	300.7	77.3
	---	---	SS1-1	lab	130.59	227.0	47.0
	---	---	SL2	lab	182.22	281.7	111.1
	spring	October	SL2, SL1	*in situ*	1		
	spring	October	SL2, SL1	lab	715.47	1061.3	298.6
Acropora digitifera	autumn	March	SL4	*in situ*	1		
	autumn	March	SL2-1	lab	514.05	761.4	342.8
	autumn	March	SS2, SL2, SL1, SL3, SS1, SL4	lab	651.28	1259.9	237.3
	autumn	March	SL3, SL4	lab	540.85	1116.7	219.2
	autumn	March	SL4	lab	548.93	880.4	287.7
	autumn	April	SL3, SL4	*in situ*	2		
	autumn	April	SL3, SL2, SL1	*in situ*	2		
	autumn	---	SS2, SL2, SL1, SL3, SS1, SL4	*in situ*	1/2		
Acropora florida	autumn	April	SL2-1	*in situ*	2		
	spring	October	SL2	*in situ*	1		
	spring	October	SL3-1	lab	575.92	780.5	391.4

Species	Inferred spawning time		Location	Method	Score /	Max.	Min.
	Season	Month			Egg size	size	size
Acropora gemmifera	autumn	March	SL2, SL4, SL3	lab	529.36	964.7	217.8
	autumn	March	SS2, SL2	*in situ*	1		
	autumn	March	SL2, SS2, SL1	lab	660.08	1163.8	261.8
	autumn	March	SL4	lab	659.43	1103.6	259.2
	autumn	April	SL2, SL1, SL3, SL4, SS2	*in situ*	2		
	autumn	April	SL2, SL4, SL3	*in situ*	2		
	autumn	---	SL2, SS2, SL1	*in situ*	1/2		
	---	---	SS2, SL4, SL2	lab	276.74	985.3	72.2
	spring	November	SL3	*in situ*	2		
	spring	October	SL4, SL3	lab	413.03	1221.0	8608.0
	spring	October	SL3	*in situ*	1		
	spring	October	SL3	lab	594.76	1030.2	236.6
	spring	October	SL3	lab	635.44	1319.9	231.4
Acropora granulosa	autumn	March	SL2	*in situ*	1		
	autumn	March	SL2	*in situ*	1		
	autumn	March	SL2	lab	522.85	915.3	298.3
	autumn	April	SL4	*in situ*	2		
	---	---	SL3, SL4, SS1	lab	109.09	162.3	52.5
Acropora humilis	autumn	March	SL3, SL2, SL1	*in situ*	1		
	autumn	March	SL1	lab	568.35	821.3	287.5
	autumn	March	SL2, SL3, SL4, SS2, SL1	lab	580.05	1013.7	257.4
	autumn	March	SL2, SL3, SL4, SS2, SL1	lab	585.12	970.1	276.5
	autumn	April	SL2, SL3, SL4, SS2, SL1	*in situ*	2		
	autumn	April	SL4, SL3, SL2	*in situ*	2		
	autumn	---	SL3, SL2, SL1, SL4	*in situ*	1/2		
Acropora hyacinthus	autumn	March	SL2	lab	470.62	799.7	223.8
	autumn	March	SL4, SL1, SL2, SL3	lab	567.65	956.9	165.8
	autumn	April	SS2, SL4, SL3, SL2, SL1	*in situ*	2		
	autumn	April	SL4, SL1, SL2, SL3	*in situ*	2		
	autumn	---	SL2	*in situ*	1/2		
	---	---	SL1, SL2, SL3, SL4, SS2	lab	141.9	740.9	73.2
	---	---	SL2	lab	228.8	404.2	122.0
	spring	October	SL4-1	lab	562.45	1197.6	220.3
	spring	October	SS1, SL2	*in situ*	1		
	spring	October	SS1, SL2	lab	651.26	1381.9	233.1
Acropora indonesia	autumn	March	SS2, SL2	lab	444.16	798.7	179.2
Acropora intermedia	autumn	March	SL3	lab	701.46	943.4	443.9
	autumn	March	SL2, SL1	lab	504.67	754.8	246.3
	autumn	March	SL1	lab	489.97	642.0	318.7
Acropora latistella	autumn	May	SL4	*in situ*	2		
	autumn	April	SS2, SL4	lab	302.83	777.8	62.1

Species	Inferred spawning time		Location	Method	Score /	Max.	Min.
	Season	Month			Egg size	size	size
	---	---	SS1-1	lab	107.72	192.0	23.9
Acropora listeri	autumn	March	SL1, SL2	lab	628.67	926.5	324.1
	autumn	March	SL2, SL1	lab	552.88	957.2	254.8
	autumn	April	SL1, SL2	*in situ*	2		
	autumn	---	SL2, SL1	*in situ*	1/2		
Acropora loripes	autumn	April	SL4	*in situ*	2		
	autumn	March	SL1	*in situ*	1		
	autumn	---	SL1	*in situ*	1/2		
Acropora microclados	autumn	March	SS2, SL2, SL1	*in situ*	1		
	autumn	March	SL1, SL2	lab	693.65	1018.5	356.6
	autumn	March	SL1, SS2	lab	590.52	944.1	253.8
	autumn	March	SL2, SL1	lab	605.08	960.5	276.5
	autumn	April	SL3, SL1	*in situ*	2		
	autumn	April	SL1, SL2	*in situ*	2		
	autumn	---	SL1, SS2	*in situ*	1/2		
	---	---	SL2	lab	171.44	596.8	81.2
Acropora microphthalma	autumn	March	SL3	lab	461.92	806.9	261.8
	autumn	March	SL4, SL1, SL2	lab	547.71	1156.7	178.4
	autumn	March	SL1	lab	562.66	1110.0	225.2
	autumn	March	SS1, SL4, SS2, SL1, SL3, SL2	lab	509.22	1015.0	228.4
	autumn	March	SL2, SL1, SS2	lab	472.61	781.6	206.5
	autumn	March	SL1	*in situ*	1		
	autumn	April	SL2, SL1, SL3, SS2	*in situ*	2		
	autumn	April	SL3	*in situ*	2		
	autumn	---	SS1, SL4, SS2, SL1, SL3, SL2	*in situ*	1/2		
Acropora millepora	spring	October	SS1, SL2, SL3	*in situ*	1		
	spring	---	SS1	*in situ*	1/2		
	---	---	SL2	lab	136.89	213.6	83.4
Acropora monticulosa	autumn	March	SS1	*in situ*	1		
	autumn	---	SS2	*in situ*	1/2		
Acropora nasuta	autumn	March	SL1	*in situ*	1		
	autumn	March	SL2, SL3	lab	509.98	1016.3	181.7
	autumn	March	SL2, SL3	lab	482.82	894.6	178.4
	autumn	April	SL1, SL2, SL3, SL4, SS2	*in situ*	2		
	autumn	April	SL2, SL3	*in situ*	2		
	---	---	SL2	lab	173.63	283.0	72.6
	autumn	---	SL1	*in situ*	1/2		
	---	---	SL2	lab	173.63	283.0	72.6
Acropora polystoma	autumn	March	SL1, SL2	*in situ*	1		
	autumn	March	SL3, SL2	lab	635	814.0	156.5
	autumn	March	SL3, SL1	lab	521.48	814.0	156.5
	autumn	March	SL1, SL2	lab	625.59	1115.4	329.1
	autumn	March	SL4, SL3, SL1, SS1, SL2	lab	629.5	968.3	350.0
	autumn	April	SL3, SL1	*in situ*	2		
	autumn	---	SL3, SL2, SL1	*in situ*	1/2		

Species	Inferred spawning time		Location	Method	Score /	Max.	Min.
	Season	Month			Egg size	size	size
	---	---	SS2	lab	174.44	281.6	86.5
Acropora samoensis	autumn	March	SL4, SL2	lab	593.21	1107.3	278.5
	autumn	March	SL2, SL1, SL4	lab	593.55	909.3	282.1
	autumn	March	SL1	*in situ*	1		
	autumn	April	SL1, SL2	*in situ*	2		
	autumn	April	SL2, SL1, SL4	*in situ*	2		
	spring	October	SL2	lab	595.93	1015.2	247.1
	spring	---	SL2	*in situ*	1/2		
	autumn	---	SL4, SL2	*in situ*	1/2		
	---	---	SL2	lab	193.08	371.4	54.8
Acropora secale	autumn	March	SS2	*in situ*	1		
	autumn	---	SS2	*in situ*	1/2		
	autumn	April	SL4, SS2, SL2	*in situ*	2		
Acropora spicifera	autumn	April	SL1, SL3, SS2, SL4, SL1, SL2	*in situ*	2		
	autumn	April	SL3	*in situ*	2		
	autumn	March	SL2, SL4	*in situ*	1		
	spring	October	SL3	*in situ*	1		
	autumn	---	SL2, SL3, SL4, SS2, SL1	*in situ*	1/2		
Acropora subglabra	autumn	March	SL2	lab	509.5	992.9	165.2
	autumn	March	SL2	lab	555.61	958.6	269.8
	autumn	March	SL2	lab	490.93	764.0	222.5
	autumn	March	SL2	lab	567.09	754.7	371.9
Acropora tenuis	autumn	March	SL3	lab	598.37	1067.8	282.4
	autumn	March	SL1, SL4, SL2, SS2, SS1, SL3, SL4	lab	625.41	1075.8	310.6
	autumn	March	SL1, SS2, SS1, SL2, SL3	lab	527.85	943.6	227.8
	spring	October	SL1, SL2, SL3, SS1	lab	659.42	1096.3	287.3
	autumn	April	SS2, SL2, SL4, SL3, SL1	*in situ*	2		
	autumn	April	SL3	*in situ*	2		
	spring	October	SL4, SL1	lab	449.07	1152.6	82.0
	spring	October	SL1, SL2, SL3, SS1	*in situ*	1		
	spring	---	SS1	*in situ*	1/2		
	---	---	SL2, SS2	lab	112.63	170.9	60.9
	autumn	---	SL1, SS2, SS1, SL2, SL3	*in situ*	1/2		
Acropora valida	autumn	March	SL1	lab	857.53	1367.6	330.5
	autumn	March	SL3	lab	525.33	937.1	238.1
	autumn	March	SL1	*in situ*	1		
	autumn	April	SL3, SL4	*in situ*	2		
	autumn	---	SL1	*in situ*	1/2		
	autumn	March	SS2, SL4	lab	584.5	812.7	330.5
Echinopora lamellosa	---	---	SL3-1	lab	274.04	506.5	108.6
	autumn	March	SS1-1	lab	334.65	625.1	195.4
Favia danae	autumn	---	SL3	*in situ*	1/2		

Species	Inferred spawning time		Location	Method	Score / Egg size	Max. size	Min. size
	Season	Month					
Favia matthaii	autumn	---	SL4, SL3	*in situ*	1/2		
Favia pallida	autumn	---	SL3	*in situ*	1/2		
	autumn	March	SL1	lab	342.58	673.9	159.0
	autumn	March	SL3	lab	384.95	661.2	191.0
Favia stelligera	autumn	---	SL3, SL4	*in situ*	1/2		
	---	---	SL3, SS2	lab	282.84	615.4	96.9
	autumn	---	SL4, SL3	*in situ*	1/2		
	---	---	SS1	lab	288.6	538.5	144.5
	autumn	March	SS1	lab	310.45	730.6	132.2
	autumn	March	SL4, SL3	lab	314.22	663.7	96.9
Goniastrea favulus	autumn	---	SL4, SL3	*in situ*	1/2		
Goniastrea edwardsi	autumn	---	SL4	*in situ*	1/2		
Montipora encrusting spp.	autumn	March	SS1-1	lab	448.19	890.8	154.6
Montipora encrusting spp.	autumn	March	SS1-1	lab	427.27	1379.4	131.3

3.6 Sedimentation and water temperature

Introduction

Elevated sedimentation and water temperatures have 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 lead to the smothering of corals, abrasion of coral tissue, reduced sexual recruitment and growth, lower coral growth rates and excess energy expenditure (Rogers 1990; Crabbe and Smith 2005). 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). 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 benefiting 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. We present physical data associated with the coral reef communities developing at Scott Reef, an isolated atoll system in the north-east Indian Ocean.

Materials and Methods

Study area and sampling regime

This component of the Project 1 study is focused on capturing the temporal and spatial sedimentation and water temperature dynamics of the shallow reef slope at Scott Reef. Sedimentation rates were estimated by deploying five replicate sediment traps at each of the six locations (SL1 SL2, SL3, SL4, SS1, SS2) at Scott Reef from March 2007 to April 2009. 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.

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 mg cm^{-2} d^{-1}, was calculated for each replicate sample from the equation:

Sedimentation rate (mg cm^{-2} d^{-1}) = (Weight of sample / Area of trap entrance) / Duration

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 CO2 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 CO2 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.

Data analysis

Two-way Analysis of Variance (ANOVA) were used to determine if sedimentation rates differed significantly among locations and/or periods of sampling, with location and period considered fixed factors. Prior to subjecting the sedimentation rates to ANOVA data were Log_{10} (n + 1) 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 year-long duration sampling. All other deployments lasted no more than approximately 3 months. Analyses used STATISTICA v 7.1 statistical software.

The sediment grain-size fractions were analysed using Principal Component Analysis (PCA) to explore any differences in grain-sizes among locations and periods. Two-way crossed ANOSIM was conducted using a Euclidian dissimilarity matrix constructed from the same data to ascertain whether the grain-size compositions differed significantly among locations and/or periods. The PRIMER 6.1 statistical package (PRIMER-E, Plymouth, UK) was used for PCA and ANOSIM tests.

Results & Discussion

Sedimentation rates in shallow (<12 m) water depths at Scott Reef differed significantly among locations ($P < 0.001$) and among time periods ($P < 0.001$) and there was a significant interaction ($P < 0.001$) between these two factors. The mean square was higher for time period (2.561) than for the interaction between location and period (1.472) or the main effect of location (1.065). Mean sedimentation rates (mg cm^{-2} d^{-1} ± 95% C.I.) ranged from a minimum of 0.8 (0.2) during the early dry period of 2008 and increased to a maximum of 6.9 (7.1) during the wet period, before declining to 1.1 (0.3) in the early dry period of 2009 (Fig. 3.6.1). Among localities, there were no clear seasonal trends in sedimentation rates with highest rates occurring over the summer (October to February) at SL3 and SL4 in both years of the study (Fig. 3.6.2).

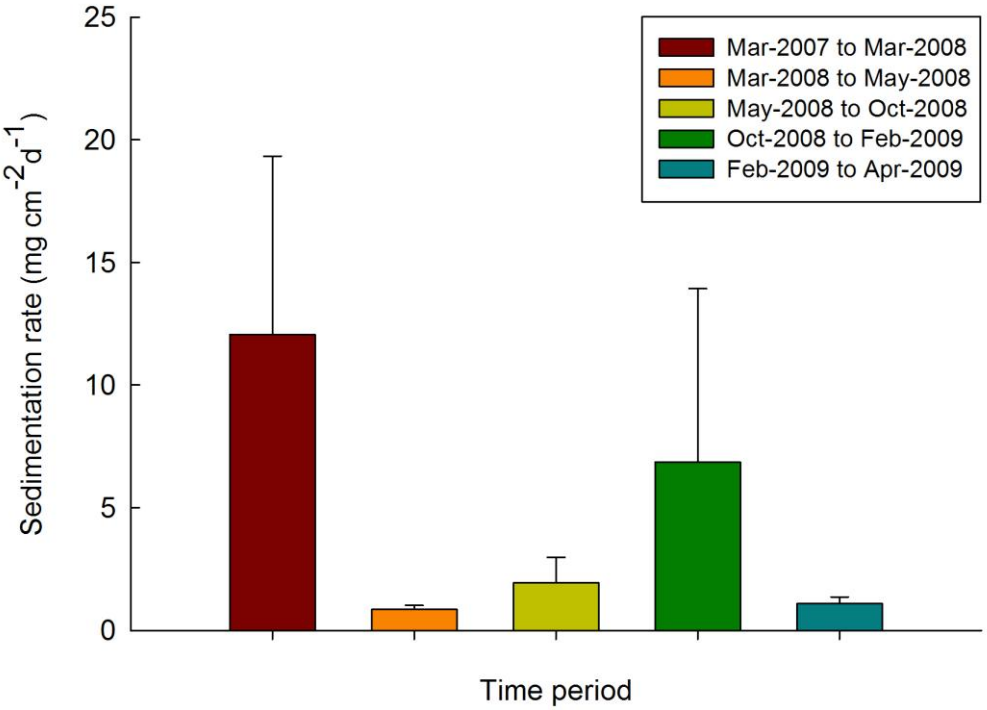


Fig. 3.6.1 Mean sedimentation rates (± 95% CI) in five time periods at Scott Reef between 2007 and 2009.

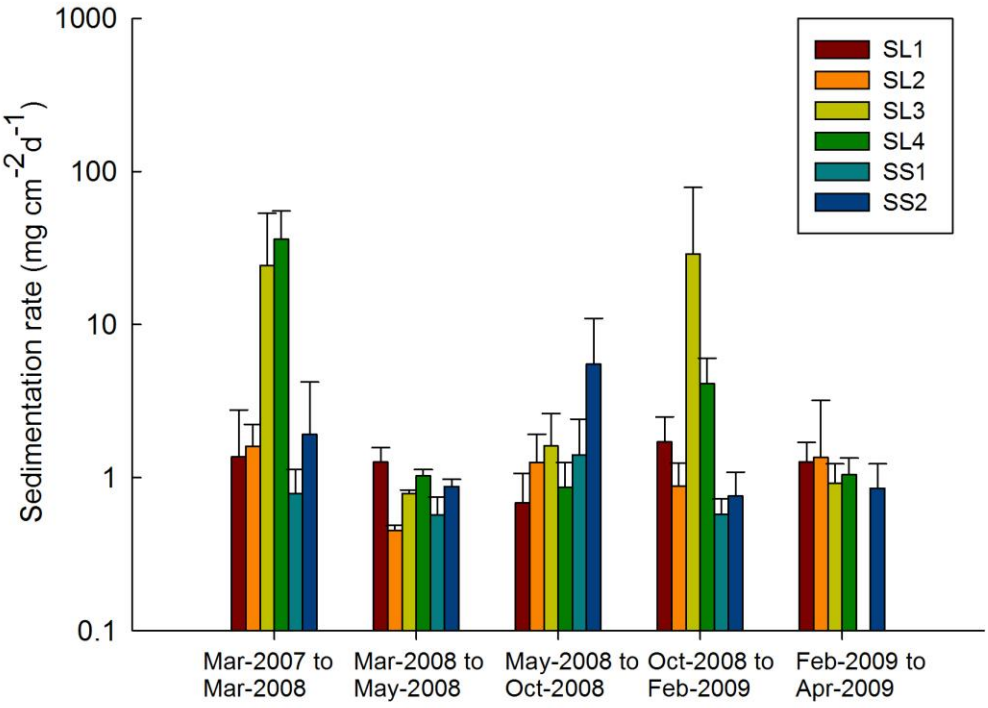


Fig. 3.6.2 Mean sedimentation rates (± 95% CI) at six locations at Scott Reef between March 2007 and April 2009. N.B. There are no data for SS1 in Feb-2009 to Apr-2009 as rough seas prevented sediment trap retrieval.

Comparisons with other regions

The mean sedimentation rates at Scott Reef between February/March 2008 and April 2009 are at the lower extent of the range (< 1 to 10 mg cm^{-2} d^{-1}) observed at reefs not subjected to stresses from human activities (Rogers 1990). 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 the wet period, this was largely driven by higher levels at two locations, namely SL3 and SL4, and was only greater than 10 mg cm^{-2} d^{-1} at the former location. The overall increase in sedimentation rate at Scott Reef during the wet period is presumably driven by the increase in wind and wave activity associated with storms passing through the region, as is the case at 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 mg 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).

Particle size distribution

Two-way ANOVA showed that mean sediment grain-size differed significantly among locations ($P < 0.001$), among time periods ($P < 0.001$) and there was a significant interaction ($P < 0.001$) between these factors. The mean square was greater for the main effects of location (50.894) and time period (46.746) than for the interaction (24.364). Mean grain size was consistently smallest (*ca* 50 µm) at SL2 and reached *ca* 260 µm at SL3 and SS2 in the wet and late dry periods, respectively (Fig. 3.6.3). Mean grain size at SL1 and SS2 was greatest in the late dry period of 2008 and decreased throughout the wet season to minimum values in the early dry period of 2009.

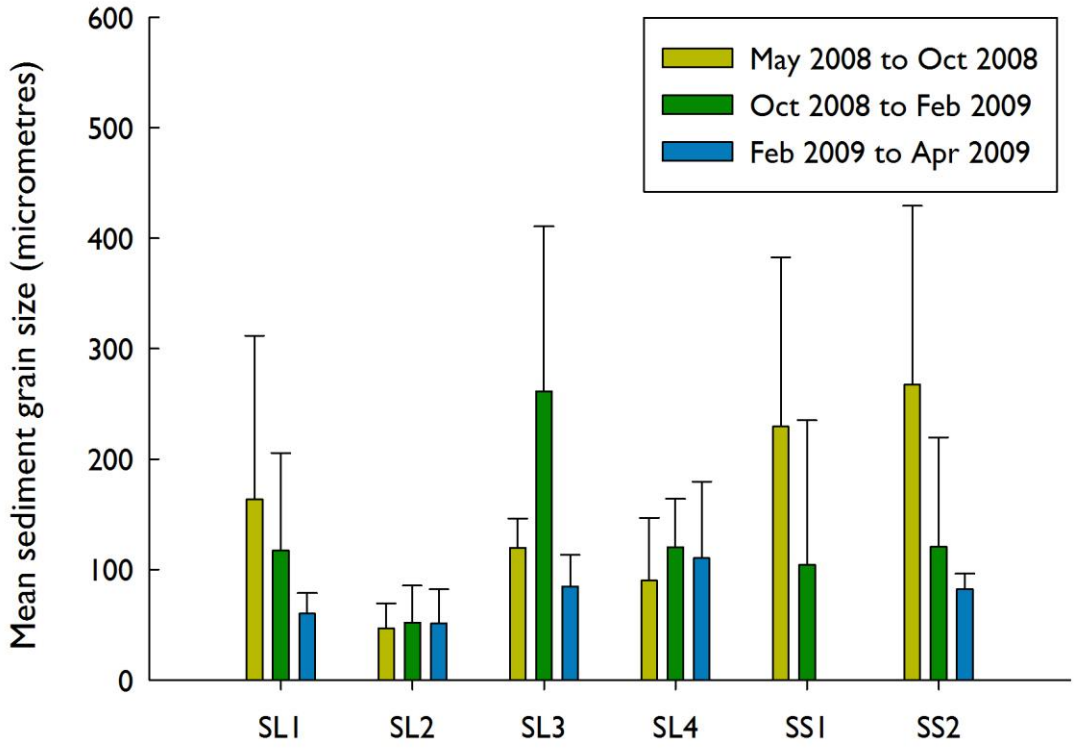


Fig. 3.6.3 Mean sediment grain size (µm ± 95% C.I.) at the six locations at Scott Reef during three periods between May 2008 and April 2009.

Representative particle size distributions are summarised in frequency histogram plots from replicate data at selected locations (Fig. 3.6.4). Larger sized sand fractions made a higher contribution during the wet period than the dry period and there was a bi-modal distribution of grain sizes at SS2 during the wet period, whereas the contributions of the larger sand sized fractions dominated the samples at SL3 during that period. At SL2 the greatest contributions were from fraction sizes < 63 µm (clay and silt), with only a small component of larger (> 100 µm) grains (sands) at the time of the late dry season, whereas the reverse pattern occurred at

SS2 at this time. Plots of the mean grain size fractions for each period at each location further illustrate the trends observed in the particle size distribution plots (Fig. 3.6.3). During the late dry period, clay and silt sized fractions contributed the most to the composition of the sediments at all lagoon locations, particularly in the case of SL3 (Fig. 3.6.4A). In contrast, larger, sand-sized grains made the highest contributions at the exposed slope locations at SS1 and SS2 at this time. At the most protected location (SL2) > 80% of the sediment was composed of clays and silts at all times, while these constituents were only important at other locations during the during the early dry period. The larger sand-size fractions contributed > 85% of the sediment at SL3 during the wet period, with the coarsest size fraction comprising *ca* 25% (Fig. 3.6.4B).

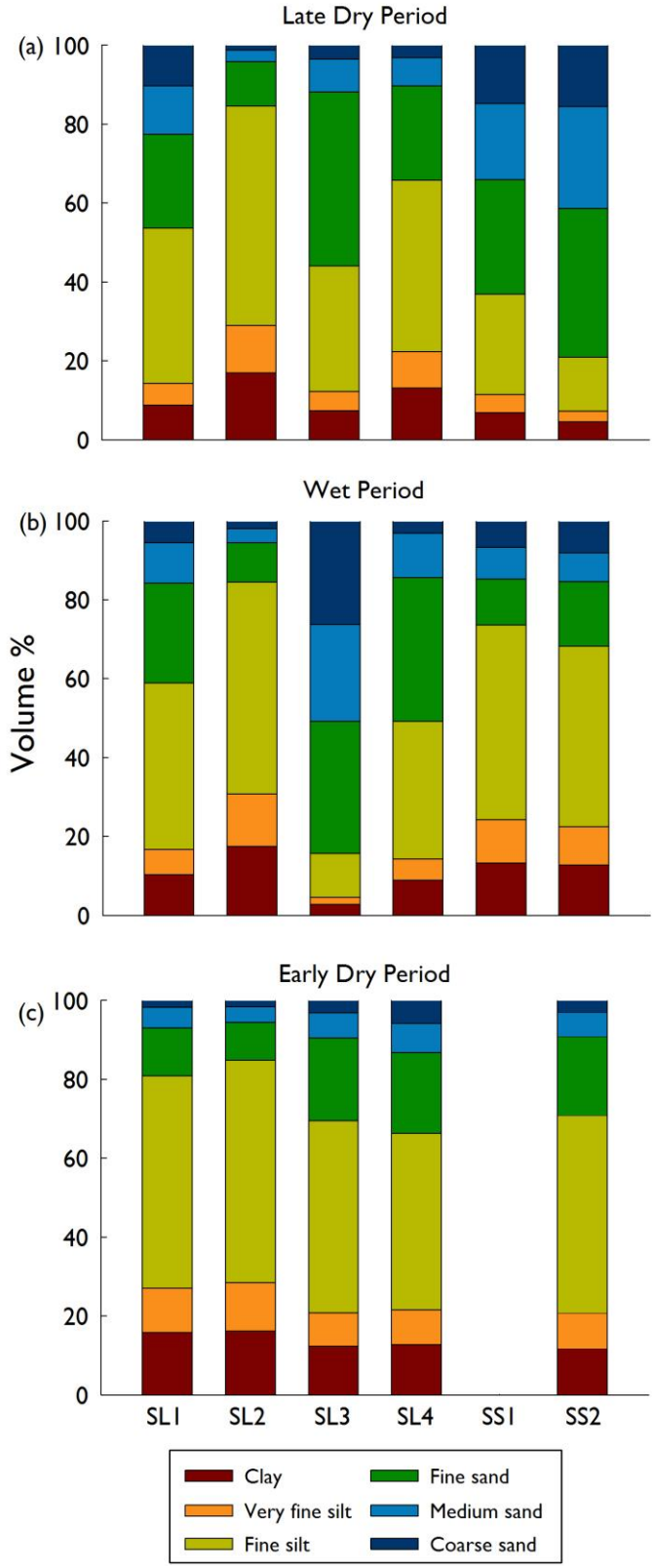


Fig. 3.6.4 Mean percentage contributions of the various grain size fractions at each location at Scott Reef in three periods between May 2008 and April 2009.

Two-way crossed ANOSIM, using the matrix derived from replicate samples, showed that sediment grain size differed significantly among locations ($P < 0.001$, *R*-statistic = 0.406), and among seasons ($P < 0.001$, *R*-statistic = 0.378). PCA of the data for the various sediment grain-size fractions accounted for 93.8% of the total variation, which was encompassed by principal component axes 1 and 2. The samples from SS2 during May to October 2008 and SL3 during October 2008 and February 2009, tended to lie on the left of the PCA plot, whereas those from SS1 and SS2 during October 2008 to February 2009 occupied a position on the right below the group formed by all the samples from SL2. (Fig. 3.6.5). The samples from the late wet period (February to April 2009) showed a tendency to group together on the right of the PCA plot, whereas those from the dry period (May to October 2008) did not form a group, but tended to spread towards the left of the plot. Samples collected from February to April 2009 and from all periods at SL2 contained large contributions of the finest grain-size fractions (< 63 µm), whereas those from SS2 during May to October 2008, were composed greater amounts of the coarser (> 250 µm) fractions.

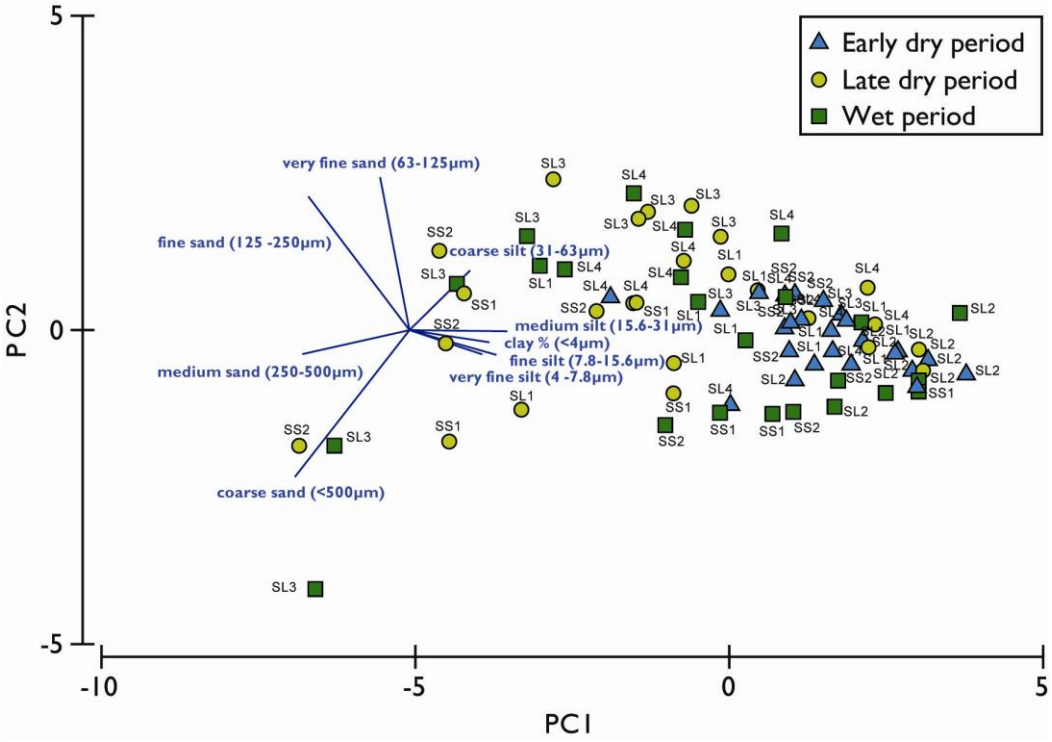


Fig. 3.6.5 Principal component analysis (PCA) plot derived from the percentage contributions of the various sediment grain size classes to the replicate sediment samples at each location in each period between May 2008 and April 2009.

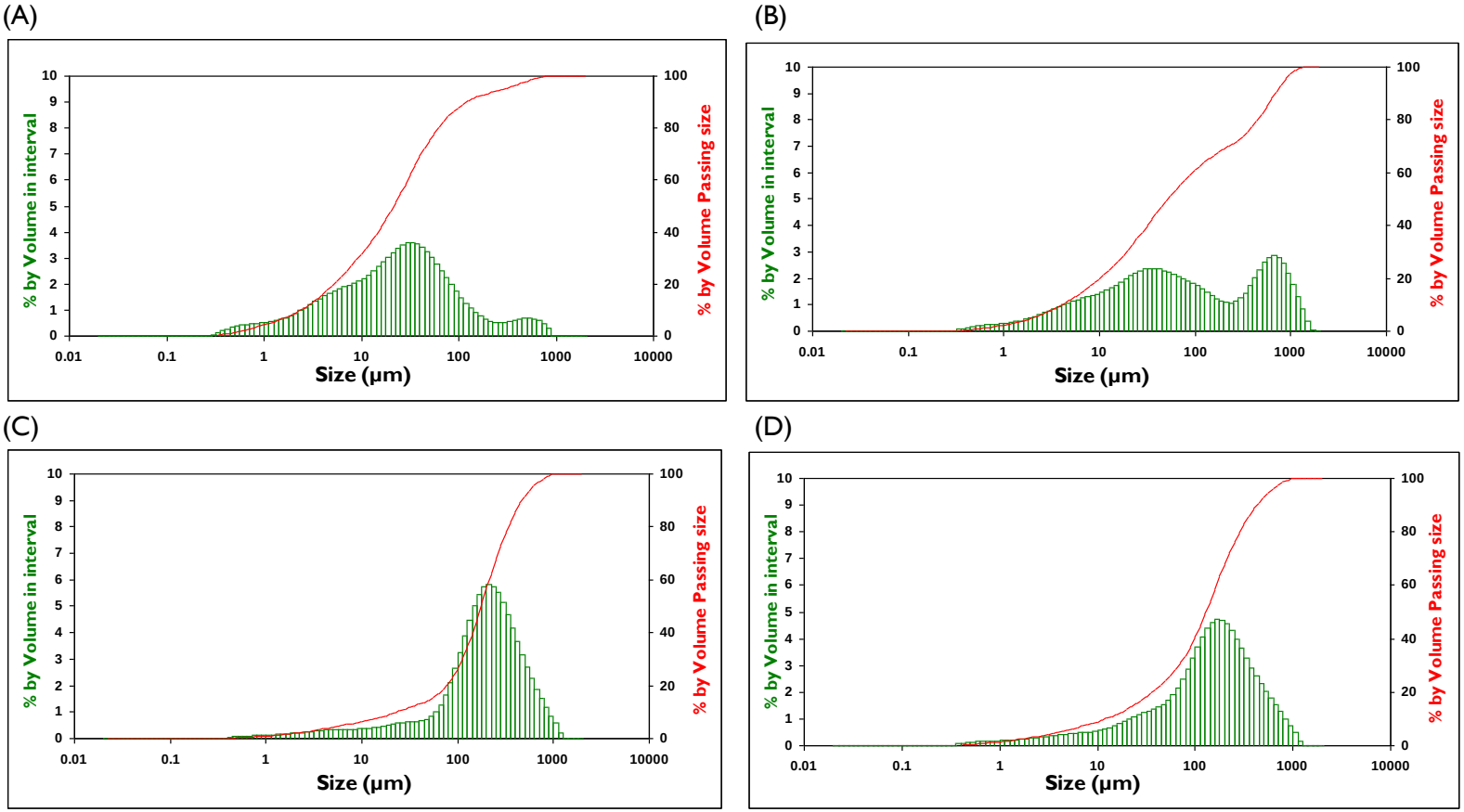


Fig. 3.6.6 Sediment grain size distribution by volume at (A) SL2 (Late dry 2008) (B) SS2 (Wet period) (C) SS2 (Late dry 2008) (D) SL3 (Wet period)

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. This combination of small sediments and protected aspect may also influence the composition of the coral community at this location, which has relatively high abundances of foliose corals. Foliose 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 3.6.1). SEM analyses demonstrated that the sediment was mostly calcium based.

Table 3.6.1 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

Water temperature

Water temperatures in shallow (*ca* 9 m) waters at Scott Reef between 2007 and 2009 followed a seasonal cycle of high temperatures in early summer followed by a secondary peak in autumn (April/May) with periods of lowest temperature occurring in late winter (August/September). Mean daily water temperatures ranged from a low of 25.7˚C at SL3 on 9 August 2007 to a maxima of 31.9˚C at SL3 on 22 November 2008 (Fig. 3.6.7). Temperatures were consistently greater than 31˚C during the periods April/May 2008, November/December 2008 and again in April 2009. In 2009, temperatures were increasing through April to *ca* 31˚C at all locations reaching a high of 31.6˚C at SS1. Although there was minimal variation in mean daily water temperature among locations in 2008 and 2009, temperatures were consistently 0.5˚C lower at SL3 throughout most of 2007 and the summer of 2007/2008. The cooler temperatures at SL3 are a consequence of the regular tidal incursions of cooler oceanic water between West Hook and Sandy Islet (Steinberg et al. 2003; Bird et al. 2004). The cooler temperatures at this location may have ecological significance in relation to the susceptibility of corals to bleaching.

There have been no visible signs of coral bleaching at Scott Reef since a few isolated colonies were observed at North Reef in October 2008. Although there have been five "bleaching watches" (issued by the National Oceanic and Atmospheric Association (NOAA) for Scott Reef between April 2007 and August 2009, no "bleaching alerts" have been issued. This indicates that the water temperature at Scott Reef during this period did not exceed critical coral bleaching thresholds.

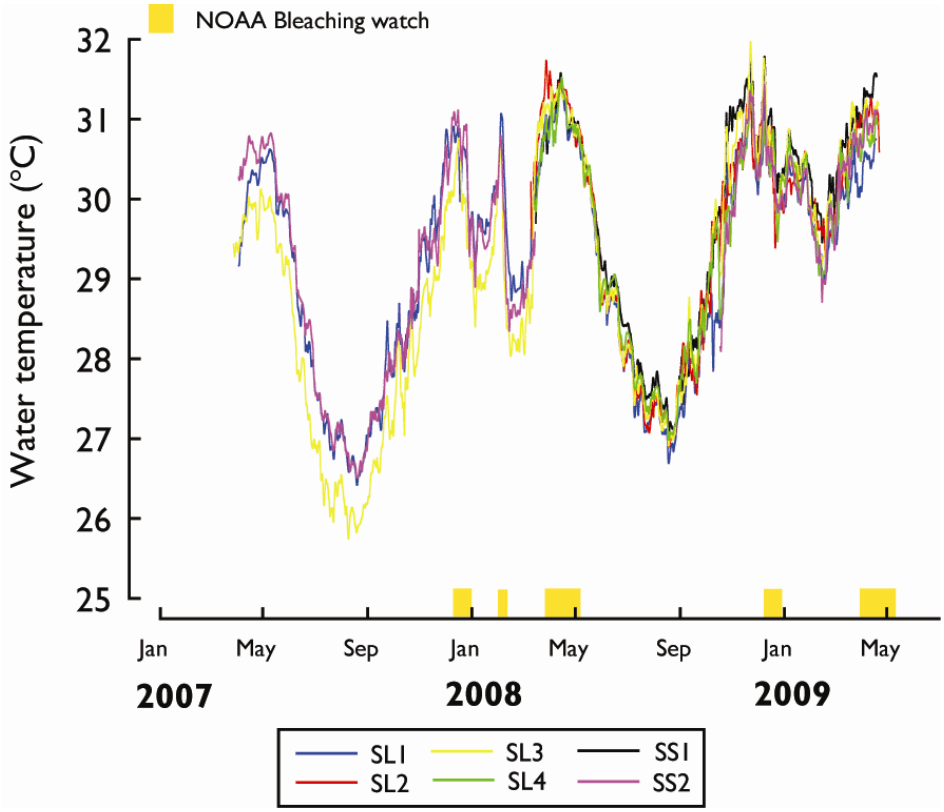


Fig. 3.6.7 Mean daily water temperatures at shallow (9m) locations at Scott Reef between April 2007 and April 2009.

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. In: Kasim Moosa M, Soemodihardjo S, Nontji A, Soegiarto A, Romimohtarto K, Sukarno, Suharsono (eds) Proceedings of the Ninth International Coral Reef Symposium, Bali, Indonesia, October 23–27 2000. Ministry of Environment, the Indonesian Institute of Sciences and the International Society for Reef Studies, Bali, Indonesia, pp 245

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

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

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

Clarke KR, Warwick RM (2001) Change in Marine Communities: an Approach to Statistical Analysis and Interpretation, 2nd edn. PRIMER-E, Plymouth Marine Laboratory, Plymouth

Coles SL, Brown BE (2003) Coral bleaching - Capacity for acclimatization and adaptation Advances in Marine Biology, Vol 46, pp 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 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 Biologia Tropical 56: 1179-1187

Hubbard JAEB, Pocock Y (1972) Sediment rejection by recent scleractinian corals: a key to paleo-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

Rogers CS (1990) 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

Steinberg C, Brinkman R, Bird J, McLean C (2003) Biological and Physical Environment at Scott Reef: 1994-2003, III: Physical Environment. Australian Institute of Marine Science

Syvitski JPM (1991) Principles, Methods and Applications of Particle Size Analysis. In: Syvitski JPM (ed). Cambridge University Press, New York, pp 225-236

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