Appendix F22

Gilmour et al. 2010

Long-term Monitoring of Coral and Fish Communities at Scott Reef Annual Report, 2010

BROWSE FLNG DEVELOPMENT
Draft Environmental Impact Statement

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BROWSE LNG DEVELOPMENT
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Long-term monitoring of coral and fish communities at Scott Reef

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PRODUCED FOR
WOODSIDE ENERGY LTD
as operator of the
BROWSE LNG DEVELOPMENT

Australian Government | Australian Institute of Marine Science

PERTH, Western Australia
September 2010

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DISCLAIMER

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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 Ltd (Woodside), as operator of the Browse LNG Development , on 28 February 2008, to undertake a three year research program at Scott Reef. For the purpose of this report, this research program is known as the Scott Reef Research Project (SRRP).

The research 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 Annual Report for 2010 is the third Annual Report to Woodside within the SRRP, and 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.

This report also integrates the most relevant findings from Project 2 (Deep-water corals) and Project 3 (Physical and biological oceanography) to update our current state of knowledge about the patterns of connectivity and resilience of coral communities at Scott Reef.

1.2 Structure of this report

The Executive Summary highlights additional data and analyses conducted during 2009/10, and specifically outlines the additional data and analyses in table form. The subsequent chapters are divided into two sections.

A brief summary of recent data and analyses is followed by an integration of all relevant data collected in the SRRP to address two key management issues, as follows:

- Chapter 2 briefly discusses the coral communities at Scott Reef in a regional context.
- Chapter 3 summarises the exposure of coral and fish communities at Scott Reef to major disturbances during 2009/2010.
- Chapter 4 provides a summary of the status of benthic and fish communities at Scott Reef.
- Chapter 5 integrates data from all Scott Reef Research Projects to address two key management issues for Scott Reef, focused on the patterns of connectivity and resilience of its biological communities. In particular, biological, oceanographic and genetic data are integrated in

    - Chapter 5.1to infer patterns of reproduction and connectivity of coral and fish communities among locations at Scott Reef and its neighbouring reef-systems, and
    - Chapter 5.2 relates the resilience of coral communities in habitats across Scott Reef to likely disturbances in the future.

Following the Summary and integration chapters, are more detailed updates of data and analyses for each Sub-Project, as follows:

- Chapter 6 updates the Long-term monitoring of benthic and fish communities (Project 1.1)
- Chapter 7 updates the Demography of coral populations (Project 1.2)
- Chapter 8 updates the Gene flow and connectivity among populations of reef fish (Project 1.3)
- Chapters 9 to 11update Patterns of reproduction and recruitment in corals communities (Project 1.4)
- Chapter 12 updates Patterns of reproduction and recruitment in fish communities (Project 1.4)
- Chapter 13 updates Water temperature and sediment regimes at Scott Reef (Project 1.1).

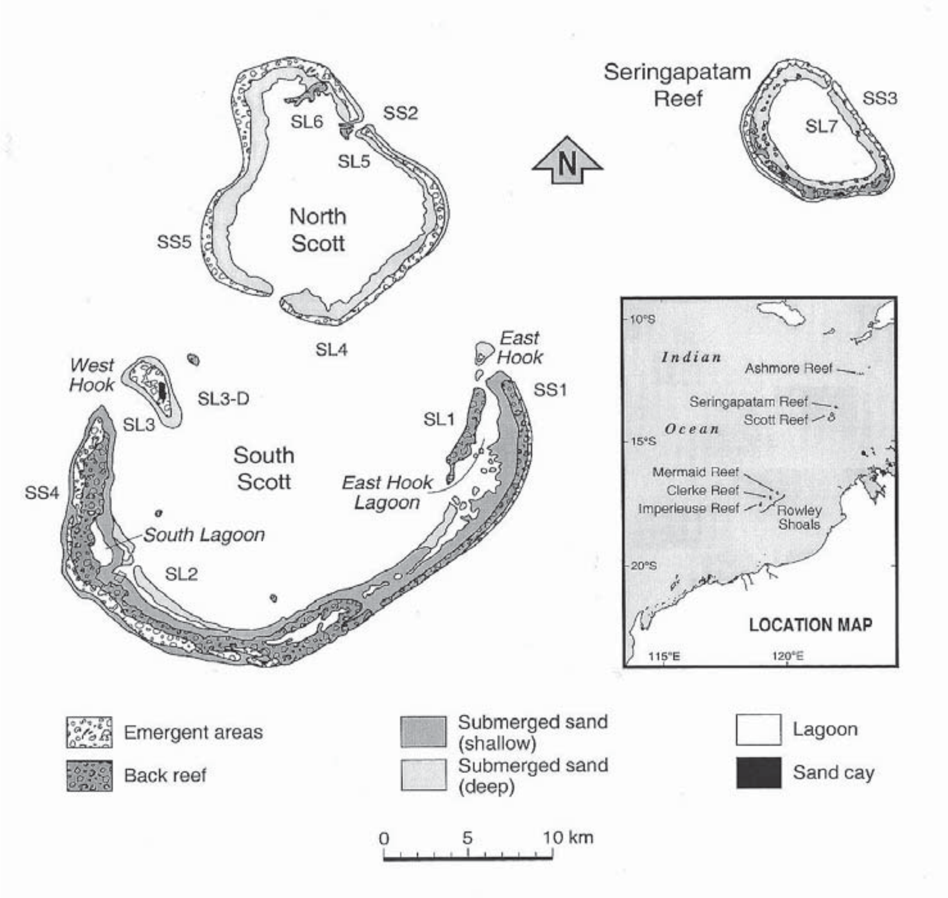


Figure 1.2.1. Location Map of Scott Reef and Seringapatam Reef off the West Australian Coast showing the monitoring locations within the reef Lagoon (SL1-SL7) and on the outer shelf (SS1-SS5).

1.3 Executive Summary

This third Annual Report updates the data collected and/or analysed for Project 1 during 2009/10, in the context of all historic data collected at Scott Reef. The key findings from the additional collection and analyses of data for 2009/10 are:

- In 2009/10 there has been increased incidence of disease among some corals at Scott Reef, but this has largely been restricted to a limited number of locations (SL2, SL1) and groups of corals (table corals). At the worst affected location (SL2), more than half the table corals have been infected by disease or have died in the last two years.
- Elevated water temperatures between March and May 2010 caused coral bleaching at Scott Reef, but the worst impacts were limited to a few locations (SL2, SL1, SS2) and groups of corals (*Pocillopora*, *Fungia, Goniastrea, Pavona*). Species of *Pocillopora* corals were worst affected by the bleaching, whereas the incidence of bleaching among the most abundant *Acropora* corals was relatively low, compared with the mass-bleaching in 1998.
- Further analyses of data collected in 2008, which will be updated in October 2010, confirms the extent to which the recovery of coral communities following the mass-bleaching in 1998 has varied according to the severity of the impact, subsequent exposure to cyclones, and the life history of the most abundant corals at each location. Communities least affected by the bleaching and/or by subsequent cyclone disturbances have returned to a similar cover and structure to that prior to the bleaching, whereas those most severely affected by bleaching and cyclones have not yet returned to a similar cover or structure. Analyses in 2009/10 also highlight the susceptibility of some groups of corals to the mass-bleaching, due largely to their life histories, and the extent to which this has influenced the recovery of communities at different locations. In particular, soft corals and brooding corals at the locations worst affected by bleaching are still far from their previous cover, primarily due to their limited recruitment or dispersal.
- Further analyses of data collected in 2008, which will be updated in October 2010, confirms the extent to which the changes in trophic groups (e.g. herbivores) of fishes are strongly linked to the changes in often highly specific groups of corals (e.g. soft corals, table corals), given the requirement for food and shelter. For example, the decline in abundance of certain species of butterflyfish was linked to the reduction in the soft coral or branching and bottlebrush *Acropora* on which they feed, and the increase in abundance of certain herbivorous fish following the bleaching linked to increases in turf-algae and coralline-algae. These relationships are far more specific that initially thought. The structure of the fish communities remains very different to that prior to the bleaching in 1998. However, not all changes in fish communities can be explained by the changes in corals, such as the increased abundance of large mobile fish (Lethurinidae, Lutejanidae, Serranideae) throughout the study. The reason for the increases in larger fish is still unknown.
- Additional data from autumn 2009 to autumn 2010 supports previous conclusions about the times of reproduction by spawning and brooding corals at Scott Reef, but also highlights that during some years (e.g. 2010) mass-spawning can be split over consecutive months during a single season (e.g. March/April), due to the timing of the full moon. Most corals at Scott Reef reproduce by mass-spawning during autumn (usually March) each year, but there are exceptions to this pattern of reproduction. Most notably, many corals also spawn during spring (usually October), spawning may be split over consecutive months in autumn (March/April) and spring (October/November) during some years, and massive *Porites* and

brooding corals (e.g. *Isopora*, *Pocillopora*) reproduce over several months throughout the year. Analyses of reproductive data in 2009/10, coupled with the relative abundances of corals at Scott Reef, has provided an index of reproductive output during different periods of the year. Based on coral cover during 2008 and general patterns of reproduction from 2007 – 2010, approximately 40% of the community reproduces during one month in autumn (usually March), 16% during one month in Spring (usually October), and 44% during other months of the year.

- Rates of coral recruitment following the autumn spawning in 2010, confirm that since 2008, recruitment at Scott Reef is similar or greater than that prior to the mass-bleaching in 1998. Analyses in 2009/10 of patterns of coral recruitment during years of high coral cover, indicate that some locations at Scott Reef act as sources (SL4, SS1) and sinks (SL1, SS2) for coral recruits, due to coral cover and current flow. Analyses in 2009/10 also summarised coral recruitment at the deep-water communities at south reef. The number of recruits and the proportion in the Family *Acroporidae* was less in the deep-communities than for the shallow, although this was confounded by longer and more variable periods of deployment. Recruits to the deep-water communities settled preferentially on the tops of plates, rather than the undersides of plates in the shallow-communities, probably due to the low light levels at depth.
- Additional data and analyses in 2009/10 of the changes in the size-structure of coral communities at Scott Reef compliment existing data on percentage cover, recruitment, growth and survival. Recent increases in coral recruitment at Scott Reef, and variation among locations and groups of corals, are evident in size-structure data as cohorts grow through size-classes. These complimentary data confirm that some locations act as sources (SL4, SS1) and sinks (SL1, SS2) for coral recruits, some groups of corals (brooding corals) are particularly susceptible to severe disturbances, and that background rates of growth and survival of corals at Scott Reef are high.
- Additional data and previously unreported analyses in 2009/10 indicate that a large proportion of bicolour damselfish spawn around April, with a potential peak in settlement occurring in July, although some settlement occurs over several months of the year. The juveniles of different fish species tended to settle among different micro-habitats and reef zones, with the bicolour damselfish settling predominantly onto bare substrates in the shallower reef crest zone, whereas scaly damselfish juveniles displaying a preference for soft corals in the deeper slope zone. These data further highlight the often specific relationship between some fish and coral species.
- Genetic analysis of fish populations in 2009/10 further support that populations of corals and fish communities at Scott Reef are isolated from other reef systems in the region and recovery following disturbances will be largely facilitated by the survivors. Many coral larvae are likely to settle within a week of spawning, whereas many fish larvae are likely to settle within a month of spawning. Within Scott Reef, there is limited exchange of coral larvae among locations separated by distances of more than 10-20km for spawning corals, and more than 1km for brooding corals, but a much higher degree of connectivity among all locations for fish communities.

This September 2010 Report contains new data and updated analyses of data presented in previous reports (Table1.3.1). To ensure the findings are presented comprehensively and that the report can be read alone, all historic data for Scott Reef are included. Some data were collected as early as 1994. All of the most recent data are presented in the report tables, figures or text, and in some instances, these were collected in 2010. In other instances, no additional data have been collected.

Table 1.3.1 Summary of new data and analyses in this report. All historic data are presented and the range of data presented in each chapter is in the 'Data Collected' column. All chapters include additional data collected during 2009/2010, and/or additional analyses and summaries of previously collected data.

Data	Chapter	Data collected	Summary
Disturbances at Scott Reef	3	2010	Moderate coral-bleaching and spread of disease during summer of 2010
Status of coral and fish communities.	4	1994-2008	Most recent survey was in 2008, next survey October 2010. Additional analyses of data to highlight changes in functional groups of corals and fish. For example, highlighting the susceptibility of soft corals and brooding corals to widespread disturbance, and the strong association between corals and species of fish based on their trophic group.
Connectivity and resilience of Scott Reef communities	5.1	1994-2010	Summary of all available data across three Projects to infer patterns of reproduction, dispersal and connectivity among communities at Scott Reef and the Rowley Shoals and Ashmore Reef.
Coral communities at Scott Reef and their resilience to disturbances.	5.2	1994-2010	Summary of all available data across three Projects to infer the susceptibility and resilience of coral communities at different habitats (shallow, deeper, deep), and at different locations within the shallow-habitat, to likely disturbances at Scott Reef.
Percentage cover of benthic communities.	6.1	1994-2010	Additional statistical analyses of changes in groups of corals through time and among locations, the influences of key physical parameters on communities, and the responses of functional groups of corals to disturbances based on growth form and reproductive mode.
Size-structure of coral communities.	6.2	1994-2008	Most recent survey 2008, next survey October 2010. Additional analyses of changes in size-structure of coral communities and their recovery from disturbance. Changes in size-structure interpreted relative to most recent information about coral reproduction, recruitment and percentage cover.
Abundance, diversity and composition of fish communities.	6.3	1994-2008	Additional statistical analyses of changes in trophic groups of fish and their association with functional groups of corals.
Demography of coral populations.	7	2006-2010	Additional data on growth, survival and changes in population structure of corals during a survey period in which moderate bleaching and disease that affected some locations.
Patterns of gene flow and connectivity among reef fish populations.	8	2006-2008	Genetic analysis of damselfish populations at Scott Reef and Rowley Shoals and updated summary of patterns of connectivity for all coral and fish populations analysed.
Patterns of reproduction for coral communities at Scott Reef.	9	2008-2010	Additional data on reproduction of spawning and brooding corals. Summary of patterns of reproduction for spawning and brooding corals and analyses of percentage reproductive output by communities throughout the year.
Patterns of recruitment for coral communities at Scott Reef.	10	1996-2010	Additional data on recruitment of corals at locations across Scott Reef. Additional analyses and summary of variation in recruitment across locations and among coral families.
Patterns of coral recruitment for deep-water communities in the south-lagoon.	11	2008-2010	Additional data and summary of coral recruitment in deep-water communities at south reef.
Reproduction, recruitment and juvenile habitat use of fishes	12	1995-2010	Additional data on reproduction and recruitment of fish and the habitat associations of recruits. Summary of patterns of reproduction and recruitment.
Water temperature and sedimentation regimes at Scott Reef.	13	2007-2010	Additional data on variation in water temperature and sedimentation among locations at Scott Reef.

Status of Scott Reef: 2010

2. SCOTT REEF'S CORAL COMMUNITIES: HABITAT ASSOCIATIONS AND REGIONAL CONTEXT

The current literature is full of reports of both sudden and insidious decline of coral reefs over large areas as a result of anthropogenic pressures, including overfishing, pollution and rising sea temperatures causing coral bleaching and diseases (Hoegh-Guldberg 2004; Hoegh-Guldberg et al. 2007; Sriver and Huber 2007). These anthropogenic changes compound natural pressures and impacts that have always been a part of the reef environment. The most severe manifestation of decline is a fundamental shift (phase shift) from dominance by reef-building corals to non-reef-building macro-algae (Done 1992; Hughes 1994), and often increased activity of reef-eroding taxa (e.g. sea-urchins and bio-eroding sponges). Hard coral communities that return to previous cover within years to decades after impact, may be considered as being 'resilient' (Smith et al. 2008; Done et al. 2010). However, restoration of a prior percentage cover alone is a low criterion for recovery. Of greater relevance to the restoration of reef building capacity, and biodiversity of coral-associated reef species, is the rate and degree to which the density, composition and size structures of the reef-building corals are restored; and how the new spatial mosaic of coral communities (Done 1992; Ninio and Meekan 2002) compares to what was present prior to the reef's decline. The degree to which communities have returned to their prior state can be measured as both the composition of recovering patches, and their spatial heterogeneity through time. The underlying drivers that determine whether communities recover, and the rate and extent to which the recovery trajectory converges towards a prior state, include the supply of new recruits (numbers and types), the prevailing conditions at the location (physical and biological), and the rates of growth and survival of the corals and their competitors.

Scott Reef has provided an invaluable opportunity to investigate these issues: its oceanic setting insulates it from coastal influences (e.g. flood plumes; terrigenous sediments); its remoteness from other reefs suggests that brood-stocks for coral recruitment (settlement and metamorphosis of larvae) are primarily located within the reef system. Scott Reef is a biologically diverse system with approximately 720 species of fish, 300 species of corals, and thousands of other species of marine invertebrates. Genetic and oceanographic studies within the Scott Reef complex (Gilmour et al. 2009a; Underwood 2009) suggest that there is connectivity among coral and fish sub-populations within the reef system, and that the strength of connections are variable.

Scott Reef has been providing an invaluable ecological data set since the early 1990s. This has been made possible by the co-investment by Woodside and AIMS, supporting detailed multidisciplinary research programs on the regional significance of Scott Reef and its function as a biophysical system. The catastrophic coral bleaching of 1998 has provided important insights into the functioning of atoll communities (Smith et al. 2008). The major coral monitoring program over the last fifteen years is a rich mine of information that allows us to document basic issues of the rates and direction of change following the 1998 catastrophe, and also to gain a better understanding of underlying ecological and bio-physical processes that have broader relevance to coral reefs globally.

The coral communities at Scott Reef, from shallow to deep, have been the subject of ecological studies since 1993 (Done et al. 1994). Based on an ecological and taxonomic reconnaissance in the shallow-habitat (<15 m) in 1993, Scott Reef was characterized as having '*extremely dense and diverse coverage of corals and very significant accumulation of three dimensional coral framework over large areas*', representing '*a very good example of a pristine oceanic coral reef*' (Done et al. 1994) Figure 2.1.1. Done et al. (1994) defined five shallow-water coral 'communities' or 'assemblages'. Assemblages were defined as characteristic groupings of coral species and growth forms that occur together, due largely to the shared environmental preferences and tolerances of their constituent species (e.g. wave energy, light penetration, sedimentation regime, substratum). These environmental conditions are all heterogeneous within the reef-habitats of Scott Reef (e.g. reef flats, reef crests, outer reef slopes, lagoon slopes: (Gilmour et al. 2006; Smith et al. 2006a), and each habitat is occupied by two to four coral assemblages (Done et al. 1994). Such zonation of coral assemblages in parallel with environmental conditions across reef flats and down slopes is typical of all surface-breaking coral reefs of substantial size. Within reef-habitats, there is further patchiness in the distribution of different coral assemblages that reflects underlying variability in site characteristics and history, which include disturbance regimes, stochastic patterns of community colonisation and succession.

Figure 2.1.1 Scott Reef is home to highly diverse communities of corals, fish and associated flora and fauna

The first comprehensive list of coral species across shallow-habitats of Scott Reef (reef slopes and lagoonal habitats mainly < 30 m) was compiled in 1987 (Veron and Marsh 1988). The Scott Reef coral data (indicating a moderately high diversity of coral species and no endemics) contributed to the definition of global biogeographic patterns in coral composition and diversity whose general form remains valid to this day: the centre of highest diversity in the Indonesia-Philippines-Solomon Islands area (so called 'Coral Triangle'), and a decline of richness with increasing distance from the equator. This general pattern is robust, though the detail changes as a result of ongoing discovery of new species and species previously unrecorded in particular places. Coral Geographic (Veron et al. 2009) places Scott Reef (~300 species) in a richer coral 'ecoregion' than the Rowley Shoals, and a species poorer ecoregion than the Coral Triangle (~605 species) (Figure 2.1.2) Moreover, the Scott Reef corals are primarily a subset of the Coral Triangle corals, not a set of different species.

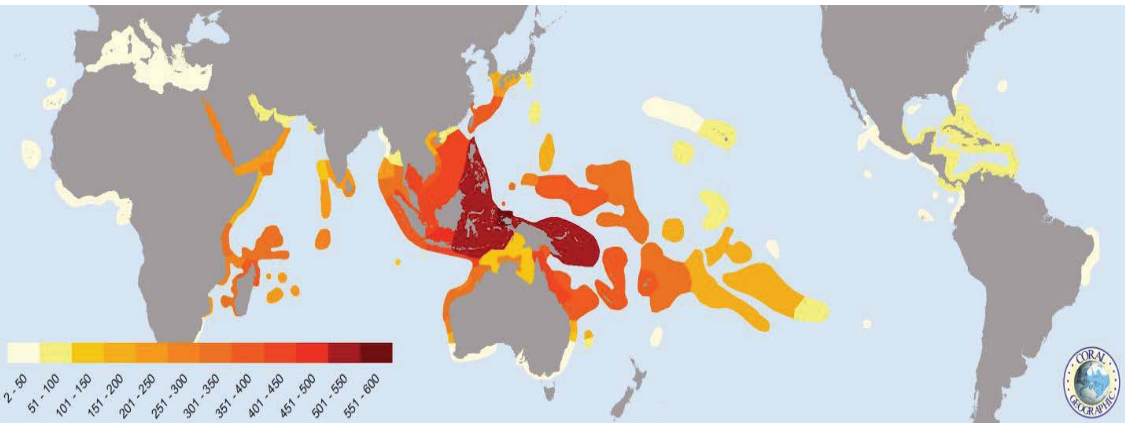


Figure 2.1.2 Scott Reef's coral communities are placed in a rich 'ecoregion', below the centre of diversity in the coral triangle and above reefs at the Rowley Shoals and Ningaloo (source Coral Geographic; www.coralreefresearch.org)

The strong development of coral assemblages at Scott Reef in 1993 (Done et al. 1994) was attributed at the time to the absence of major physical disturbances or predator outbreaks within the preceding years to decades. The absence of major disturbances in recent years had allowed coral cover, diversity and median sizes of corals all to attain high levels. However the subsequent, decade was not so benign, and Scott Reef was exposed to a prolonged heat-wave in 1998 that killed most corals, along with many other reefs in the Indian and Pacific Oceans. In 2004 (Cyclone Fay) and 2007 (Cyclone George), Scott Reef was then exposed to cyclone-generated waves sufficient to break, dislodge and kill corals, and to move large volumes of sediment and substrata. The impacts of these disturbances were documented in the monitoring transects established in 1994 on the outer and lagoonal slopes of north- and south-reef. At each location there is 750 m of permanent transect. This monitoring program showed that the 1998 heat-wave bleached and killed > 80% of the shallow-water corals (Figure 4.1.2a) (Smith et al. 2008) and reduced the diversity of coral genera by half (Figure 4.1.2b); by contrast, the prolific coral beds in the deep-lagoon (30-70 m) of south-reef were apparently unaffected (Smith et al. 2006a). Among the corals most severely reduced in 1998 were key species that defined the shallow-water coral assemblages (Done et al. 1994), notably *Acropora* and *Isopora* species. Following the bleaching, these coral assemblages were no longer recognisable (much as a forest becomes unrecognizable after a severe bush-fire), with dead coral becoming colonized by algal turfs and encrusting coralline algae. As with forests, there is an expectation that the same type of assemblages would re-establish in the damaged areas given sufficient time, possibly following transitional stages when different species have the ascendancy. Moreover, the initial assemblages may themselves have had a transient composition (in terms of relative abundance of species, diversity, evenness and size structures) given sufficient time without serious setback (c.f. Done et al. 2010).

The long term monitoring showed that by 2004, the shallow water hard corals overall had returned to approximately 40% of their pre-bleaching cover, and the local diversity of hard corals had increased from ~ 10 to ~15 genera per site (Figure 4.2.2). However coral recovery was patchy and the structure of most hard coral communities was still very different to that prior to the 1998 bleaching: previously dominant staghorn corals (*Acropora*) were still relatively sparse (< 25% of their previous abundance), leaving the massive corals that had better survived the bleaching (notably *Porites*) still in the ascendancy. By 2008, there had been a sharp increase in hard coral cover (to 70 – 100% of pre-1998 levels), and there were once again an average of ~20 hard coral genera in each monitoring location. Changes in coral community composition associated with the sharp decline in 1998 and following recovery are well documented in AIMS Long Term Monitoring program (See Chapter 4).

3. DISTURBANCES AT SCOTT REEF

The location of Scott Reef on the shelf-edge means it is free of many of the stressors affecting coral reefs closer to the mainland. However, coral communities at Scott Reef are exposed to a range of natural disturbances, some of which are being amplified by climate change. Additional pressure to communities also comes from traditional fishing of targeted stocks. A more detailed discussion of potential disturbances at Scott Reef and the resilience of its coral communities follows in Chapter 5.2. Historically, the most common disturbances and stressors likely to impact communities at Scott Reefare:

1) elevated water temperatures and mass-bleaching;
2) severe storms and cyclones;
3) outbreaks of coral diseases or predators;
4) overfishing.

During the 2009/2010 survey period, Scott Reef coral communities have been impacted by elevated water temperatures, outbreaks of disease and overfishing, but not severe storms or cyclones.

3.1 Elevated water temperatures and coral-bleaching in 2010

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

Although not as severe as the event in 1998, mass-bleaching also occurred at Scott Reef between March and May 2010. Colonies from a range of coral species were fully- and partially-bleached at locations across Scott Reef (Figure 3.1.5). The bleaching event coincided with the 2009-2010 El Niño-Southern Oscillation (ENSO) warming conditions and sustained surface temperatures above 31˚C (Figures 3.1.1, 3.1.2). The NOAA Bleaching Watch issued for Scott Reef on 18 February 2010 was upgraded to a Bleaching Warning on 22 March 2010, and to a Bleaching Alert Level 1 (≥ 4 Degree Heating Weeks) on 12 April 2010 (Figure 3.1.3). This is the first bleaching alert for Scott Reef since NOAA began monitoring in 2000.

Figure 3.1.1 El Niño-Southern Oscillation (ENSO) monitoring graph issued by the Australian Bureau of Meteorology. Showing the peak in the Nino 3.4 SST index in December 2009 and the period of bleaching at Scott Reef between March and May 2010. Monthly values > +0.8 indicate typical El Niño conditions.

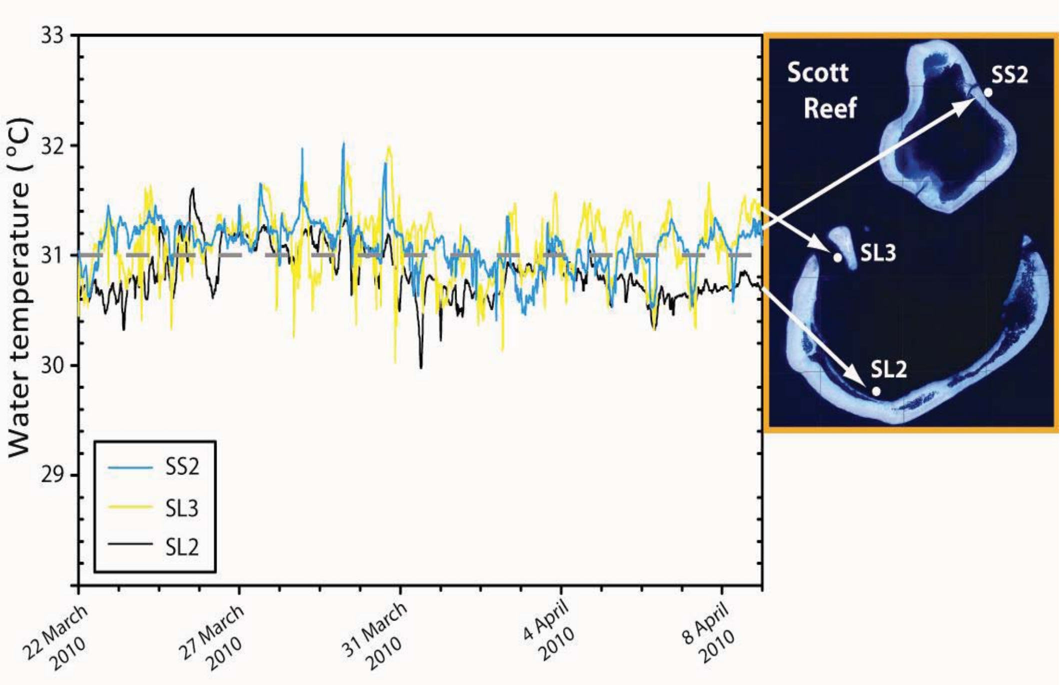


Figure 3.1.2 Water temperatures at 9 m depth at three monitoring locations at Scott Reef over the period of bleaching in 2010. Horizontal grey dotted line indicates the 31˚C bleaching threshold for Scott Reef, which is calculated by NOAA as 1˚C above the maximum monthly mean for Scott Reef at the surface (not 9 m depth).

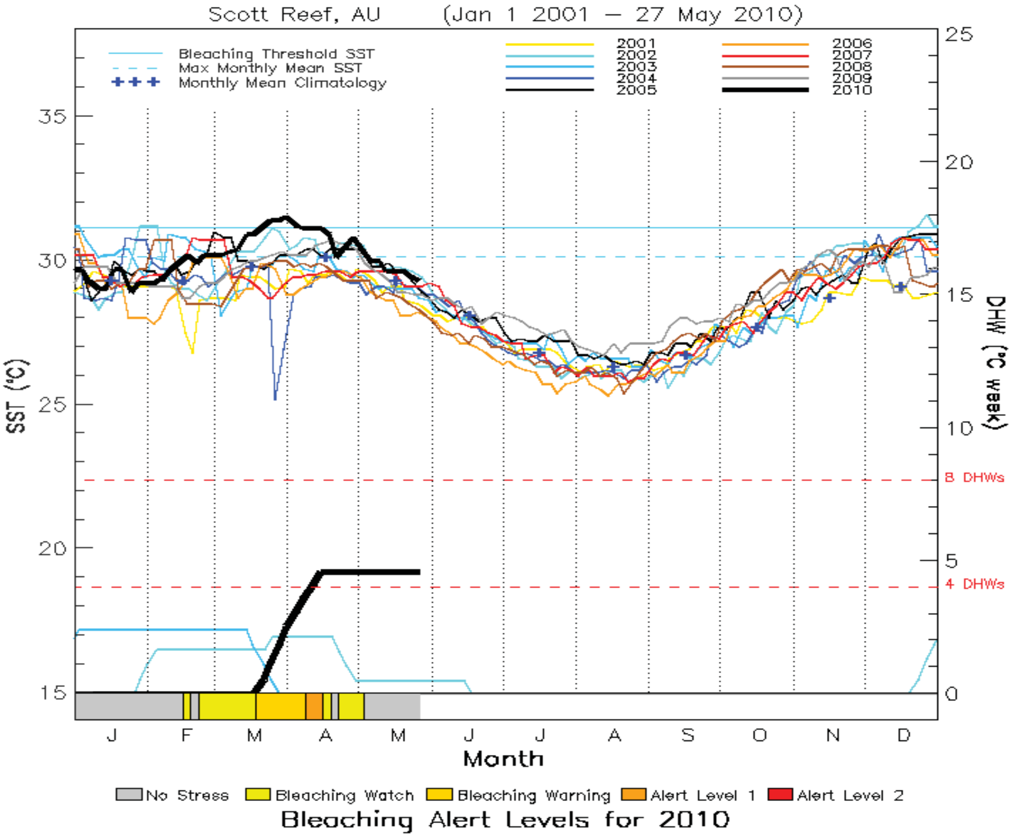


Figure 3.1.3 NOAA bleaching alert levels for Scott Reef in 2010. Remotely sensed sea surface temperature (SST), degree heating weeks (DHWs) and the Alert Level 1 initiated on 22 March 2010. Coral bleaching degree heating week (DHW) values are a cumulative measurement of the intensity and duration of thermal stress, and are expressed in the unit °C-weeks. DHWs over 4°C weeks have been shown to cause significant coral bleaching, and values over 8°C-weeks can cause widespread bleaching (NOAA, 2010b).

Based on observations of communities during May 2010, the severity of the bleaching varied among locations and coral genera at Scott Reef (Figure 3.1.5). Locations SL2, SL1 and SS2 were perhaps the worst affected by the bleaching, as were corals in the genus *Pocillopora*, *Fungia*, some massive *Goniastrea,* and some foliaceous *Pavona*; the *Acropora* corals were moderately affected (Figures 3.2.4; 3.1.4). All estimates of the proportion of corals bleached are qualitative.

- At Locations SL1, the majority of *Pocillopora* colonies had partially- or fully-bleached, in addition to a moderate proportion of massive *Goniastrea* and around 5 to 10% of the remaining coral community.
- At Location SL2, around 80% of *Pocillopora* colonies bleached and 20% of *Acropora* were bleached, diseased and/or recently dead (Figure 3.2.8; See Chapter 3.2). Some foliaceous *Pavona* had also bleached, as had many of the fungiid corals that were abundant in the 9 m habitat.
- At Location SL3, there was moderate to low bleaching, which mainly affected the *Pocillopora*. Bleaching at SL3 was less severe than at other locations (as with the 1998 bleaching) and the brooding coral *Isopora brueggemanni* that was so severely impacted in

1998 appeared not to be affected. The lower level of bleaching of communities at SL3 may be related to their proximity to the deep-water channel (Figure 3.1.2).

- At Location SL4 and the outer-reef location SS2, there was moderate to severe bleaching of the *Pocillopora* and some massive *Goniastrea*, in addition to some *Acropora* colonies at SS2.

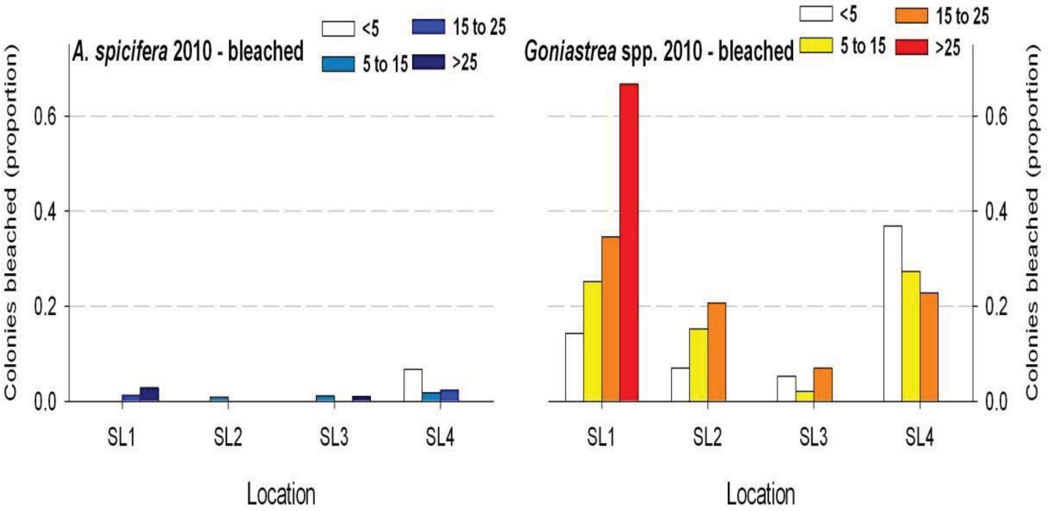


Figure 3.1.4 Proportion of tagged *Acropora spicifera* and *Goniastrea spp*. (*edwardsiii/retiformis*) colonies partially- or fully-bleached in May 2010. Of the bleached colonies, only 14% (n = 2) of *A. spicifera* and 17% (n = 27) of *Goniastrea spp*. were completely bleached. The high proportion of large *Goniastrea* bleached at SL1 is a consequence of low replication (n=3). See Location Map Figure 1.2.1.

In addition to qualitative estimates of bleaching among locations and genera, quantitative estimates at monitoring locations (not SS1, SS2) were obtained from tagged colonies of *Acropora spicifera, Goniastrea edwardsii/retiformis;* although these corals were not among those (e.g. *Pocillopora* spp.) worst impacted by the bleaching. Based on the tagged colonies, the bleaching was most severe at Locations SL1 and SL4, followed by SL2, then SL3. Bleaching was far more prevalent in *Goniastrea spp*. than *A.spicifera,* with around 20% of *Goniastrea* bleached at SL1 and SL4, around 10% at SL2, and around 5% at SL3 (Figure 3.1.4).

Coral bleaching does not always result in mortality, and some corals may survive the stress. The extent of mortality and the reductions in coral cover arising from the bleaching event in 2010 will be assed in field surveys in October 2010.

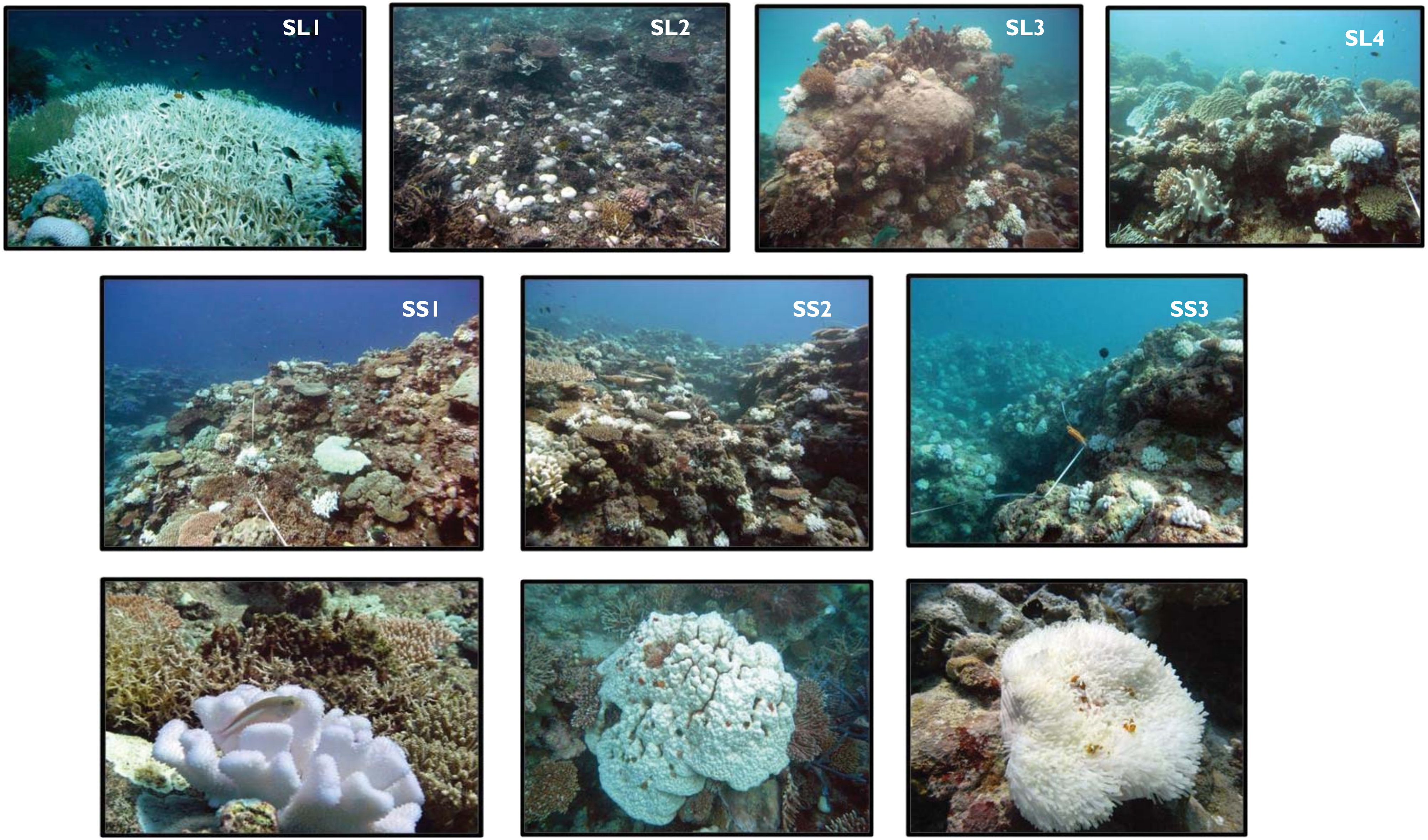
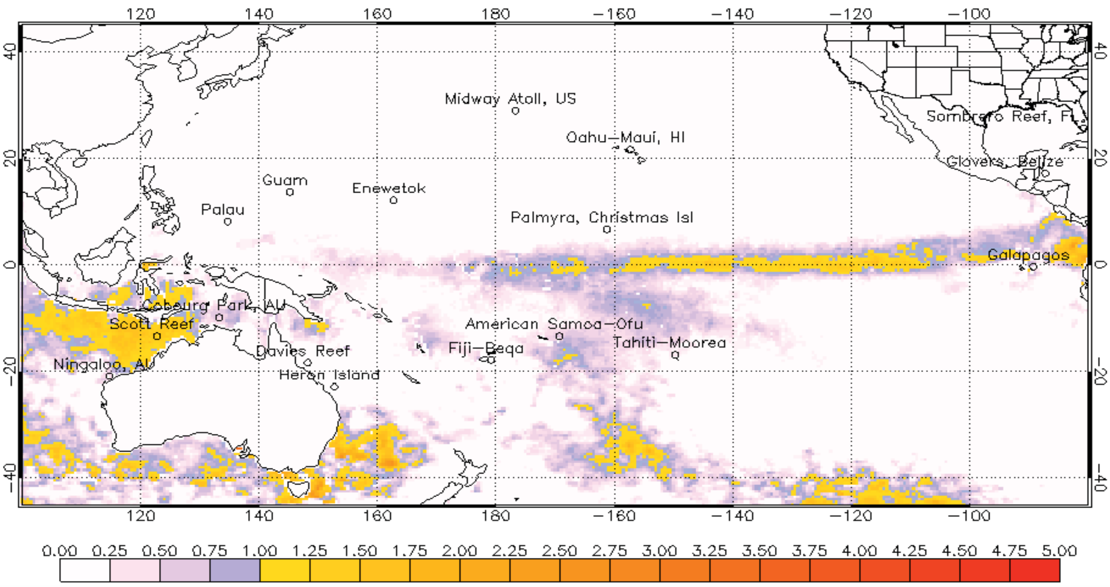
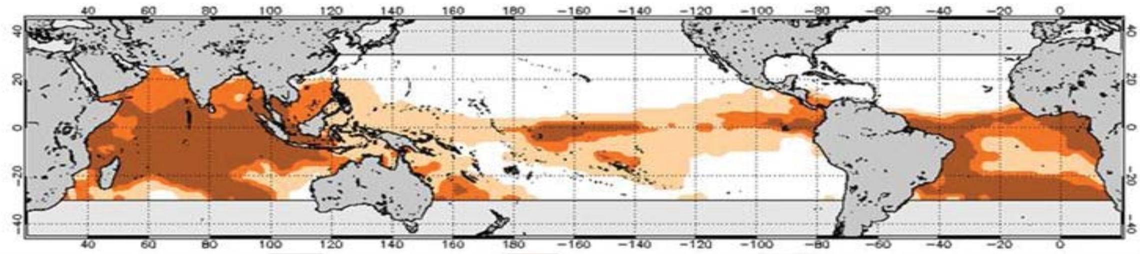


Figure 3.1.5 Coral bleaching at Scott Reef in May 2010. Although not as severe as in 1998, some corals at most locations had bleached in 2010. Corals in the Family Pocilloporideae were the worst affected, but the Acropora, Porites and Fungiidae had also bleached, as did some anemones. Bleaching of these organisms also affects the fish communities, such as hawkfish, which use *Pocillopora* colonies as a habitat, and anemone fish. See Location Map Figure 1.2.1.

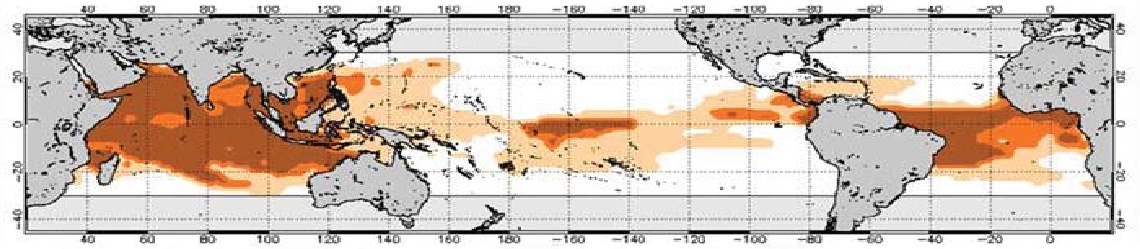
NOAA/NESDIS Coral Bleaching HotSpots, 3/29/2010



2010 Feb 23 NOAA Coral Reef Watch Coral Bleaching Thermal Stress Outlook for Feb–May 2010



2010 Mar 30 NOAA Coral Reef Watch Coral Bleaching Thermal Stress Outlook for Mar–Jun 2010



2010 Apr 13 NOAA Coral Reef Watch Coral Bleaching Thermal Stress Outlook for Apr–Jul 2010
(Experimental Product)

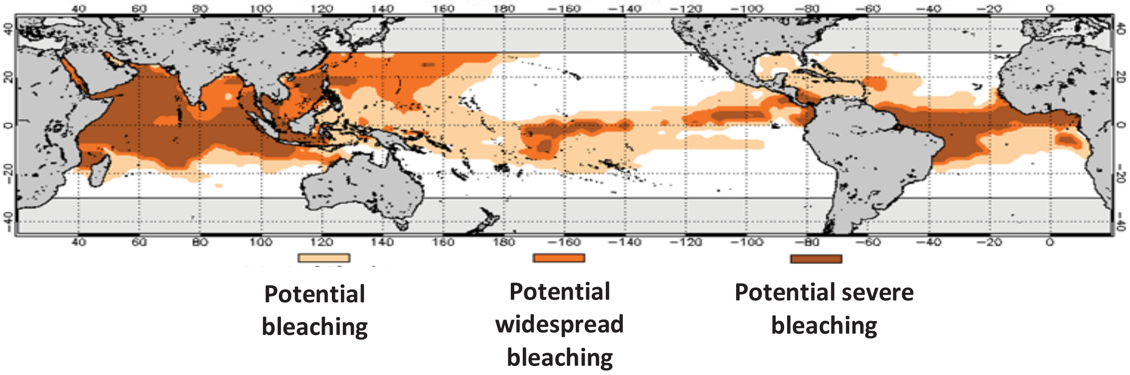


Figure. 3.1.6 NOAA Coral Bleaching Hotspots image issued on 29th March 2010, and bleaching alerts issued for the months of February to April, highlighting the extent of ocean-warming through the northern Indian Ocean and south-east Asian regions (http://www.noaa.gov).

The mass-bleaching of coral at Scott Reef in 2010 was part of global elevation in ocean temperatures in the Indian Ocean and Southeast Asia regions (Figure 3.1.6), with mass-bleaching documented on reefs in the Maldives, the Andaman Sea and Gulf of Thailand, Malaysia, Singapore, Cambodia and parts of Indonesia and the Philippines (NOAA 2010). Within the region of Western Australia, bleaching was also observed at Ashmore Reef at the same time as at Scott Reef. The bleaching at Scott Reef in 2010 was not as severe as that in 1998, but on other reefs around the world, the bleaching was more severe than in 1998. Some reefs, such as Ashmore Reef or those around Singapore, were not impacted in 1998 but bleached in 2010, while other reefs throughout the coral triangle have suffered dramatic reductions in cover following bleaching this year (Normile 2010).

The elevated water temperatures off north-western Australia and the bleaching of corals at Scott and Ashmore Reefs in 2010 reflect global patterns of climate change (Figure 3.1.7; NOAA; *www.ncdc.noaa.gov/sotc*). Between January and July 2010:

- *Land and ocean temperatures were the second warmest on record (after 1998);*
- *Land temperatures were the warmest on record;*
- *Ocean temperatures were the fifth warmest on record.*

Global temperatures in 2010 are already exceptionally warm. Around Australia, warmer than normal sea-surface temperatures in the first half of the year increased the probability of extreme temperatures during the following summer, and/or extreme cyclonic events. These data suggest an increased likelihood of mass-bleaching and/or cyclone damage to coral communities at Scott Reef during 2011. The survey of long-term monitoring locations at Scott Reef in October 2010 will assess the recent impacts of bleaching (and disease), and consider the most appropriate response should more severe impacts become likely in the summer of 2011. The regional scale of disturbances associated with climate change highlight the need to conduct monitoring programs over similar spatial scales, over replicate reef systems, to ensure that local activities are not inappropriately attributed to impacts (Lough 2007).

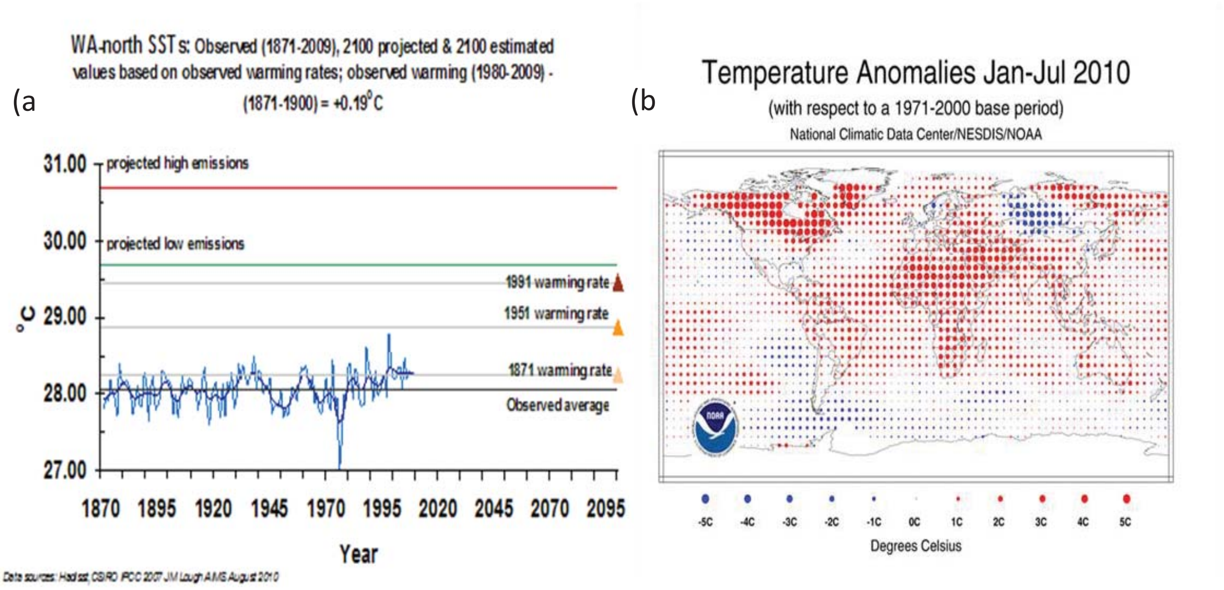


Figure 3.1.7 a) Observed and predicted increases in sea-water temperatures off Western Australia, north of 20°C (updated from Lough 2007). b) Global temperature anomalies for the period of January to July 2010 (www.ncdc.noaa.gov/sotc).

3.2 Outbreak of coral diseases in 2009-2010

Through 15 years of monitoring, a low incidence of coral disease is usually observed at Scott Reef. However, since October 2009, disease has caused widespread mortality of some *Acropora* corals in at least one location near the southern part of south-lagoon (SL2), and there is concern that outbreaks could spread to other locations following the May 2010 bleaching (Figure 3.2.1). From 2009, there has been a noticeable increase in the incidence of coral disease at Location SL2. Most notably, the majority of infected and recently dead colonies are table *Acropora* (e.g. *A. hyacinthus, A. cytherea*; Figure 3.2.1). The recent outbreak of disease among table *Acropora* at SL2 is possibly 'white-syndrome' disease, caused by the bacteria *Vibrio coralliilyticus* (Sussman et al. 2008 & Pollock et al. 2010). Low water circulation, increased sedimentation and high water temperatures, all can trigger an outbreak of white-syndrome, and high water temperatures and high cover of susceptible species can sustain the outbreak (Bruno et al. 2003; Sutherland et al. 2004; Heron et al. 2010) Miller et al. 2009; Heron et al. 2010); all of these conditions characterise the recent outbreak at Location SL2.

Figure 3.2.1 White-syndrome disease in table *Acropora* at Location SL2. a) The spread of disease through an individual colony is readily recognised, as is b) the apparent infection from one adjacent colony to another. c+d) In addition to infected colonies, there are also many huge table *Acropora* over a metre in diameter that have recently died from infection. Although most prevalent in table *Acropora*, some other branching and corymbose *Acropora* have been infected. See Location Map Figure 1.2.1.

Location SL2, at the southern part of south-lagoon, has comparatively poor water quality, low circulation, limited flushing with the open ocean, and high turbidity (see Chapter 5.2). Cyclone George in 2007 increased wave energy around Location SL2, which resuspended accumulated sediments and associated in fauna. Additionally, the density of large table *Acropora* corals at SL2 had increased in recent years and many colonies are in close proximity to each other. In many instances, the spread of disease can be tracked from one adjacent colony to the next (Figure 3.2.1). In addition to the number of infected colonies, in May 2010 there was also an abundance of huge dead *Acropora* plates that had died from the outbreak in the last year.

During the most recent survey in May 2010, the outbreak of disease seemed to have spread to a greater number of species and locations including a range of *Acropora* and to Location SL1. Importantly, currents at the southern part of the south-lagoon, near SL2, are most likely to flow towards Location SL1 inside east hook, albeit at a slow rate; the communities are genetically similar and some coral larvae produced at SL2 are likely to recruit to SL1 (if they have not already settled) (see Chapter 5.1 'Reproduction and Connectivity).

Of the tagged corals at monitoring locations across Scott Reef (not SS1, SS2), *Acropora spicifera* had a much higher incidence of disease than did the massive *Goniastrea* colonies, and the proportion infected was highest (> 10%) for the large colonies at Locations SL2 (see Chapter 7 'Demography of Coral Populations). However, around 5% of larger *A. spicifera* colonies at other locations were also infected by disease, and a much higher proportion of table *Acropora* were infected at all locations, particularly SL1. The spread of disease through a greater number of species and locations is more likely following the bleaching in May, and surveys of monitoring locations in October 2010 will provide insights into the extent of the mortality and the reductions in percentage cover.

Associated with the recent bleaching and outbreak of diseases were increases in the number of crown-of-thorns and particularly *Drupella* spp. observed feeding on colonies, although the predators were in relatively low abundance and were probably opportunistically feeding on coral already affected by the other stressors.

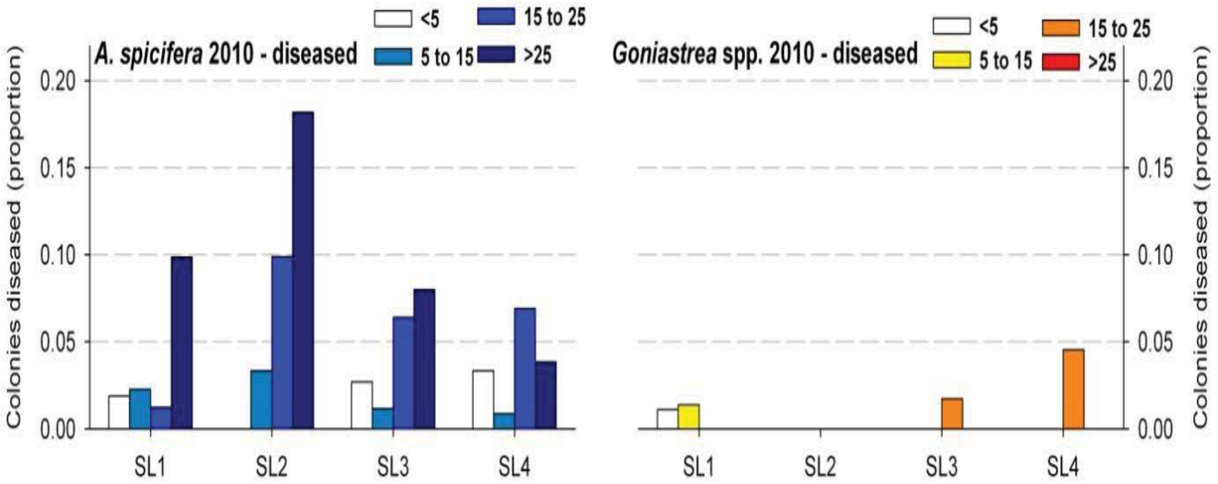


Figure 3.2.2. Proportion of tagged *Acropora spicifera* and *Goniastrea spp*(*edwardsii/retiformis*) colonies infected by disease at monitoring locations (not SS1, SS2) in May 2010. Most corals infected by disease were table *Acropora*, and a comparatively low proportion of *A.spicifera* were infected. See Location Map Figure 1.2.1.

3.3 Overfishing

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 with close to 100 vessel visits per year in recent years (ERM 2008; ERM 2009). Fishing by Indonesians now involves the collection of a range of animals, but principally targets sea cucumbers (bêche-de-mer), trochus (topshell), reef fish and particularly sharks (Figure 3.3.1). Studies have shown this fishing has severely depleted shark populations at Scott Reef, compared to the Rowley Shoals, with the most plausible reason being overfishing (Meekan et al. 2006). Stocks of sea cucumber and trochus are also heavily exploited (Skewes et al. 2005; Bryce 2007). Overfishing of sharks has been shown to release numbers of tertiary feeders elsewhere (DeMartini et al. 2008; Sandin et al. 2008) andmight explain the trend of an increasing number of piscivore and invertivore species over the duration of the study, despite an unknown level of fishing for fish other than sharks also occurring (see section 6.3).

Figure 3.3.1 Fishers in traditional vessels have historically targeted trepang (sea-cucumbers) and trochus, but have shifted focus to shark-fin and potentially other species of reef fishes.

Although the major disturbance events at Scott Reef generally involve threats posed to corals by thermal bleaching, disease and the impacts of cyclonic wave, a recent threat to the reef ecosystem has emerged in the form of the targeting of large keystone fish species by traditional Indonesian fishermen. Recent survey data indicate that traditional fishers at Scott Reef are now targeting a wider range of fish species, using new fishing methods and gear. In 2009, the Australian Fisheries Management Authority (AFMA) conducted creel surveys of traditional fishers at Scott and Seringapatam Reefs and observed a wide range of reef fish species being collected. In particular, fishers were increasingly using underwater torches and spears to catch large numbers of the giant humphead parrotfish *Bolbometopon muricatum* as they rested at night (Figure 3.3.2; J. Prescott (AFMA) pers. comm. 30 June 2010). Although the survey was mainly focused on sea cucumbers, catches of a wide range of other reef fish were also reported, including the endangered humphead Maori wrasse (*Cheilinus undulatus*), various emperors (*Lethrinus* spp.), red bass (*Lutjanus bohar*), coral trout and species of shark.

Giant humphead parrotfish are one of the largest coral reef fishes (1.2.m) and play a critical role in reef ecosystem processes (Bellwood et al. 2003). (Figure 3.3.2). This large coral eroding species is listed as vulnerable on the IUCN Red list (Chan et al. 2007), in recognition of its slow growth, late sexual maturity (Hamilton et al. 2008), and ease with which stocks can be devastated by spearfishers (Dulvy and Polunin 2004). Consequently, populations of large bioeroders such as *B. muricatum* have been reduced across much of their range, and are now common only in remote areas or areas where fishing is prohibited, such as the Rowley Shoals (Dulvy and Polunin 2004; Chan et al. 2007).

The reduction or loss of a keystone species such as *B. muricatum* is predicted to result in an increase in fast growing, grazing susceptible corals such as tabulate *Acropora* and *Pocillopora* (Bellwood et al. 2003). As herbivorous reef fishes played an important role during the post-bleaching period at Scott Reef (Chapter 2.3), further studies investigating the potential impact their removal may have on maintaining the coral-algal balance and thus resilience of coral reefs to disturbance in the region are required.

Figure 3.3.2 School of browsing giant humphead parrotfish *(Bolbometopon muricatum*)

4. STATUS OF CORAL AND FISH COMMUNITIES

4.1 Abundance and diversity of coral and fish communities

Between 1994 and 2008, 52 genera of hard coral were recorded at Scott Reef. However, many of these genera were rare and the 9 most abundant genera usually accounted for more than 90% of total cover of hard corals. In approximate order of abundance, these genera were *Isopora, Acropora, Porites, Montipora, Seriatopora, Echinopora, Fungia, Pocillopora* and *Faviidae*. These abundant genera were further grouped into functional categories based on growth form and life history traits : massive and encrusting corals (*Porites*, *Montipora*, massive Faviidae), Acropora, *Isopora*, *Pocilloporidae* (*Seriatopora* and *Pocillopora*), folioaceous corals (including *Echinopora*) and soft corals. Of these groups, the pre-bleaching community at Scott Reef was dominated by massive and encrusting corals (15%), *Isopora* (7%) and soft corals (9%).

In 1998 bleaching reduced cover of hard coral on Scott Reef from an average of approximately 48% to 10% (Figure 4.1.1 (a)), and the number of genera from approximately 19 to 9 (Figure 4.1.1(b)). Since this time, cover of hard coral has generally increased, despite exposure to two major cyclonic events. In 2004, Cyclone Fay noticeably reduced cover of hard coral at four of the six monitoring locations, but overall cover of hard coral on Scott Reef continued to increase around this disturbance. Total cover of hard coral at Scott Reef in 2008 was 38% and the number of genera at each location had returned to pre-bleaching levels.

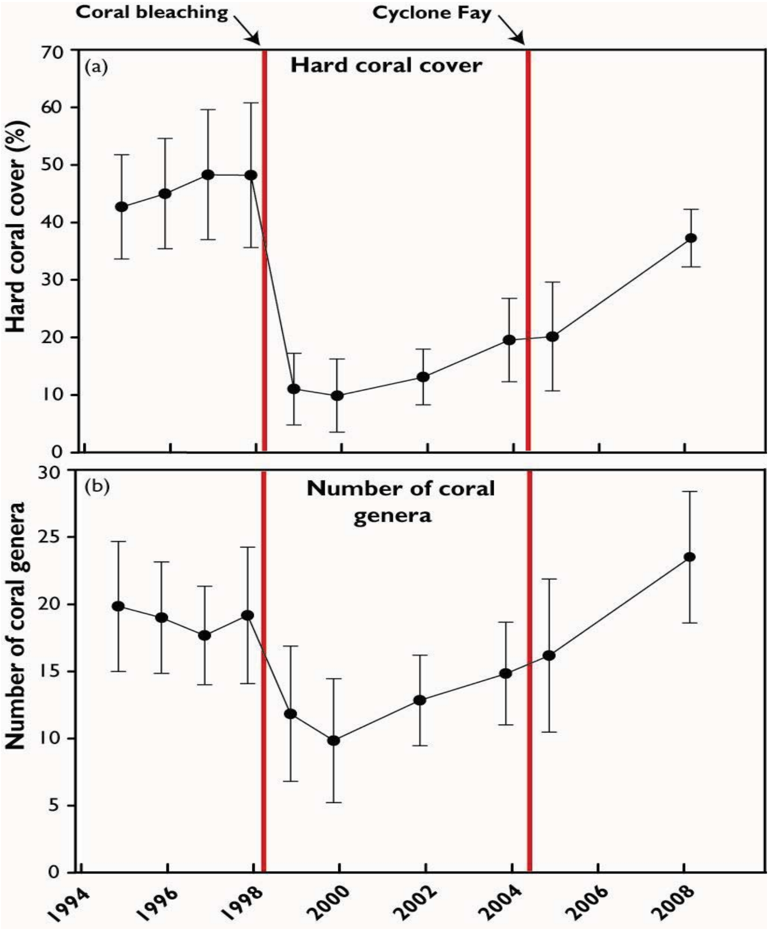


Figure 4.1.1 Mean (± 1 SD) plots of (a) live hard coral cover and (b) number of hard coral genera at Scott Reef between 1994 and 2008.

The coral bleaching also structured the subsequent changes in damselfish (Pomacentridae) populations at Scott Reef because it altered the habitat that many damselfishes rely on for food and shelter (Figure 4.1.2.a). In contrast, the densities of larger and more mobile fishes (non-Pomacentridae) and numbers of fish species increased throughout 15 years of monitoring (Figure 4.1.2a,b). The number of larger reef fishes is now 50% greater than at the start of monitoring, and species richness is 20% greater. These increases in reef fishes were apparently unaffected by bleaching and cyclones disturbances and could reflect traditional fishing pressure that has targeted the largest predatory reef fish and sharks over the last decade (Sandin and Pacala 2005; DeMartini et al. 2008).

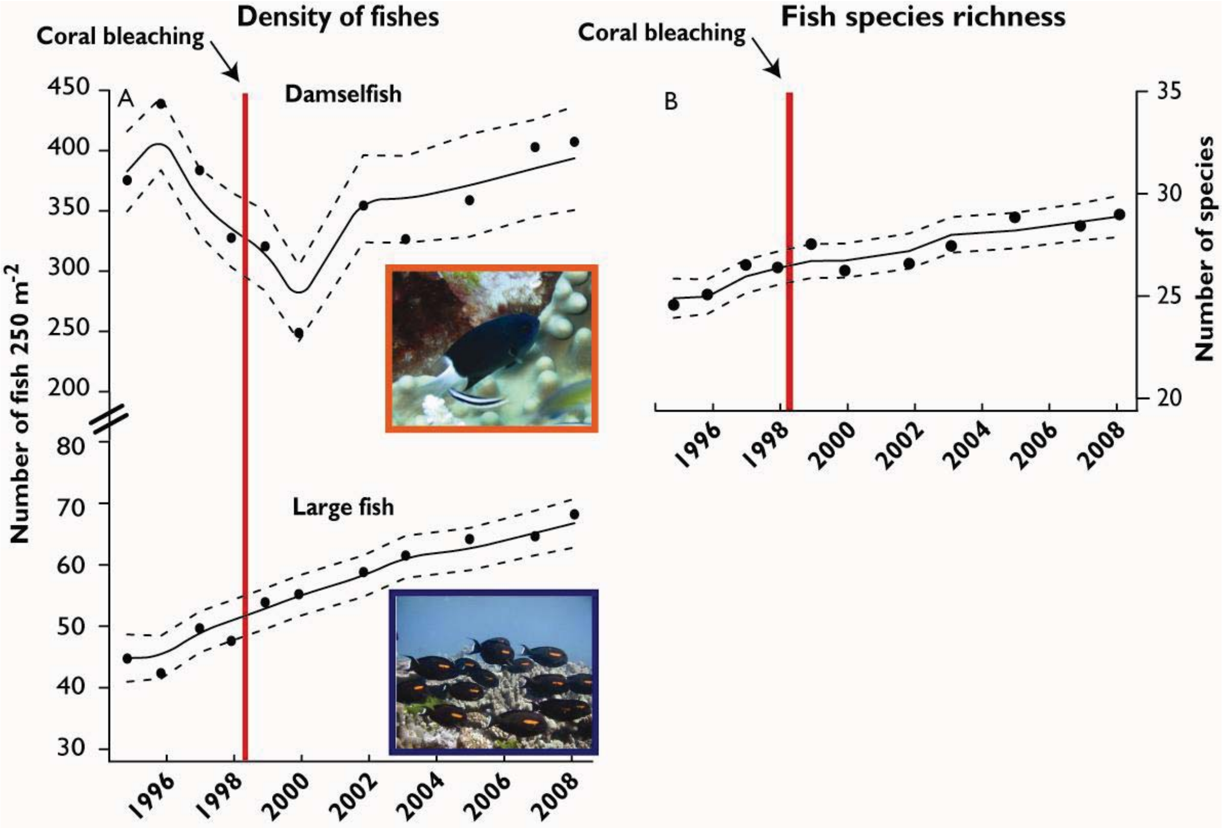


Figure 4.1.2 Mean (± 95 C.I.) densities of (a) damselfishes and large (non-Pomacentridae) fishes and (b) mean numbers of all species recorded at Scott Reef between 1994 and 2008. The circles represent the observed mean densities. Solid line represents mean densities and dashed line 95% confidence limits.

Coral cover and number of genera at Scott Reef are now similar to that prior to the bleaching, but these broad indicators provide few insights into whether the community structure is also similar to that prior to the bleaching and the degree to which the communities have fully recovered. Throughout the monitoring period, changes in coral cover have led to a net decrease in cover of branching *Acropora*, *Isopora* and soft corals, and increases in the cover of table *Acropora*. These changes in functional groups of corals can be divided into four distinct periods (Figure 4.1.3a): 1) pre-bleaching (1994-1997); 2) bleaching (1998-2001); 3) initial recovery and cyclone (2003-2004); and 4) further recovery and cyclone (2008). These changes are driven by the differences in susceptibility of groups to disturbances and their recovery (Figure 4.1.3).

As with the corals, communities of fishes also underwent a cycle of change initiated by the bleaching event in 1998 and are yet to return to the pre-bleaching structure (Figure 4.1.3.b). Fish communities underwent three distinct periods of change: 1) pre-bleached community characterised by habitat and dietary specialists (predominantly coral and plankton feeders); 2) bleaching community characterised by species that have a preference for the resulting habitats, coral rubble, turf algae; and 3) the current (2008) community, characterised by fish that have generalist diet and habitat requirements, or higher order consumers such as certain lutjanid and lethrinid species that feed on crustaceans and other fishes.

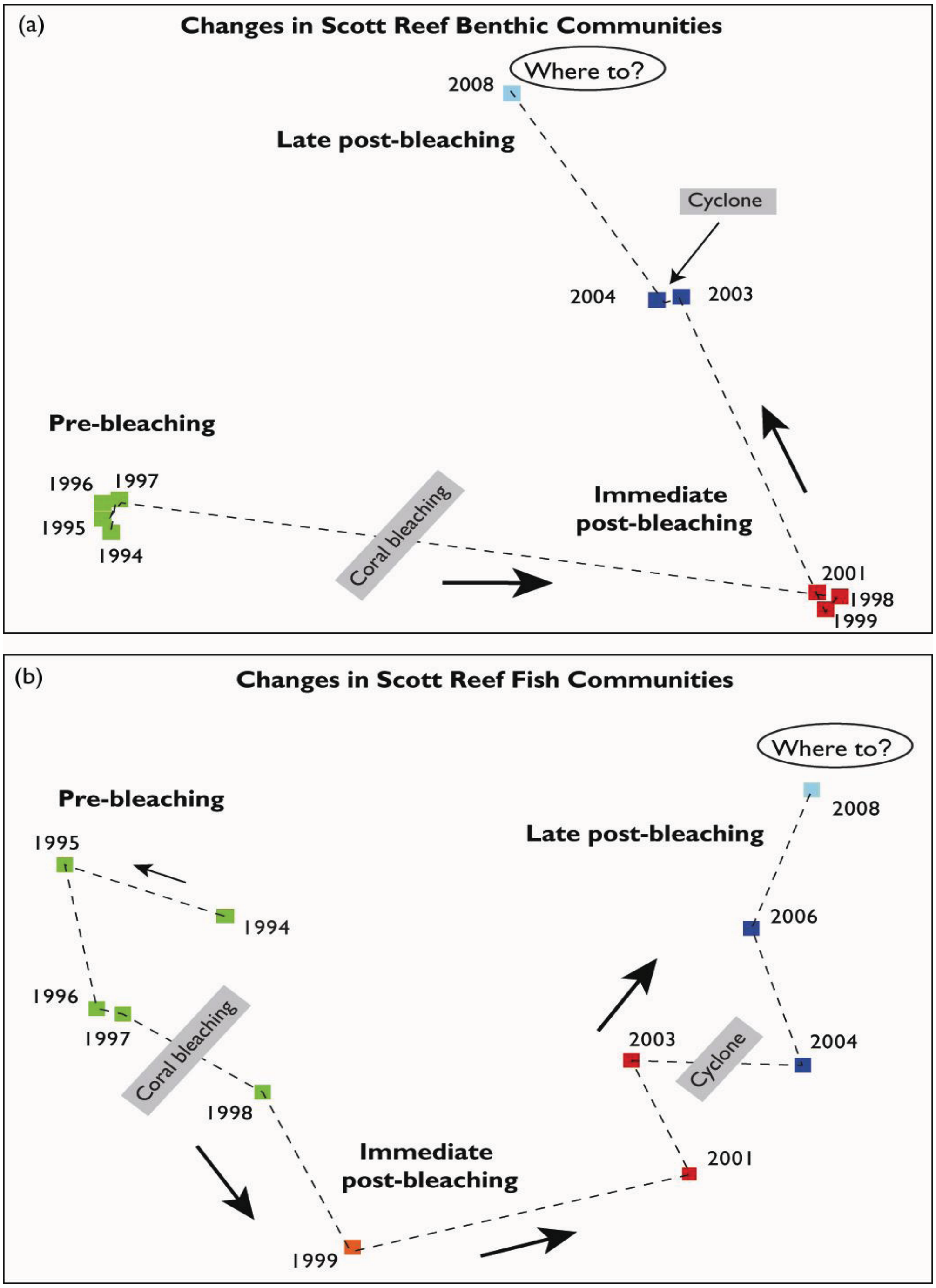


Figure 4.1.3 Changes in the structure of (a) benthic and (b) fish communities at Scott Reef from 1994-2008. The distances between the years reflect the degree of similarity in community structure

4.2 Functional changes in coral and fish communities

For the coral communities at Scott Reef, the cover of massive and encrusting corals at all locations was reduced by the mass-bleaching, but their subsequent increases in cover were comparatively rapid because some colonies were injured rather than killed (Figures. 4.2.1(h), 4.2.2). After the bleaching, the cover of those hard corals (*Montipora, Porites and Faviidae*) most likley to be injured and then regrow, had increased at all locations from an average of 9% in 1999 to 21% in 2008.

In contrast to the massive and encrusting corals, the bleaching event killed most soft corals and *Isopora* corals, dramatically reducing their cover at all locations (Figure 4.2.1(h)). The soft corals can have low rates of growth and sexual recruitment, often reproducing asexually, and there has been little increase in their cover since the bleaching. Before the bleaching event, cover of soft corals ranged from around 1% at SL2 to 20 % at SL4. Bleaching reduced cover to < 5% at all locations and the average cover of soft corals in 2008 ranged from <1% at SL2 to 10% at SL4 (Figure 4.2.2). Similarly, the cover of *Isopora* prior to bleaching was particularly high (7 – 20%) at three of the monitoring locations (SL3, SS1, SS2), but was reduced to undetectable levels at all but one location (SL3) after the bleaching. In 2008, the cover of *Isopora* remained very low (< 1%) at most locations, with the exception of SL3. Increases in cover at location SL3 were driven by the production of brooded larvae by the surviving corals. The limited dispersal of these brooded larvae means they have not recolonised other locations in which few *Isopora* survived the bleaching. Net decreases in relative cover of the previously dominant soft corals and *Isopora* have coincided with increases in relative cover of *Pocillopora* and *Acropora*, and after an initial lag period, these corals show good capacity to recover over wide spatial scales (Figure. 4.2.2). Most notably, corymbose and digitate *Acropora*, followed by table *Acropora*, were responsible for much of the recent increases at many locations at Scott Reef.

In coral reef ecosystems, there is a strong mutualistic relationship between the corals and fish, to the extent that changes in community structure of corals, result in corresponding changes in certain trophic groups of fishes (Figure 4.2.1a-g). Consequently, the mass-bleaching resulted in striking changes in fishes that are obligate associates of live coral, whether using coral for food (e.g. butterflyfishes; (Cole et al. 2008) or for protection (e.g. planktivorous damselfishes; Wilson et al. 2008)(Figure. 4.2.1c). Following the death of bleached corals and their overgrowth by algae, the abundances of herbivores increased, as did numbers of detritivores that benefitted from the trapping of detritus by rubble and algal turfs. It was during this phase that grazing herbivorous fishes played a role in controlling the algal community at Scott Reef and maintained suitable substrata for coral larvae to recolonise (Mumby 2006); the lack of macroalgae communities at Scott Reef also ensured that suitable substrata remained for colonisation by corals.

Fish species tended to change in abundance mostly at sites where their preferred coral communities also changed. The decline in abundance of many butterflyfish (*Chaetodon* species) following the bleaching, was related to the reduction in branching, corymbose and bottlebrush *Acropora* (e.g. *A. hyacinthus*) they feed on (Pratchett 2005), or the reduction in soft corals that other species of butterfly fish (*C. melannotus*) feed on (Figure 4.2.2). Additionally, the decline in planktivorous damselfish (*Chromis ternatensis*) following the bleaching was related to the large reduction in *Isopora* corals, within which the species shelters (Figure 4.2.3). Increases in the abundance of various algal and detritus feeding fish species following the bleaching (Figure 4.2.3) was related to the changes in cover of turfing and coralline algae, and abiotic susbtrata such as sand and rubble (Figure 4.2.3).

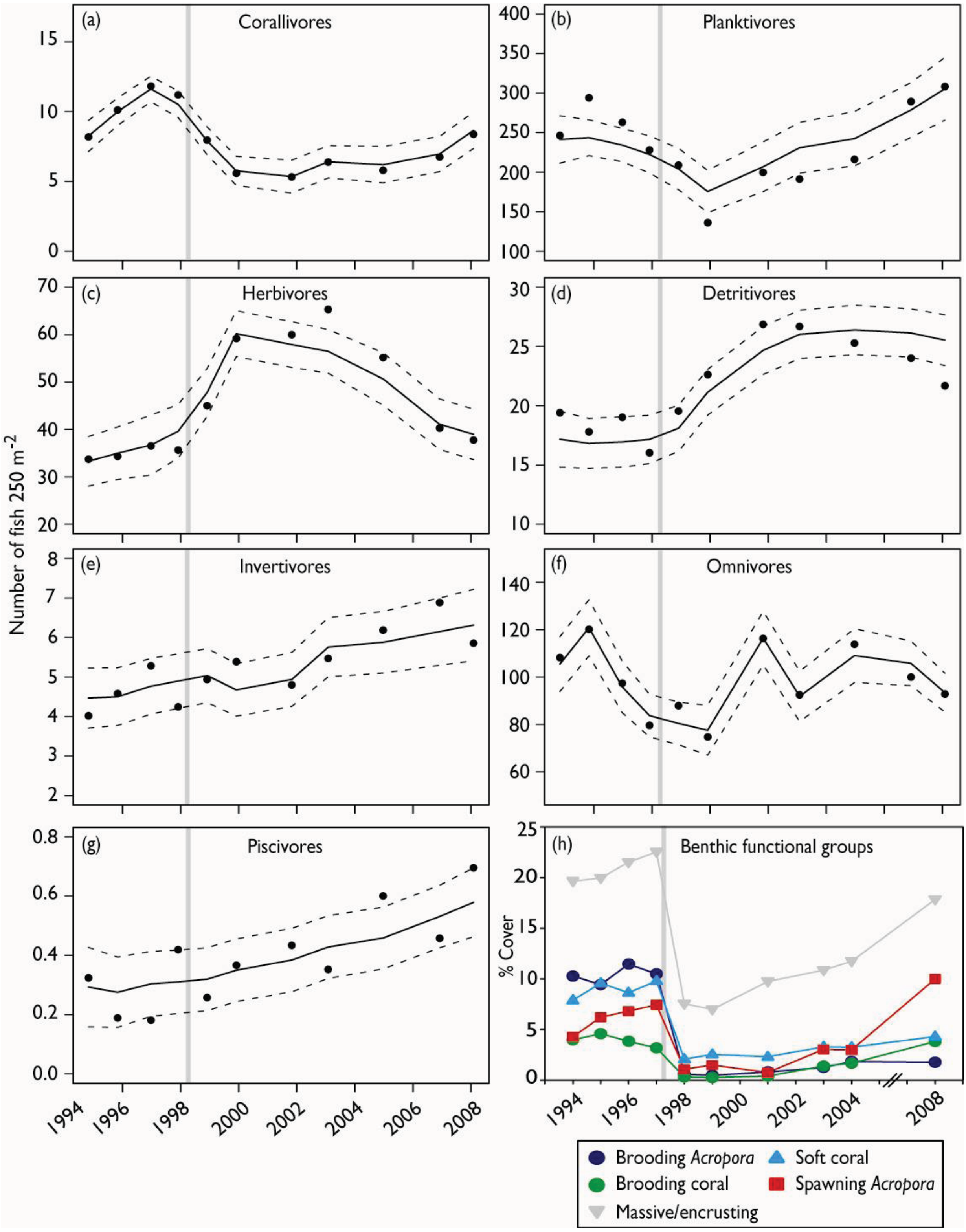


Figure 4.2.1 Plots of (a – g) the abundance of each of the main trophic groups of fishes through time and (h) change in percentage cover of functional groups of corals.

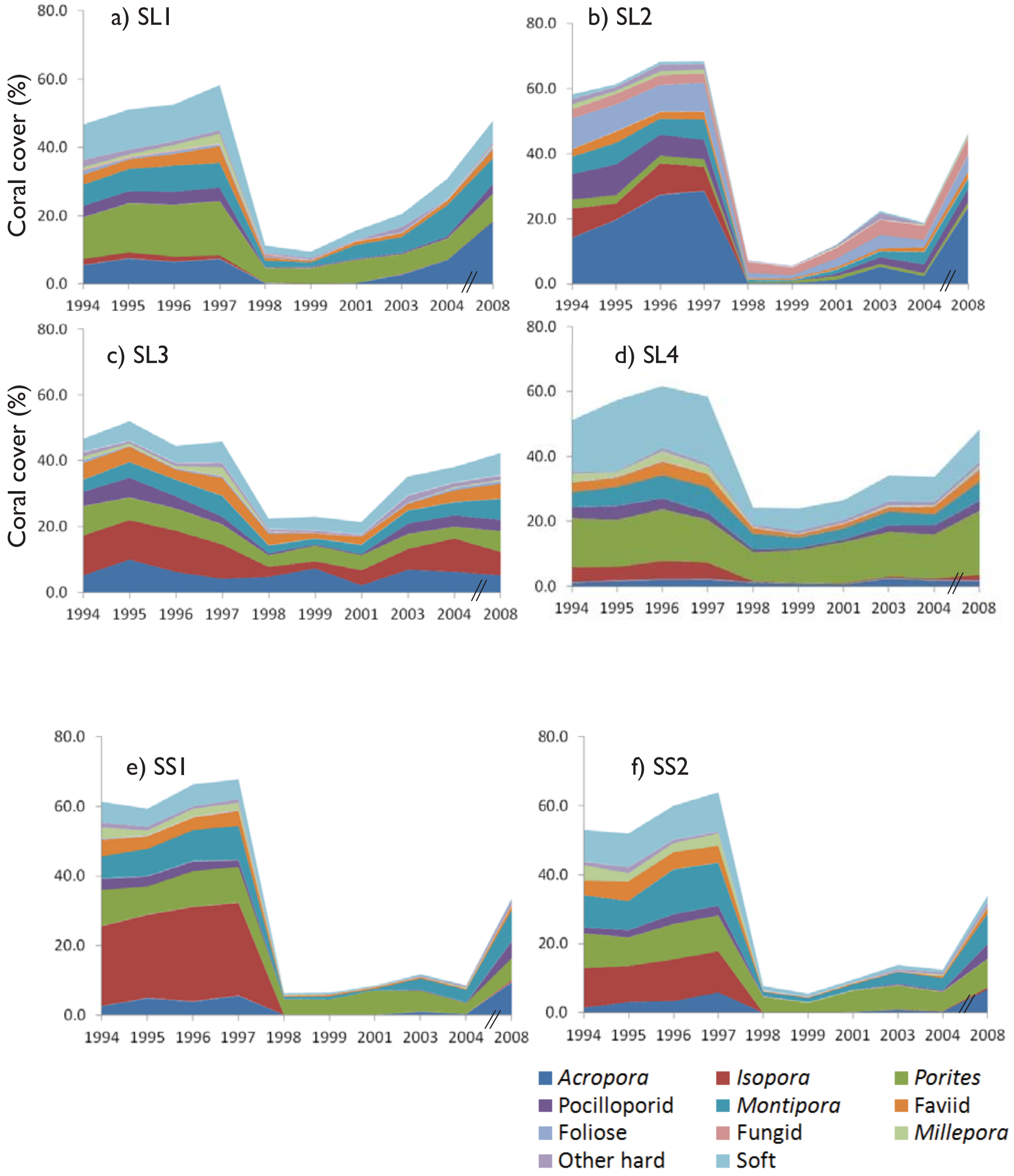


Figure 4.2.2 Percent cover of benthic functional groups at each of six locations at Scott Reef between 1994 and 2008. See Location Map Figure 1.2.1.

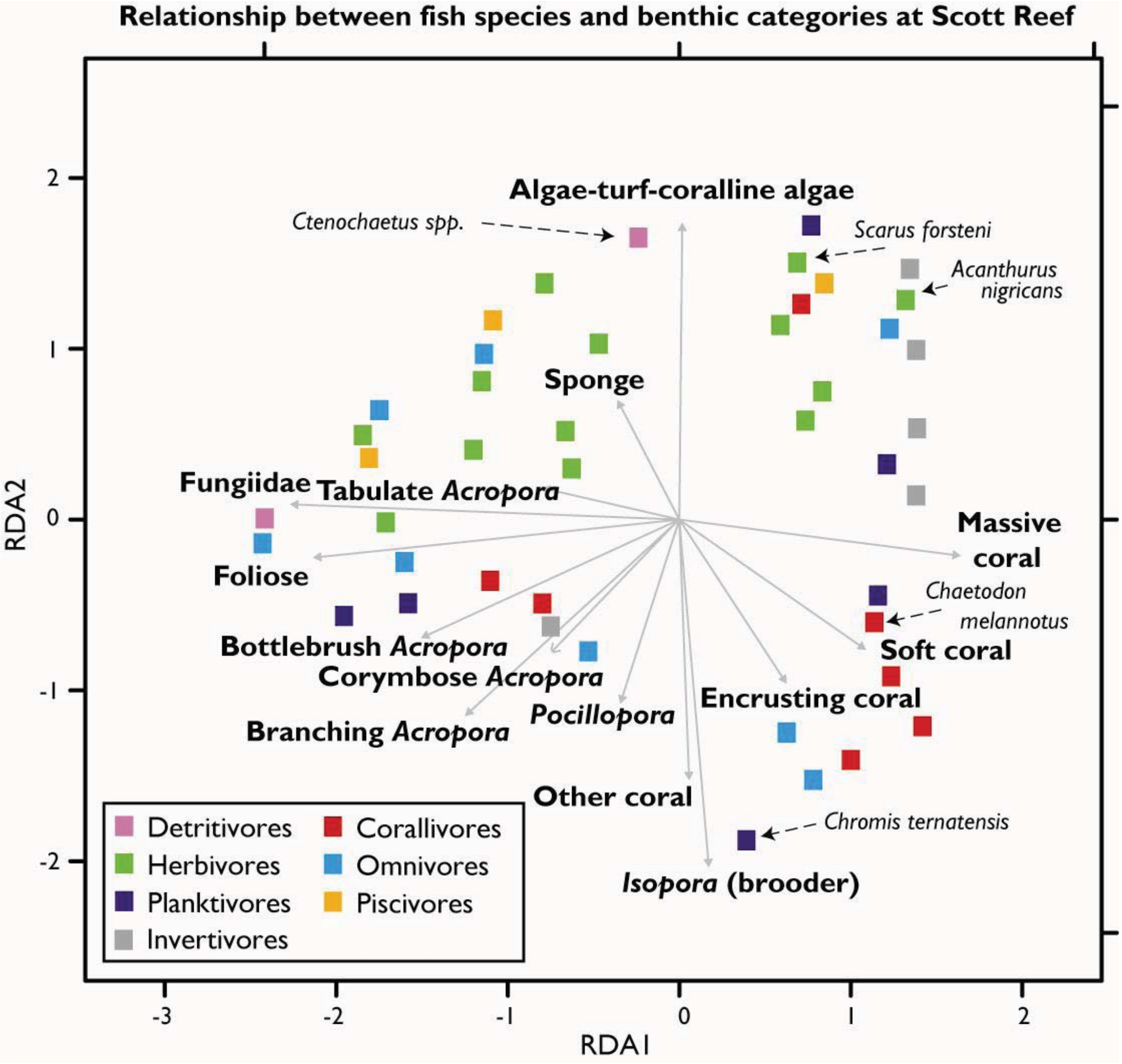


Figure 4.2.3 Relationship between groups of corals and fishes at Scott Reef. Each coloured square represents a species of fish, and the colour of the square indicates the species' food preference and their trophic group. The trophic groups of fish are positioned closest to their preferred coral habitats, according to the dominant benthic groups (arrows). For example, fish that feed on corals (corallivores) group strongly with the groups of corals they feed on (*Acropora,* soft corals).

Spatial variation of change across Scott Reef

Underlying the strong changes in coral cover and diversity of genera at Scott Reef following mass-bleaching was finer-scale variation among some locations and communities, due to their difference in habitat conditions, disturbance regimes and the life histories of their dominant corals (Figure 4.2.2). The local changes in community structure can be summarised as follows:

- Both outer-slope communities (SS1, SS2) displayed similar changes in community structure throughout monitoring (as did SS3 at Seringapatam). These communities were initially dominated by *Isopora brueggemanni,* and the subsequent mortality following bleaching dramatically altered community structure. In addition, the outer-slope communities were most exposed to Cyclone Fay, which slowed the recovery from bleaching, particularly for the *Acropora*.

- In contrast to the outer-slope communities, the communites at SL3 on the inside of west hook, and SL4 at north-reef adjacent to the deep-channel, were least impacted by the bleaching; the lower impact was possibly due to cool-water intrusions from the deep-channel at the time of bleaching. Despite the net decreases in coral cover, community structure at SL3 and SL4 were relatively stable through the period of monitoring. However, the main exceptions to this pattern were the slow recovery of soft corals and the lack of recovery of *Isopora* corals at SL4. Indeed, in 2008 the community at SL3 was the only only one in which the once abundant *Isopora brueggemanni* had returned to a relatively high cover (Figure 4.2.2).

- Location SL2 at the southern part of south-lagoon is the most sheltered of the monitoring locations, and characterised by poor circulation and high turbidity. This location has a most distinctive coral community, with a relatively high cover of fungiids, foliose corals and bottlebrush *Acropora*. The high cover of *Acropora* at SL2 was dramatically reduced by the bleaching, but was not severely impacted by subsequent cyclones and the community in 2008 was approaching that prior to the bleaching; the exception was the lack of recovery of *Isopora* corals (Figure 4.2.2) The most notable changes in community structure at SL2 are the changes from a high cover of branching *Acropora* prior to the bleaching to a high cover of table *Acropora* in 2008.

- Locaton SL1 on the inside of east hook is a mix of habitat conditions and community structures. Relative to the other locations, communities were moderately impacted by bleaching and subsequent cyclone disturbances. Depsite the reduction in coral cover associated with each disturbance, community structure has remained relatively stable throughout monitoring. Communities are located within an eddy system inside east hook and may receive larvae from several other sources (e.g. SL3, SL4, SL2), and have consistently high rates of coral recruitment that have facilitated their recovery. As with Location SL2, there has been a notable change in structure of *Acropora* corals from branching species prior to the bleaching to table species in 2008.

- Coral communities within the north-reef lagoon have not been surveyed consistently since the bleaching in 1998. Prior to bleaching, coral cover was highest (around 80%) in parts of the north-lagoon, as were the reductions in cover following the bleaching. Communities in the north-lagoon were dominated by staghorn corals and this fragile growth form is susceptable to both bleaching and cyclones. There is little evidence of recovery of coral communities in the north-lagoon, but only a subset of monitoring sites have been surveyed and recent observations of additional sites and depths (> 10 m) suggest that cover of branching corals may be greater than the 10% measured in 2008.

- Most data on changes in community structure has been collected from long-term monitoring sites at 9 m depth on the reef slopes. Additional sites in other habitats (< 9 m) are surveyed periodically, including the most recent survey in 2008. Comparable patterns of impact and recovery from disturbances were observed at all of these habitats up the reef slope and reef crest, returning to a similar pre-bleaching cover by 2008. The exception was the reef crest habitat in shallow-water (around 1m depth). Communities in the reef crest were exposed to extreme heating during the bleaching and wave energy during two cyclones, and their cover in 2008 was less than half that prior to the bleaching (≈ 20%). (Figure 4.2.4).

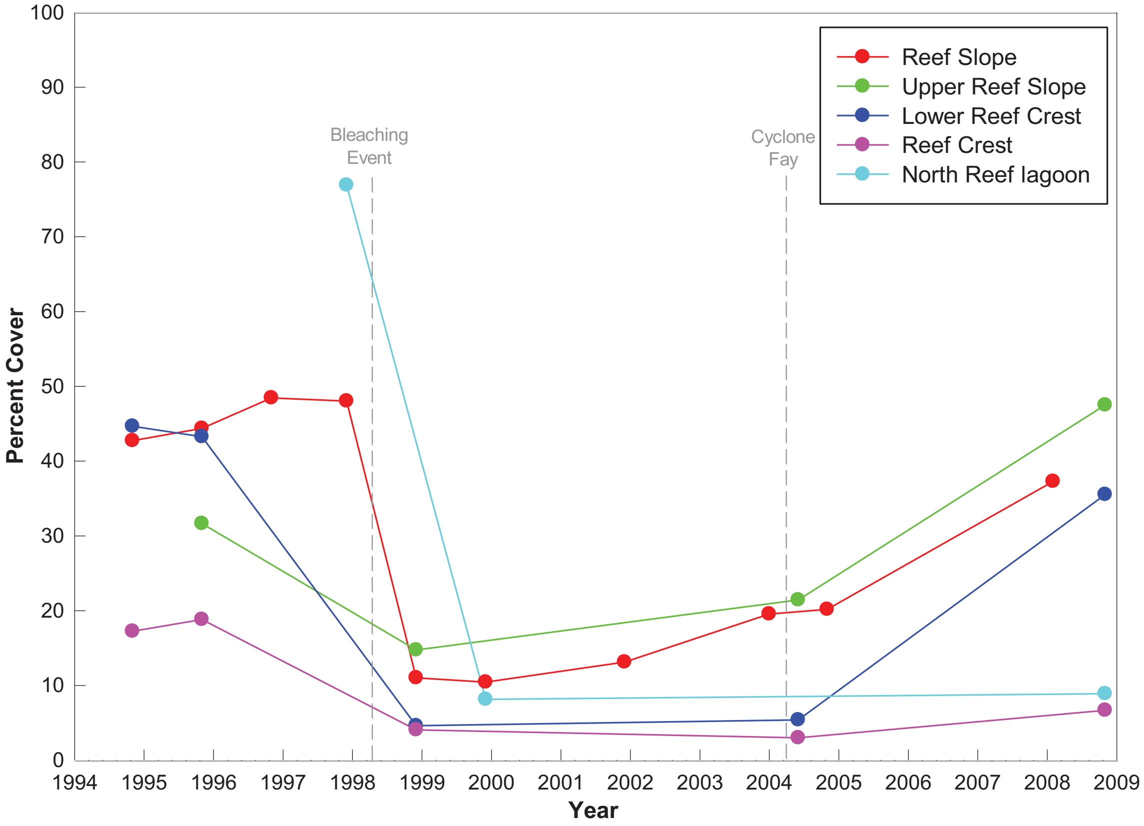


Figure 4.2.4 Percent cover of hard coral in the reef crest (1 m water depth), lower reef crest (3 m), upper reef slope (6 m), reef slope (9 m), and north-lagoon habitats at Scott Reef between 1994 and 2008. Pre-bleaching cover at the north-lagoon is derived from the mean cover of 20 sites ranging from 4 to 15 m depth, and only a subset of these sites in 2008.

Changes in reef fish communities at Scott Reef were spatially consistent, with the abrupt shift from pre-bleaching to post-bleaching assemblages being recorded at all of the monitoring locations. The structure of the fish communities at each location remained relatively constant over the period of monitoring, communities consistently grouping according to their proximity to the south-lagoon (SL1 - SL4) or outer-slope (SS1 – SS3). However, each of the lagoon communities (SL1 - SL4) also have their own unique structure. For example, the most sheltered location (SL2) has a characteristic fish community dominated by species typical of a lagoon habitat, such as the damselfish *Stegastes nigricans*, *Dascyllus aruanus* and *Neoglyphidodon nigroris*. In contrast, the fish community at location SL4, adjacent to the deep-channel, has greater abundance of the butterflyfish *Chaetodon melannotus* that feeds on the higher cover soft corals within this habitat. In contrast to the lagoon communities, those on the outer-slope at locations SS1 and SS2 have become more homogenised into a unique post-bleaching community structure, possibly reflecting the severe impact of the bleaching on the coral communities and their limited recovery due to subsequent impacts from cyclones.

5. CONNECTIVITY AND RESILIENCE OF SCOTT REEF COMMUNITIES

5.1 Reproduction and connectivity

Summary

Of primary interest to researchers, industry and managers, are the patterns of reproduction and connectivity of communities within and among coral reefs. The Scott Reef Research Project (SRRP) has integrated a range of complimentary data to infer these patterns at Scott Reef and its neighbouring reef systems. These data include:

- *The times and modes of reproduction of fish and particularly corals;*
- *The physical conditions and oceanography around the times of reproduction;*
- *The population genetics of coral and fish communities.*

The patterns of reproduction and connectivity provide important insights into the consequences of severe disturbances for the persistence of communities. In particular, whether recovery from severe disturbances will be aided by the supply of recruits from other locations on the same reef or other reefs. Communities that are not well connected do not receive a large supply of recruits from outside locations, or reefs, and their recovery will be slow because it is facilitated by the few remaining survivors; such as at Scott Reef following the mass-bleaching in 1998. The degree of connectivity also determines whether local impacts influence the persistence of communities at other locations, or reefs, potentially far away from the direct impacts of the disturbance. For example, if communities at a particular location, or reef, are largely sustained by the supply of recruits from those upstream, then their maintenance will be affected by severe disturbances upstream that reduce the production and supply of recruits.

A knowledge of reproduction and the connectivity among locations and reefs is therefore of primary importance to the management of coral reefs, but connectivity cannot be measured directly. The most accurate inferences about patterns of connectivity come from a range of complimentary studies of reproduction, larval ecology, oceanography and population genetics. The SRRP has integrated these data to make the following inferences about reproduction and connectivity among locations within Scott Reef and its neighbouring reef systems.

- *The majority of corals at Scott Reef spawn during autumn (March/April) each year, but a secondary spawning involving many corals from a subset (16%) of species also occurs in spring (October/November). However, every few years spawning during either season may occur over consecutive months, due to a 'split-spawning'. Other exceptions to the general pattern of mass-spawning also exist for some abundant corals. In particular, massive* Porites *corals apparently spawn between October and June, and many abundant brooding corals (*Isopora*,* Pocillopora*,* Seriatopora*) release larvae over a similar period. After adjusting for the relative abundance of the most common species at Scott Reef, roughly 40% of the community reproduces during one month in autumn (usually March), 16% during one month in spring (usually October), and 44% during other months of the year.*
- *Common species of reef fish at Scott Reef also reproduce throughout the year, with evidence of peaks in reproduction similar to the times of mass coral-spawning in spring and autumn.*
- *The mass-spawning of corals in autumn occurs at times of peak water temperatures, light winds and neap tides, all of which reduce larval dispersal. Most larvae probably settle within a week after dispersing less than approximately 10-20km. In contrast, most brooded larvae are released during a wider range of physical conditions, they are competent to settle when released, and probably disperse less than one kilometre from the parent.*

- *Many larvae of common reef fish species probably disperse for approximately one month among many locations across Scott Reef before settling, but some may disperse over larger distances for several months.*

- *There is currently no certain understanding of the flow of currents and patterns of connectivity between particular locations at Scott Reef, but a hypothetical model is proposed (Figure 5.1.17):*
    - *Current flow is strongest in the deep-channel between north- and south-reef, and slowest in the north-lagoon and toward the southern part of south-lagoon.*
    - *Many of the larvae produces by communities adjacent to the deep-channel are carried towards east hook, where they may be trapped in an eddy system. Therefore, rates of coral recruitment at Location SL4, on north-reef adjacent to the deep-channel, were consistently low.*
    - *Some larvae may leave the strong currents in the deep-channel and are caught in eddies on the inside of west hook. This eddy may also trap many of the larvae produced by communities around Sandy Islet and inside west hook, and Location SL3 inside west hook had intermediate rates of coral recruitment. Some larvae may also be carried towards the southern part of south-lagoon.*
    - *Slow current flow near the southern part of south-lagoon means most coral larvae are probably retained within the vicinity before settling. Location SL2 at the southern part of south-lagoon had intermediate rates of coral recruitment.*
    - *Some larvae produced within south-lagoon may be carried slowly towards east hook where they are caught in an eddy system. The supply of larvae from the south-lagoon and often from the deep-channel, mean Location SL1 inside east hook had consistently high rates of coral recruitment.*
    - *During years when coral recruitment was not highest at Location SL1, recruitment was highest at Location SS2, on the outside of north-reef. This variation in recruitment suggests that when larvae in the deep-channel are not trapped inside east hook, they are carried along the outside of north-reef before settling.*
    - *Larvae produced on the outer-slope at east hook may also be carried to north-reef, as rates of coral recruitment at Location SS1 outside east hook were consistently low.*
    - *This hypothetical pattern of connectivity applies for larvae produced following mass-spawning in March. Larvae produced at different times of the year (e.g. spring), or by brooding corals over several months, will have different patterns of dispersal. For the brooded larvae, much smaller dispersal distances mean limited connectivity among locations.*

- *The time taken for larvae to disperse between the atoll systems off northwest Australia is roughly one month between Ashmore and Scott Reef, and roughly two months between Scott and Rowley Shoals, with currents switching from a predominantly southerly flow to a northerly flow in the middle of the year. There is little evidence of connectivity between Scott Reef and the Rowley Shoals for populations of fish, and particularly corals. Routine exchange of coral larvae between Scott and Ashmore Reefs may also be unlikely, but the probability of exchange is greater for the fish larvae whose planktonic periods are around one month. Ashmore Reef is Scott Reef's closest neighbour, and impacts at either atoll system have the potential to impact communities at the other. Genetic analyses of coral and fish communities at Ashmore Reef are required.*

Coral Reproduction

Modes of reproduction

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 over a few nights each year. Fertilisation of the eggs and subsequent larval development occur over a few days within the water column, often resulting in their larvae being carried distances of tens of kilometres. Many of the most abundant species at Scott Reef are spawning corals, including most of those in the families *Acroporidae* and Faviidae (Figure 5.1.1).

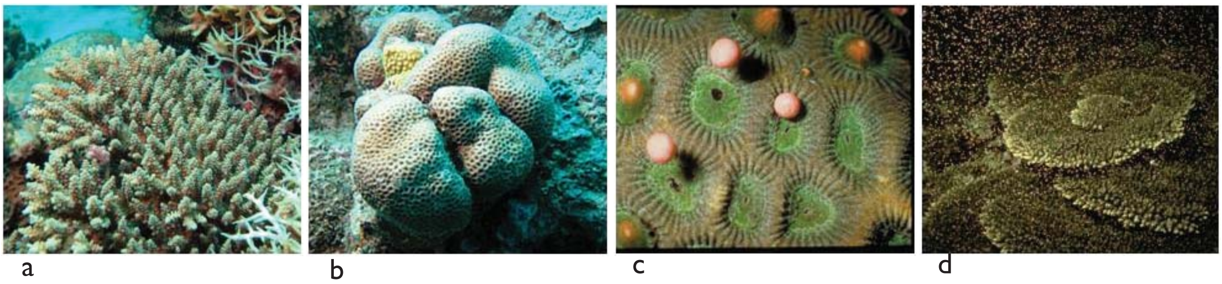


Figure 5.1.1 Common spawning corals at Scott Reef in the families *Acroporidae and Faviidae. a) Acropora tenuis; b) Goniastrea edwardsi; c)* Faviid and d) *Acropora* colonies spawning gametes**.**

Although most corals on Indo-Pacific reefs mass spawn, some abundant and functionally important species are brooding corals. These brooding corals release sperm that fertilise the eggs while still inside the coral polyp (Harrison and Wallace 1990; Richmond and Hunter 1990). Brooding corals tend to have multiple cycles of gametogenesis over many months, each culminating in the release of brooded larvae that are competent to settle close to the parent colony *(e.g. Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990; Tanner 1996; Zakai et al. 2006)*. As a result, brooding corals (e.g. *Isopora*, *Pocillopora*, *Seriatopora*) are often densely aggregated, and *Isopora brueggemanni* in particular forms large dense fields at Scott Reef (Figure 5.1.2).

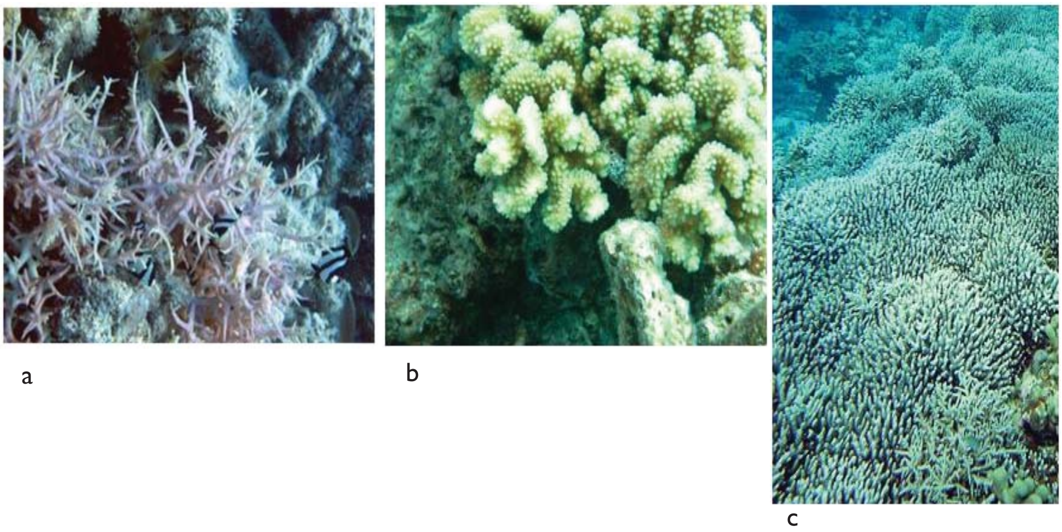


Figure 5.1.2 Common brooding corals at Scott Reef. a) *Seriatopora hystrix*, b) *Pocillopora verrucosa* and c) dense fields of *Isopora brueggemanni.*

Times of reproduction

Mass spawning by corals 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 northwest Australian reefs (Harrison and Wallace 1990). On north-west Australian reefs, mass 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. 2009a). Research in the 1990s also discovered a second spawning event on the most northern reefs (Heyward pers comm.), 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. 2009a). Of 68 species sampled from Scott Reef, most colonies of most species (59%) spawn during autumn, with a smaller percentage (16%) of species spawning during spring (massive *Porites* spp. considered 1 species only). Seventeen (25%) species participate in both spawning events, but most evidence suggests that individual colonies spawn only once at the same time each year. Although most species and colonies spawn during autumn, at least two abundant species spawn exclusively during spring (Figure 5.1.3). Additionally, the massive *Porites* colonies (Figure 5.1.3(c)) appear to spawn predominantly (86% of sampled colonies) from November to May and these are functionally very important to communities at Scott Reef. There is also consistently a small number of species and colonies that spawn during months either side of the mass-spawning in autumn and spring.

Figure 5.1.3 Common species at Scott Reef that exclusively spawn at times other than the main event in autumn; (a) *Acropora millepora*, (b) *A. cytherea*, (c) massive *Porites*.

Further variation in the times of spawning at Scott Reef occurs every few years, due to a split in spawning over two consecutive months. The month of spawning is determined by the timing of the full moon, usually occurring after the full moon in October (spring) or March (autumn); the main autumn spawning can often occur in April. The time of spawning is triggered by the time of the full moons in Autumn and Spring. However, during years in which the full moons fall early in Spring or Autumn months, gametes in all colonies may not be fully mature following the full moons in March and October, respecitively. During these years (e.g. 2010) a split-spawning occurs and a similar proportion of corals spawn in both March and April during autumn, and/or during October and November in spring.

Compared with the spawning corals, less is known about the patterns of reproduction in brooding corals because their cycles of gametogenesis are less predictable and more complex. In general, gametogenesis and larval release by brooding corals occur over several months, and a similar pattern is emerging at Scott Reef. Some brooders at Scott Reef release larvae during most months of the year, but the main periods of larval release are probably from November to July; the drop in larval output from February to April is most likely an artefeact of insufficient sampling (Figure 5.1.4).

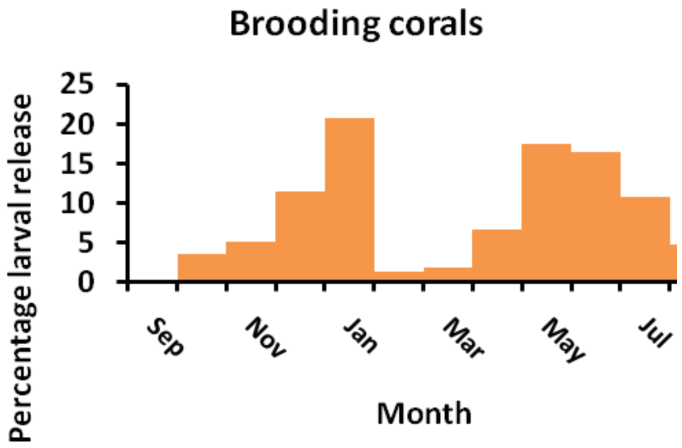


Figure 5.1.4 Months of larval release by colonies of brooding corals at Scott Reef. Reproductive patterns are summarised for all brooding corals sampled during 2008, 2009, 2010

Significance of reproductive periods and management implications

The percentage reproductive output during different months of the year at Scott Reef depends on both the proportion of coral species reproducing that month and their relative cover within the community. For most spawning corals, the percentage of reproductive output is roughly 80% in autumn (March/April) and 20% in spring (October/November), with very few corals spawning during other months (Figure 5.1.5(a)); the main exception is for the massive *Porites* that spawn over several months. For the brooding corals, the percentage reproductive output is roughly 55% from November to May, and 45% at other times of the year. Considering the entire community at Scott Reef (spawners and brooders) and the months of spawning, roughly 40% of reproductive output occurs in March, 16% in October and 44% during other months (mostly April or November) (Figure 5.1.5(c)).

The times of reproduction for spawning and brooding corals at Scott Reef appear not to vary among locations, but the percentage of reproductive output during any given month does vary among locations. This variability is determined by local differences in community structure, including the relative abundance of broadcast spawners and brooders, and the relative abundance of species and colonies within these groups. For example, communities dominated by brooding corals have a lower percentage of reproductive output during March, and a higher output from November to July. Reproductive output also varies among years, particularly during years of split-spawning. During split-spawning years, a similar reproductive output occurs over consecutive months during the autumn and/or spring spawning periods. Additionally, important groups of corals reproduce exclusively when the output by the rest of the coral community is low. At Scott Reef, community output is relatively low during summer months, but output from massive *Porites* corals is high at this time, and at least two common species spawn exclusively in spring. Managing development operations around the key periods of coral reproduction and settlement requires consideration of peak output times involving the majority of species, and times that are critical for other functionally important corals.

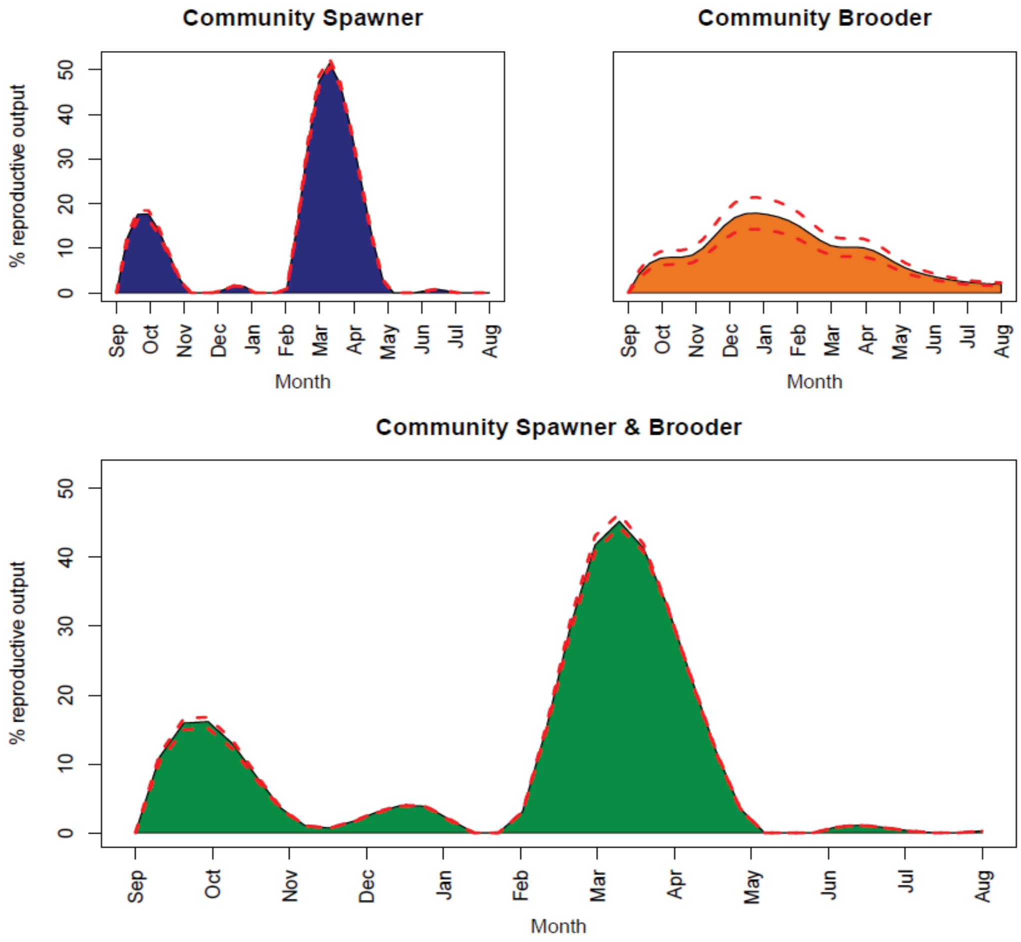


Figure 5.1.5 Percentage of reproductive output by coral communities at Scott Reef (± 95% C.I.) Reproductive patterns are summaried for all colonies within each species group sampled during 2008, 2009 and 2010. Reproductive output is adjusted for proportion of corals reproducing and their relative cover within communities for a) spawning corals, b) brooding corals, c) spawning and brooding corals combined); patterns will vary among different locations at Scott Reef according to their community structure.

Fish reproduction

Mode and timing of reproduction

Reproduction in reef fishes typically involves the production of either demersal or pelagic eggs and the subsequent hatching into a planktonic larval phase that can lasts from 9 to over 100 days (Leis 1991). In many of the smaller conspicuous families of reef fishes such as the damselfishes, females produce demersal eggs in nests that are usually built and guarded by males before the larvae hatch into the pelagic environment (Meekan et al. 1993; Robertson et al. 1999). For larger reef fishes, however, reproductively mature adults often take part in paired or group spawning in which males fertilise buoyant planktonic eggs released by females (Domeier and Colin 1997). Within the surgeonfish family (Acanthuridae), this can involve spectacular mass group spawnings in which large numbers of fish migrate to an area of the reef at specific times and move amongst the clouds of gametes released by both males and females (Robertson 1983; Domeier and Colin 1997) (Figure 5.1.6). Although the subsequent pelagic larval stage generally represents when larvae can disperse to distant reefs, there is mounting evidence of active behaviour in which they are able to sustain swimming speeds greater than the surrounding currents and use their senses in order to orientate themselves to reefs (Leis 2006). This implies some degree of retention of larvae to natal reefs is likely.

Figure 5.1.6 Spawning aggregations of parrotfish (foreground) and surgeonfish (background) gather in the late afternoon on the top of the high tide. Pairs split off from the group and fertilization occurs in a brief intense frenzy near the surface.

While some species of tropical coral reef fish spawn throughout the year, the timing of spawning and reproduction is often coupled with seasonal patterns of water temperature or productivity and with monthly changes in moon phase and tidal range, thus invariably coinciding with the most favourable conditions for larval survival and growth (Johannes 1978; Cushing 1987; Doherty and Williams 1988; Robertson et al. 1999). The degree to which patterns of spawning and recruitment are seasonal, diminishes towards the equator as seasonal changes in environmental conditions such as water temperature become less. On the Great Barrier Reef, recruitment of most fish species occurs during summer when water temperatures are at their peak (Russell et al. 1977; Talbot et al. 1978; Williams and Sale 1981; Milicich et al. 1992; Milicich and Doherty 1994). In contrast, most species of reef fish in the Caribbean spawn during months when water temperatures are minimal (Munro et al. 1973).

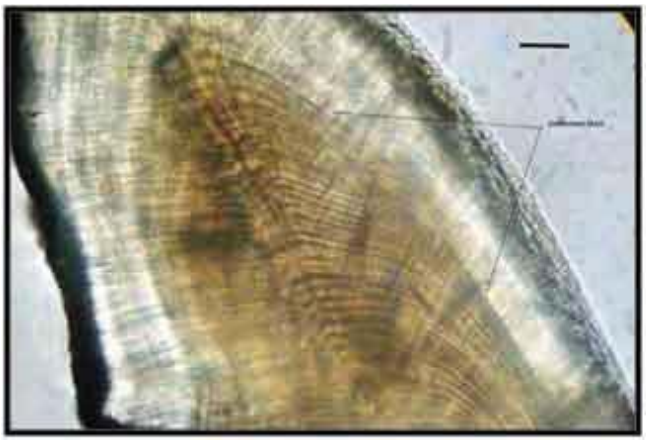


Figure 5.1.7 Photomicrograph of sagittal otolith (earbone used to age fish) of newly settled bicolour damselfish *Chromis margaritifer* showing pre-settlement increments (daily growth rings) and settlement mark at 37 days (59 day old fish). Scale bar = 20 µm

The earbones of fish, known as otoliths, contain a vast amount of information on the life history of individual fish. Growth rings within these otoliths are used to age fish in much the same way as the reading of growth rings in trees and important early life history events such as the date of hatching, length of larval life and date of settlement back to the reef can be determined (Figure 5.1.7). Previously unreported back calculations of these dates for *Chromis margaritifer* at Scott Reef show that settlement occurs throughout the year, but peaks do occur in October and July (Figure 5.1.8). The high occurrence of spawning female damselfish (*Chromis margaritifer*) at Scott Reef in April 2008 (Figure 5.1.9), and of *Pomacentrus lepidogenys* in October 2008, provides evidence that spawning occurs during autumn and spring. Fish recruitment surveys carried out between 1995 and 1997 also indicate that this species recruits throughout the year, but the greatest numbers occur in autumn and spring when water temperatures are rising and monsoonal storm fronts and associated strong wind and waves are least (Figure 5.1.13; Gilmour et al 2009a).

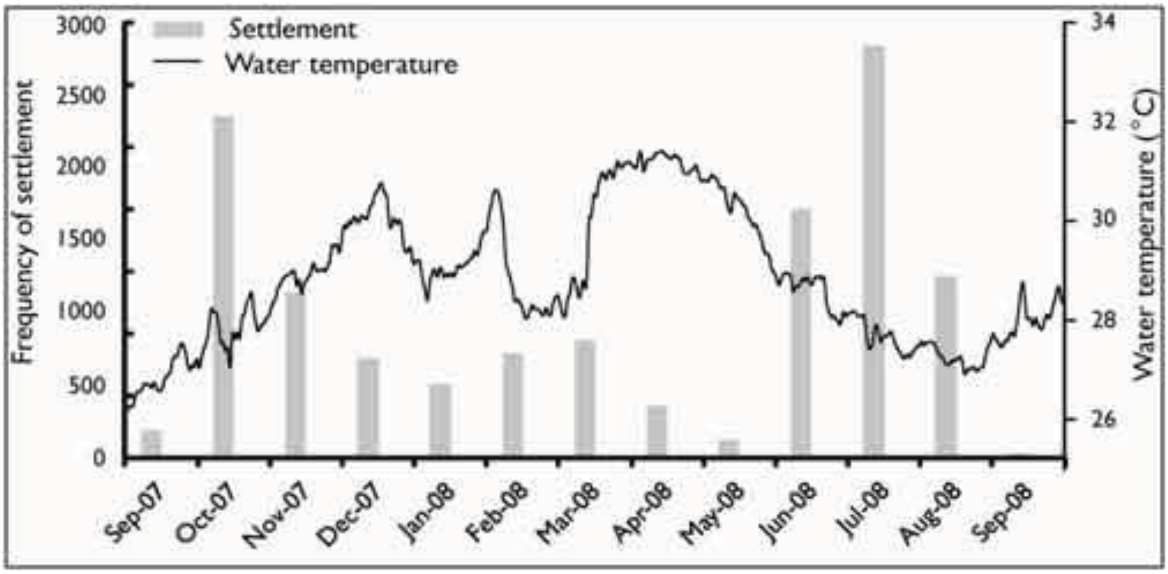


Figure 5.1.8 Frequency of settlement for *Chromis margaritifer* at Scott Reef as estimated by the back calculation of settlement dates from otoliths collected in April and October 2008. An instantaneous mortality rate of 0.1 d^{-1} has been applied. Water temperature is recorded at 6 to 9m depth.

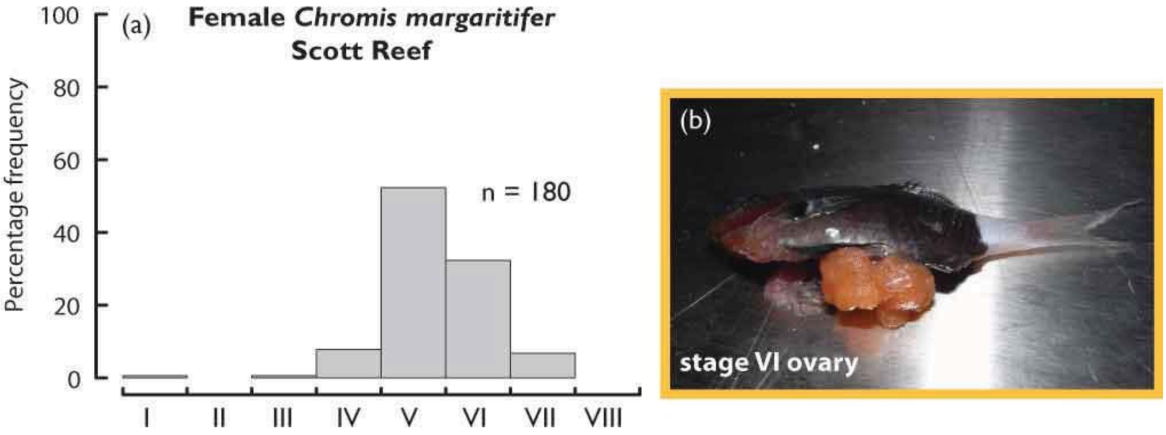


Figure 5.1.9 (a) Percentage frequencies of occurrence of sequential stages in female ovary development in *Chromis margaritifer* caught at Scott Reef in April 2008 and (b) photo of a ripe spawning stage VI ovary in a female *Chromis margaritifer*. n = sample size.

Larval dispersal

Larval dispersal in corals

The distances of larval dispersal and the degree of connectivity among locations depend on larval competency and behaviour, coupled with the strength and direction of winds and currents during the dispersal period. Following mass-spawning, coral larvae develop in the water column before they are competent to settle onto the reef and metamorphose into a coral polyp (Figure 5.1.10). The minimum developmental period is usually between 3 to 6 days, but the actual duration is influenced by a range of factors, including water temperature. In the warm waters at Scott Reef, larvae are usually competent to settle within a few days of spawning (Figure 5.1.11) (Smith et al. 2003; Gilmour et al. 2009a). Larvae that are carried off the reef will perish unless they encounter another suitable patch of reef. In this instance, larvae rely on their energy reserves to survive during their upper competency periods of several weeks (after which they are unable to settle and metamorphose).

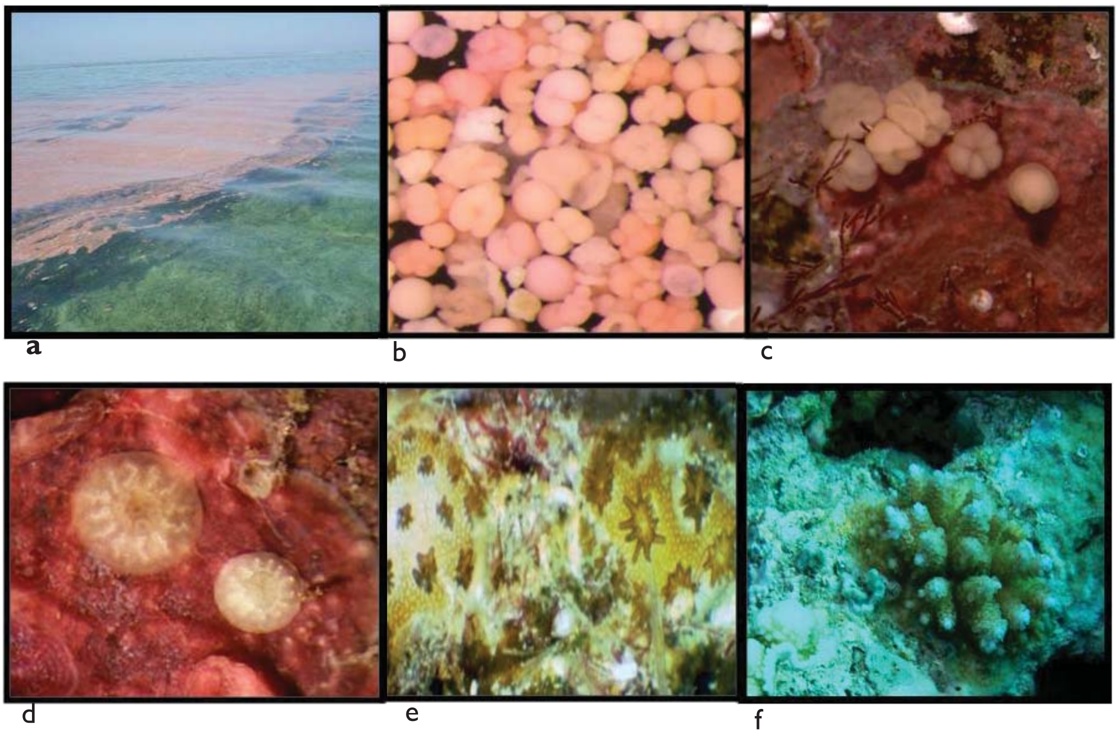


Figure 5.1.10 Dispersal, settlement and metamorphosis in spawning corals. a) Slicks of coral spawn are produced following spawning, after which eggs are fertilized, b) embryos and larvae disperse through the water column for days to weeks, then c) settling onto the substrata, d) metamorphosing into a coral polyp, and dividing repeated over e) months and f) years to produce the coral colony.

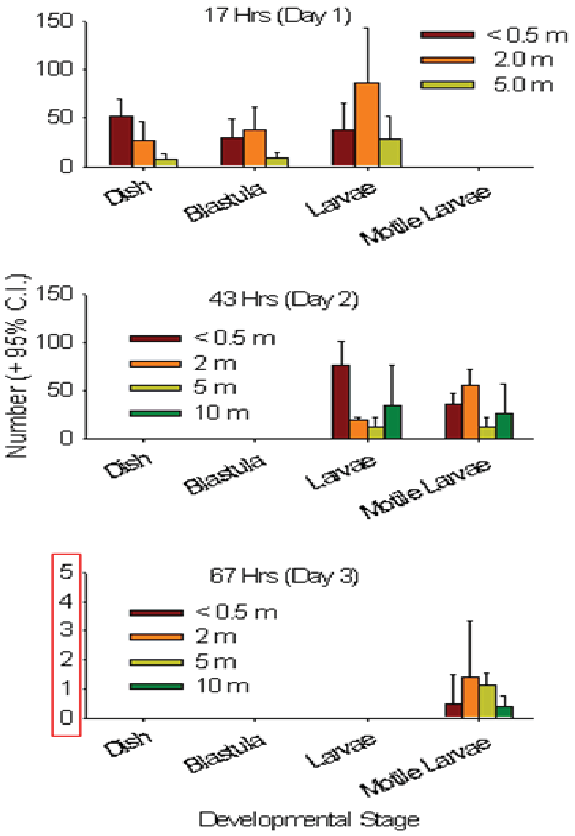


Figure 5.1.11 Rates of development of coral embryos and larvae at Scott Reef following mass-spawning. Plankton tows through the water column near Sandy Islet indicated that two days after spawning embryogenesis was complete and larvae had developed. Three days after spawning there was a dramatic reduction in the number of larvae collected in replicate tows and all larvae were motile and actively exploring the substrata (in experimental treatments), suggesting that dispersal and larval settlement occurred within approximately four days of spawning (Smith et al. 2003).

In contrast to the larvae produced by spawning corals, brooded larvae are well developed when released from the colony and competent to settle, which characteristically occurs within hours of release. However, because brooded larvae are large and better developed, they are able to survive in the water column for longer than the larvae of spawning corals, with upper competency periods of a few months (Richmond 1988; Ayre and Hughes 2000; Harii et al. 2002). At Scott Reef, most brooded larvae probably settle within hours of release, but a small proportion may disperse for several weeks before settling.

The tendency for brooding corals to release larvae that are competent to settle over several months means they can play an important role in structuring local communities. For example, a large number of brooded larvae can quickly occupy available space following a disturbance and become spatially dominant (Figure 5.1.12). For fast growing brooding corals with a fragile growth form, this is a key life history strategy that allows them to persist in the face of disturbances to which they are particularly susceptible, 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). This life history strategy can be manifest as dramatic changes in coral abundance and cover through time, which at Scott Reef is exemplified by the brooding coral *I. brueggemanni* over the course of monitoring (Figure 5.1.12) (Smith et al. 2006b; Smith et al. 2008).

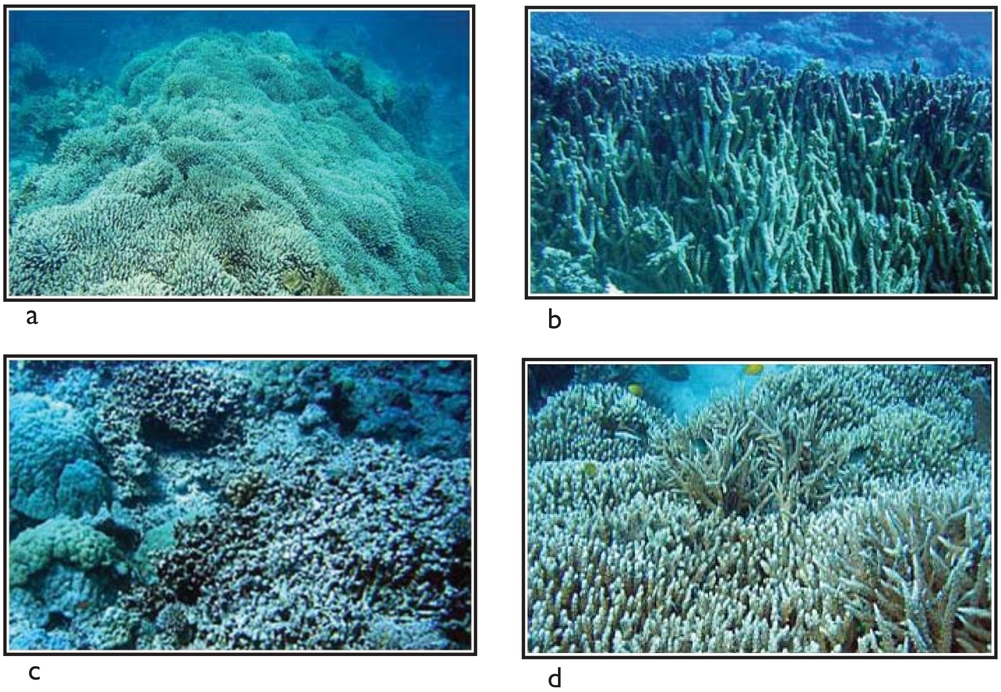


Figure 5.1.12 Changes in the cover of the brooding coral *Isopora brueggemanni* at Scott Reef. a) Large stands of *I. brueggemanni* prior to bleaching in 1998. b) & c) Mass-bleaching killed most *I. brueggemanni* colonies across Scott Reef, and there has been little subsequent recovery at the worst affected locations given the limited dispersal of brooded larvae. d) At locations least affected by the bleaching, the local production of larvae means they are now returning to high cover; recovery has been slowed by exposure to cyclone disturbances.

Buoyant slicks of coral spawn on the sea surface (Figure 5.1.10) are influenced strongly by both winds and currents, but within a day of spawning the resulting embryos and larvae (Figure 5.1.10) begin to disperse through the water column and are less influenced by winds (Figure 5.1.11). Coral spawning characteristically occurs during neap tides and calm conditions, which increases the likelihood of larvae settling on their natal reef and not being lost in the open ocean. At Scott Reef, mass-spawning during both spring and autumn occurs during neap tides, when wind speeds are low and water temperatures are high, either side of a period of stronger winds and waves during summer months (Figure5.1.13).

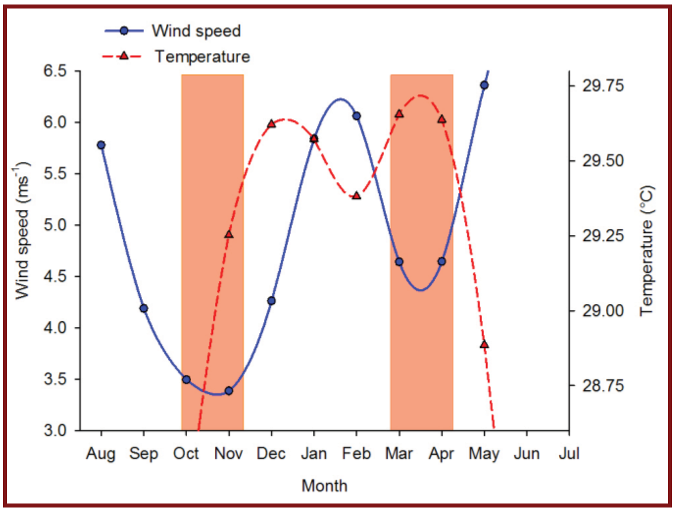


Figure 5.1.13 Mean monthly seawater temperatures (°C) and wind speeds (ms^{-1}) at Scott Reef (Gilmour et al. 2009a). Shaded bars represent the times of coral spawning.

Complementary oceanographic, ecological and genetic data indicate the nature of larval dispersal at Scott Reef. In calm conditions, surface drifters deployed around Sandy Islet in 2003 all travelled less than 10 km from their point of release within approximately 6 days of mass-spawning (Figure 5.1.14; (Smith et al. 2003)); plankton tows and settlement experiments indicated that most larvae had settled within approximately 5 days of spawning (Figure 5.1.11). Dispersal distances may be larger for larvae produced from other locations and other years, but genetic analyses of the coral *Acropora tenuis* (Figure 5.1.15) support inferences that the routine distances of dispersal for spawning corals at Scott Reef are restricted to approximately 10 to 20km (Figure 5.1.15; (Gilmour et al. 2008; Underwood et al. 2009).

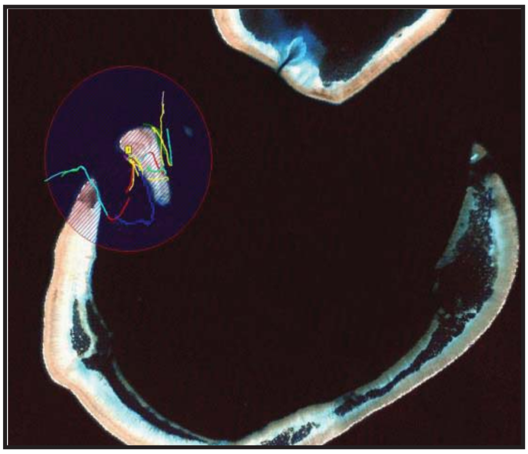


Figure 5.1.14 Tracks of surface drifters released for up to one week around the time of spawning in autumn 2003 (Steinberg et al. 2003). Circle represents a dispersal distance of 10km.

Because brooding corals release larvae over several months during the year, they are exposed to a greater range of oceanographic conditions than are the larvae of spawning corals. However, brooded larvae are not positively buoyant and are competent to settle when released, so there is less opportunity for winds and currents to influence their dispersal. Genetic analyses suggest that routine distances of dispersal for the brooding coral *S. hystrix* (Figure 5.1.15) at Scott Reef is less than a kilometre, but that rarely larvae can travel over distances of tens of kilometres before recruiting (Figure 5.1.15) (Gilmour et al. 2008; Underwood et al. 2009).

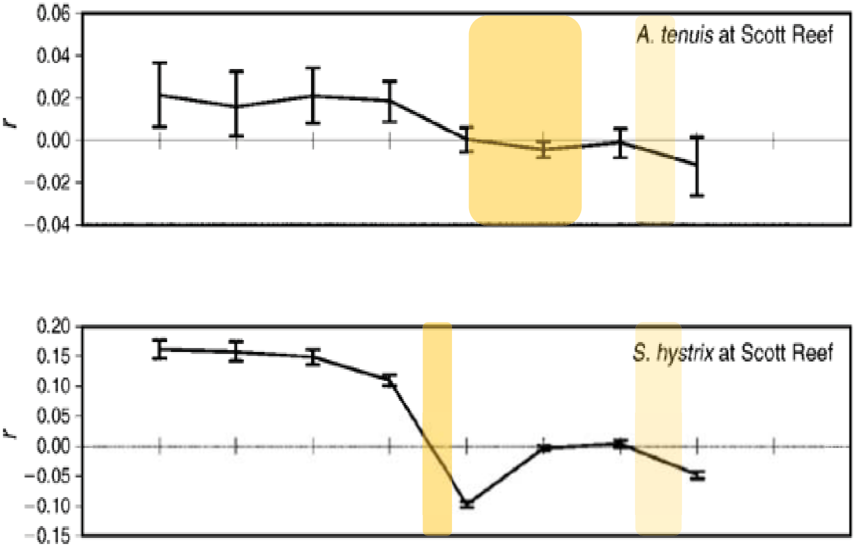


Figure 5.1.15 Inferred distances of larval dispersal in the spawning coral *Acropora tenuis* and the brooding coral *Seriatopora hystrix* based on genetic analyses (Gilmour et al. 2008; Underwood et al. 2009). The distance at which the r-value crosses 0.00 indicates the distance of routine larval dispersal (indicated by the strength of shaded bars); at Scott Reef around 10-20km for the spawning coral and a few kilometres for the brooding coral (but with rare long-distance dispersal).

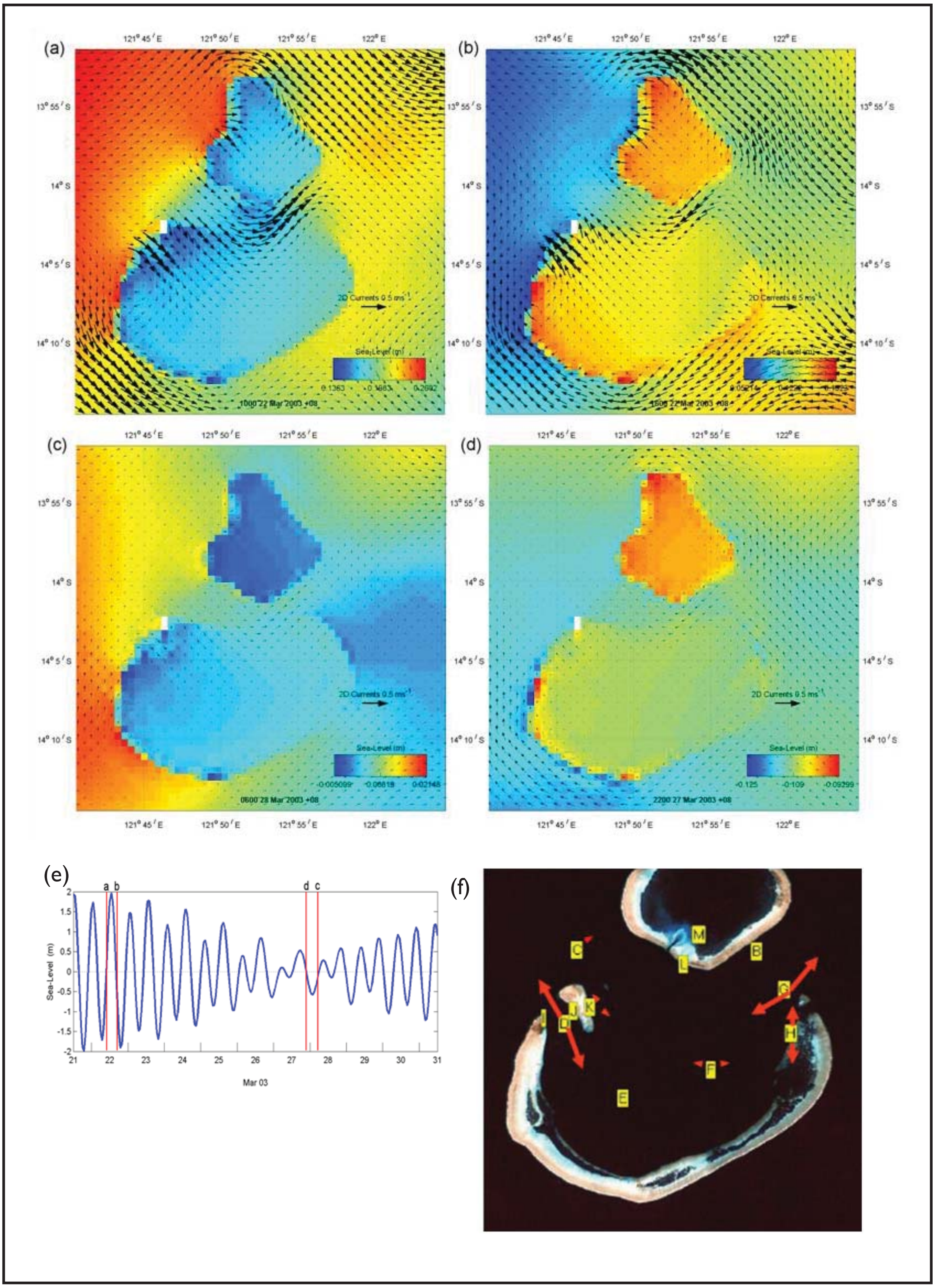


Figure 5.1.16 Current flows at Scott Reef around the times of mass-spawning in autumn 2003. a – d) Surface circulation (shown as vectors) and sea level (shown with colour) at times of maximum flood (left) and ebb (right) tides for both spring (top) and neap (southern part) tides. e) Tidal stage of each synoptic plot is indicated on the time series of sea level (Steinberg et al. 2006). f) Relative magnitude and direction of observed currents during April and May (Bird et al. 2004).

Larval dispersal in fish

While reef fish can produce either demersal or brooded eggs, the general rule is for pelagic eggs to be fertilised externally. Irrespective of the type of eggs produced, larvae hatch shortly afterwards and begin a pelagic phase that can vary in length from 9 to over 100 days. The duration of this planktonic period varies among species and depends on environmental conditions, such as prevailing ocean and tidal currents and wind-induced water flow. The swimming and sensory capabilities of many late stage fish larvae also enable them to travel faster than some prevailing currents and navigate towards reefs. For fish larvae to survive and recruit successfully into a population (distant or near) they must first survive the mortality events that occur between the pelagic larval period and post-settlement stage, and a short period of high predation within 48 h of settling. At Scott Reef and the Rowley Shoals, the mean lengths of the pelagic larval phase for a damselfish that lays demersal eggs, and two mouth brooding cardinalfish, were between 31 to 35 days, with ranges of 26 to 43 days. These pelagic larval durations are longer than for other species within these families, particularly for damselfish species associated with anemones (10 to 15 days), similar in length to many butterflyfish and groupers, but shorter than the 60 days typical of many surgeonfish and wrasse species that are also numerous in these systems.

Larval dispersal and connectivity among locations at Scott Reef

There is currently not a definitive understanding of the movement of currents and the connectivity among communities at Scott Reef following mass-spawning. However, a hypothetical pattern of larval dispersal and connectivity within Scott Reef can be proposed from existing data. These data are primarily limited to a few shallow-water locations at south Reef, but include current data, oceanographic models, coral recruitment and population genetics. The current data and oceanographic models are based on only one year's sampling at the time of spawning in 2003, and several years' data are required to determine whether they are representative. The patterns of coral recruitment are based on ten years' data and some variation in patterns among locations is clear. The population genetics reflect patterns of recruitment over many generations. The proposed pattern of dispersal is for generalised conditions following spawning in autumn during neap tides, and patterns will vary under different conditions and times of the year. This hypothetical pattern of dispersal attempts to generalise sometimes contradictory data.

The dispersal of larvae following spawning is mostly under the influence of neap tides, but the longer larvae remain in the water column the more dispersal distances will be influenced by the stronger currents associated with spring tides. At the south-lagoon, flow rates are fastest near the channel between north and south reef, and the current speeds reduce dramatically further into the lagoon (Figure 5.1.16).

Many of the larvae produced from communities within the lagoon near west hook (near Location SL3; Figure 5.1.17), are likely to remain in the vicinity through their minimum competency period, possibly becoming entrapped in a weak eddy system (Figure 5.1.16 & 5.1.17). Some larvae produced by communities closer to the tip of west hook may be carried to the outer reef or towards north reef, while some larvae produced on the south western side of north reef (near Location SL4; Figure 5.1.17) may be carried towards west hook (Figure 5.1.16 & 5.1.17). Coral communities at Location SL3 had intermediate but variable rates of coral recruitment (Figure 5.1.18). Genetic analyses of coral and fish indicate similarities between populations at Locations SL3, SL4 and SL5 on the western side of Scott Reef, but communities at Location SL4 were also similar to those at SL1 (Figure 5.1.19).

Most of the larvae produced by the communities near Location SL4 are probably carried towards east hook (near Location SL1; Figure 5.1.17) on the strong currents in the deep-channel (Figure 5.1.16), and rates of coral recruitment at SL4 were consistently low (Figure 5.1.18).

Larvae produced by communities at the southern part of south-lagoon (near Locations SL2, SL7; Figure 5.1.17), where current speeds are slowest (Figure 5.1.16), are also likely to remain within the vicinity through their minimum competency period. Communities at Location SL2 had intermediate rates of coral recruitment (Figure 5.1.18), with most recruits probably produced locally. Larvae that do not settle locally, and are produced by communities near the central or southern part of south-lagoon or within the deep lagoon (Figure 5.1.17), are probably carried slowly towards east hook. Genetic analyses of coral and fish indicated similarities between locations SL2, SL7 and SL1 (Figure 5.1.19).

Larvae travelling on the currents in the deep-channel, and from some communities in south-lagoon, are entrained in an eddy system inside east hook (near Location SL1; Figure 5.1.16 & 5.1.17). Genetic analyses of coral and fish indicate that populations at Location SL1 have affinities not only with those at SL2, but with those at SL4 and SL3 (Figure 5.1.19). Communities at SL1 consistently have among the highest rates of coral recruitment, often far higher than at other locations (Figure 5.1.18), reflecting the supply and entrapment of larvae from several locations (Figure 5.1.16 & 5.1.17).

During some years there were low to moderate rates of coral recruitment at SL1, but high recruitment at Location SS2 on eastern slope of north Scott (Figure 5.1.17 & 5.1.18). Rates of coral recruitment were consistently highest at either locations SL1 or SS2, suggesting that when larvae travelling on the currents in the deep lagoon are not retained near east hook, they continue along the outer edge of north reef to settle near Location SS2 (Figure 5.1.17). However, the larvae produced within the south-lagoon (near Location SL2) or at west hook (near SL1) are probably trapped in the eddy system at east hook and do not travel towards Location SS2 at north reef (Figure 5.1.18), given little similarity in the genetic structure of their coral and fish populations (Figure 5.1.19). Coral and fish populations at Location SS2 have a weak affinity with those at Locations SL3 and SL4, but a high degree of similarity with populations at Location SS1on the outer-slope at east hook. (Figure 5.1.17 & 5.1.19).

Rates of coral recruitment at Location SS1 were consistently low (Figure 5.1.18), and periodically very high at Location SS2, suggesting a northern drift of larvae from the outer-slope at south reef to north reef. No settlement plate data was collected at Seringapatam (SS3) however patterns of coral recruitment at Scott Reef, and genetic similarities (Figure 5.1.18 & 5.1.19) between populations at Scott Reef and Seringapatam Reef (Location SS3) suggest a possible northern drift of larvae, particularly fish larvae, between the three reefs; however, the same genetic patterns could be produced by a southern drift of larvae.

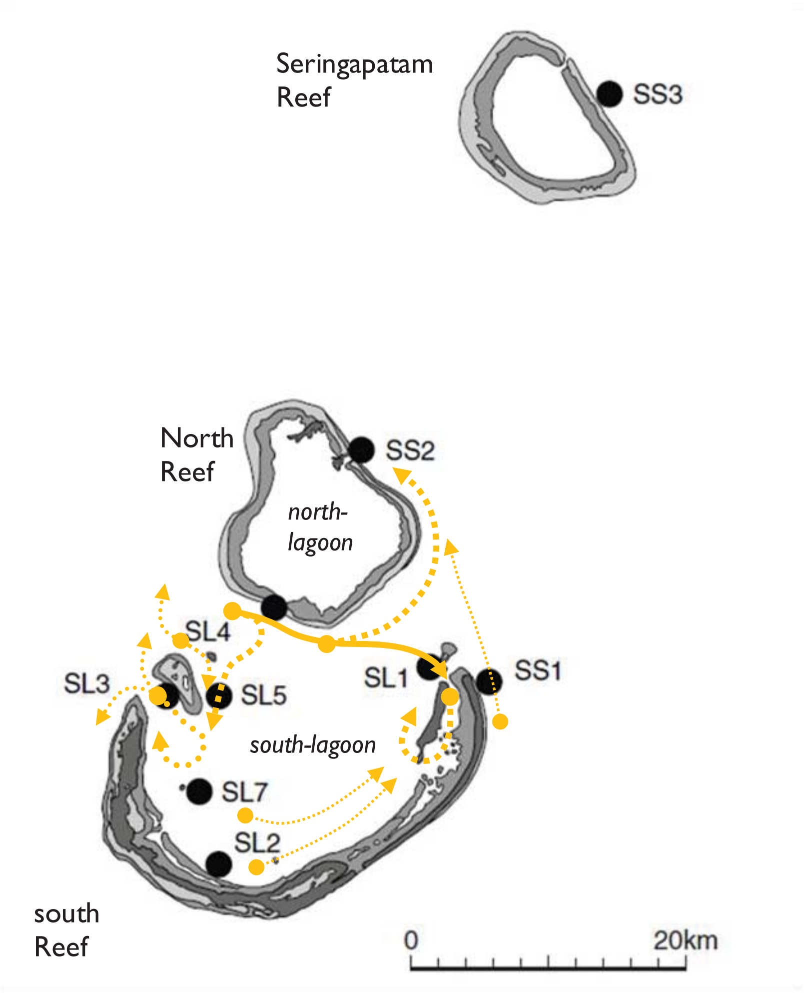
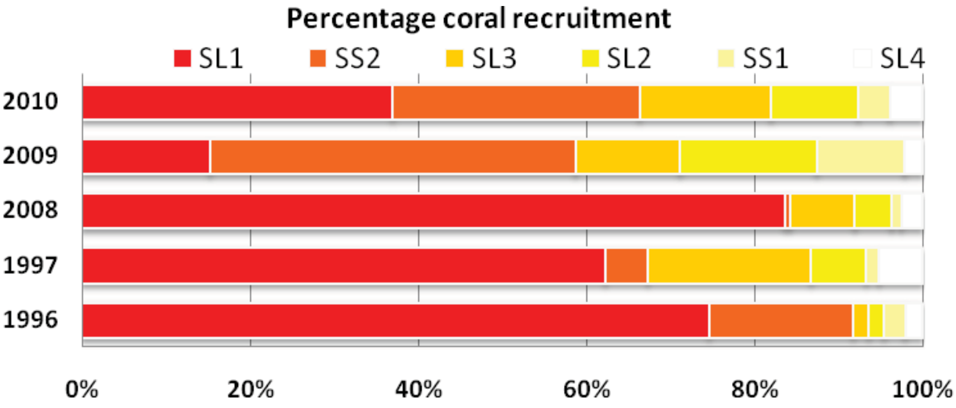


Figure 5.1.17 Study sites at Scott Reef and patterns of connectivity. Locations at which biological, genetic and/or oceanographic data were collected and the hypothetical flow of currents and patterns of connectivity among coral communities at these locations. The weight of the arrow reflects the strength of flow and/or connectivity.

a)



b)

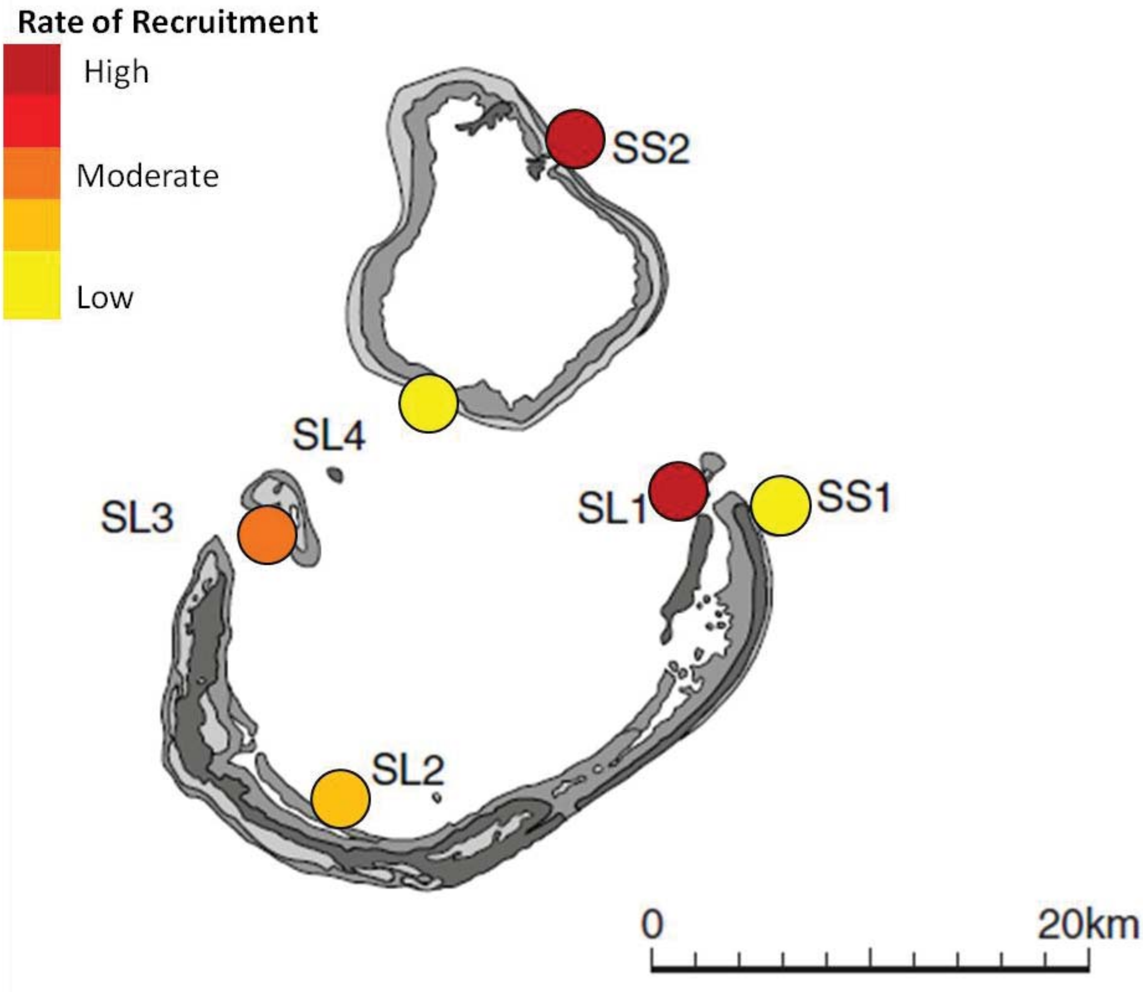
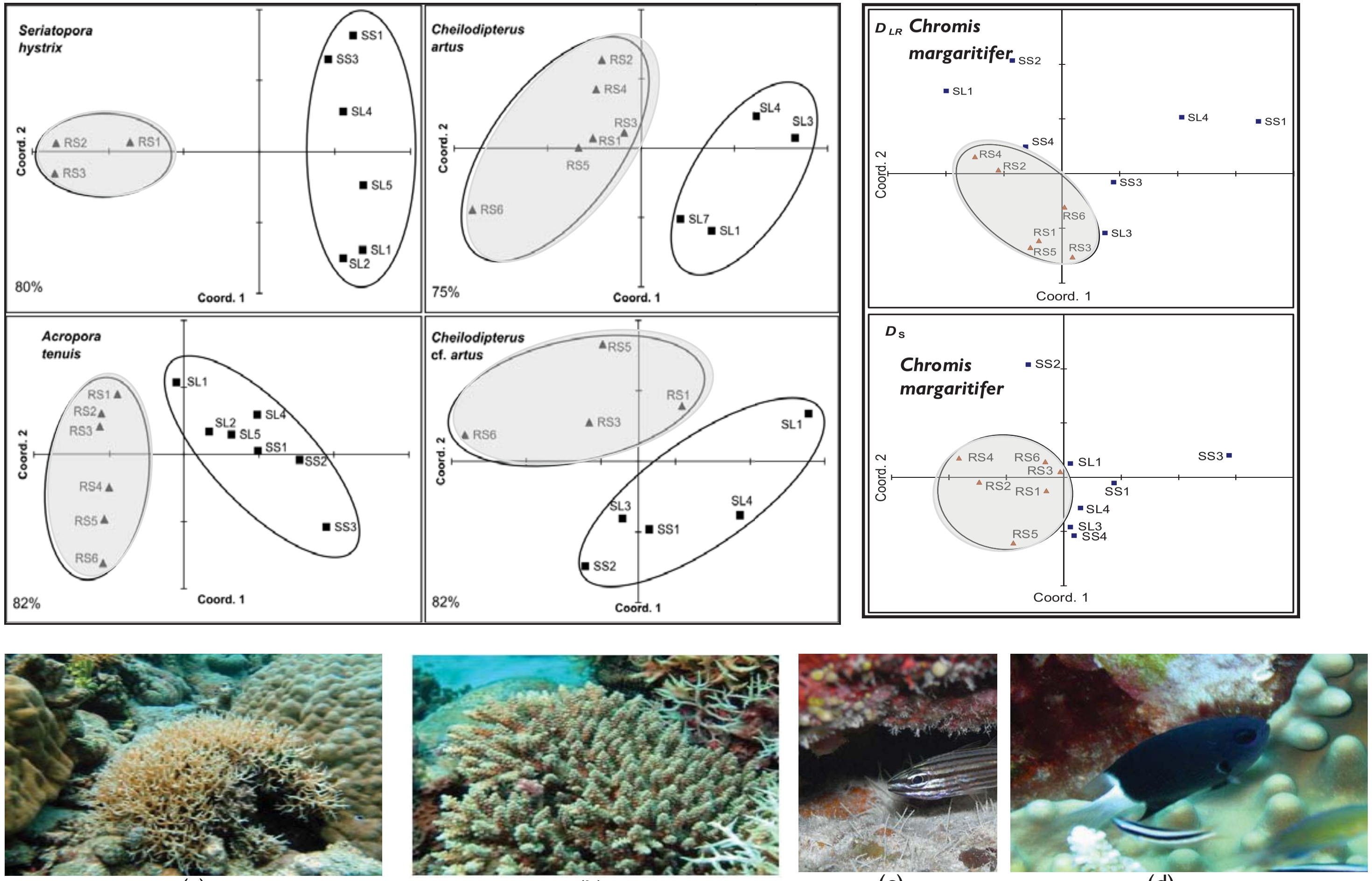


Figure 5.1.18 Relative rates of coral recruitment at locations across Scott Reef over 15 years of monitoring at Locations SL1, SL2, SL3, SL4, SS1 and SS2 (see Figure 5.1.17). No recruitment data was collected at Seringapatam (SS3).Years in which coral recruitment was particularly low, following the bleaching, are not included. a) Consistent patterns of variation among locations are evident, with Locations SL1 and SS2 having consistently the highest recruitment, and SS1 and SL4 consistently the lowest. b) Hypothetical grouping of communities at study locations based on their rates of coral recruitment.



(a) (b) (c) (d)

Figure 5.1.19 Similarity among locations at Scott Reef (Sx) and Rowley Shoals (Rx, grey ellipse) based on population genetics of the a) brooding coral *Seriatopora hystrix*, b) spawning coral *A. tenuis*, reef fish c) *Cheilodipterus artus*, *Cheilodipterus* cf. *artus* and d) *Chromis margaritifer*. Analyses are Principal Coordinates Analysis (PCoA) of pairwise genetic distances (D_{LR} or D_S) among locations for each species (Gilmour et al. 2008; Gilmour et al. 2009b). See Figure 5.1.17 for postion of Locations.

Following the mass-spawning by corals in autumn, there were consistent patterns of variation in rates of coral recruitment across Scott Reef; recruitment to communities at SL1 or SS2 were consistently the highest; SL3 intermediate; SL2 intermediate to low; and SS1 and SL4 consistently the lowest recruitment (Figure 5.1.18). Recruitment by spawning corals follows two periods of calm each year, whereas brooding corals release larvae over several months, including the summer months that characteristically have stronger winds and current movement (Figure 5.1.13). Thus, brooded larvae are exposed to a much wider range of oceanographic conditions. For example, surface drifters released in January from the southern part of south-lagoon reached the east hook within a few days, despite current speeds characteristically being slowest in this part of the reef. Although most brooded larvae probably settle within a kilometre of their parents, they also have the potential to survival in the water column for several weeks and be carried over tens of kilometres during summer months (Figure 5.1.15). The rare dispersal of brooded larvae over longer distances, and their subsequent ability to produce many local recruits, means they can potentially colonise distant areas of low coral cover following severe disturbances. This pattern of highly localised dispersal and rare long distance dispersal in brooding corals contrasts with that displayed by most spawning corals, which have more intermediate distances of dispersal during more uniformly calm oceanographic conditions.

Long-distance dispersal among atoll systems off northwest Australia

A wide range of data indicate limited larval dispersal and connectivity among coral and fish communities at Ashmore Reef, Scott Reef and the Rowley Shoals. The movement of sub-surface drifters (Figure 5.1.20) and oceanographic models (Figure 5.1.21) suggest a low probability of larval dispersal between Scott Reef and the Rowley Shoals within two months. The drifter tracks also provided evidence of the reversal of the predominant currents in the middle of the year from a southerly flow during the autumn mass-spawning to a northerly flow during the spring mass-spawning. Few coral larvae that disperse for a period of longer than one month are likely to survive and recruit successfully, whereas this is closer to the routine periods of dispersal for fish larvae (Underwood 2009). Genetic analyses suggest little exchange of fish and particularly coral larvae between Scott Reef and the Rowley Shoals over ecological time scales (Gilmour et al. 2009b; Underwood 2009) but these data do not exist for populations from Ashmore Reef that are approximately half the distance from Scott Reef (Figure 5.1.20).

The tracks of drifters and ocean models suggest a low probability of larvae dispersing from Ashmore to Scott Reef within one month (Figure 5.1.20 & 5.1.21). Over this period, some coral larvae could recruit from Ashmore to Scott Reef following the spawning in autumn, but the degree of connectivity is still likely to be low. A strong stock-recruitment relationship between coral cover and the supply of larvae is evident at Scott Reef (Figure 5.1.22), and the very low levels of recruitment following the bleaching suggest little input of larvae from other reef systems in the region. For the fish larvae, there is likely to be a greater degree of connectivity among populations at Ashmore and Scott Reef, but the extent to which each system contributes the others population maintenance is unknown. (Figure 5.1.23) Genetic analyses of coral and fish populations from Ashmore Reef are required to address these questions.

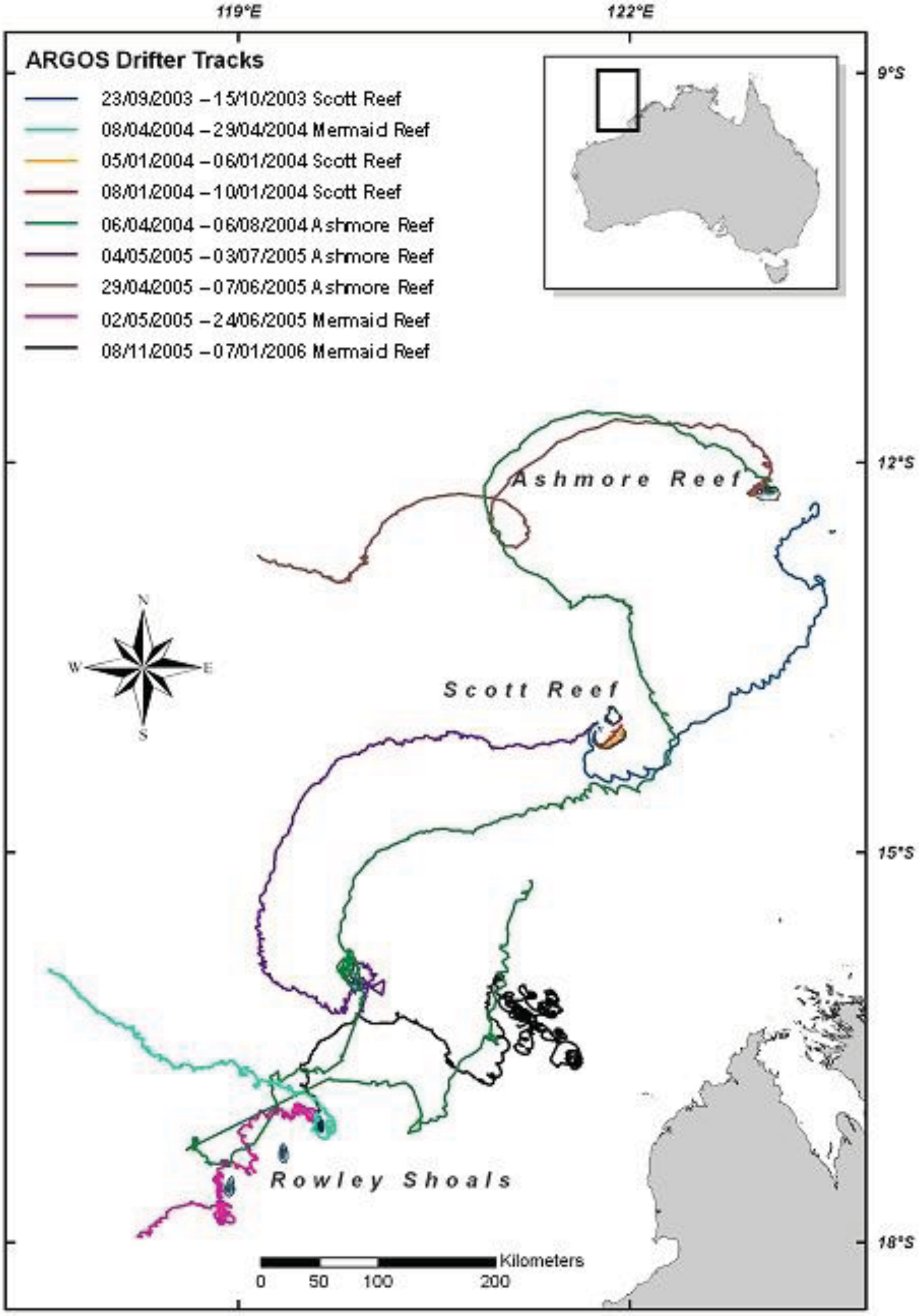


Figure 5.1.20 Tracks of sub-surface drifters released from adjacent to the Scott Reef, Ashmore Reef or Rowley Shoals reef systems around the times of spawning in autumn or spring (Smith et al. 2003; Gilmour et al. 2009b)

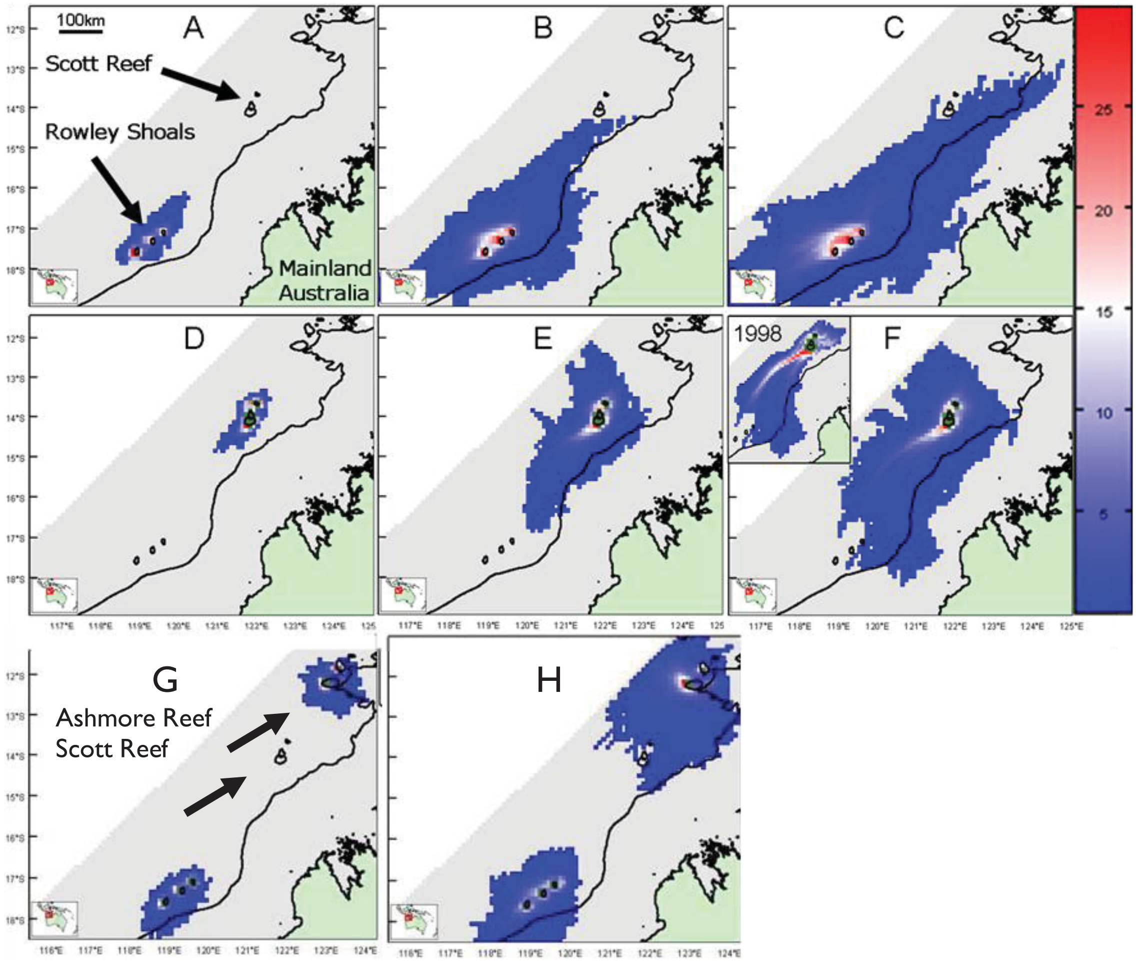


Figure 5.1.21 Dispersal kernels from a three-dimensional non-linear hydrodynamic model forced by wind, temperature and salinity fields to estimate the probability of connectivity by passively dispersed particles among reef systems (online interface, Connle, developed by CSIRO; (Condie and Andrewartha 2008). Panes A, B and C, particles released from Rowley Shoals in the first quarter and run for 7, 28 and for 56 days respectively. Panes D, E and F, particles released from Scott Reef in the second quarter and run for 7, 28 and for 56 days respectively. Panes G and H, particles released from Ashmore Reef and the Rowley Shoals in the second quarter and run for 7, 28 days respectively. All results are based on particle distributions averaged across six years (1994-1999) apart from insert in Pane F which was for 1998 only. The colour bar indicates probability of connectivity (Blue < 5%, Red >25%).

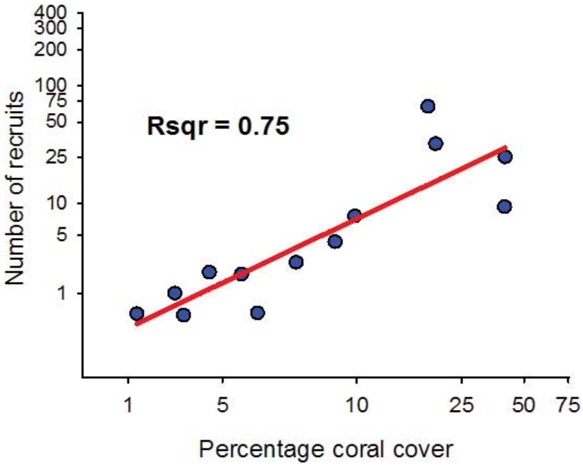


Figure 5.1.22 Stock-recruitment relationship for coral communities at Scott Reef. Correlation between coral cover and recruitment over 15 years of monitoring.

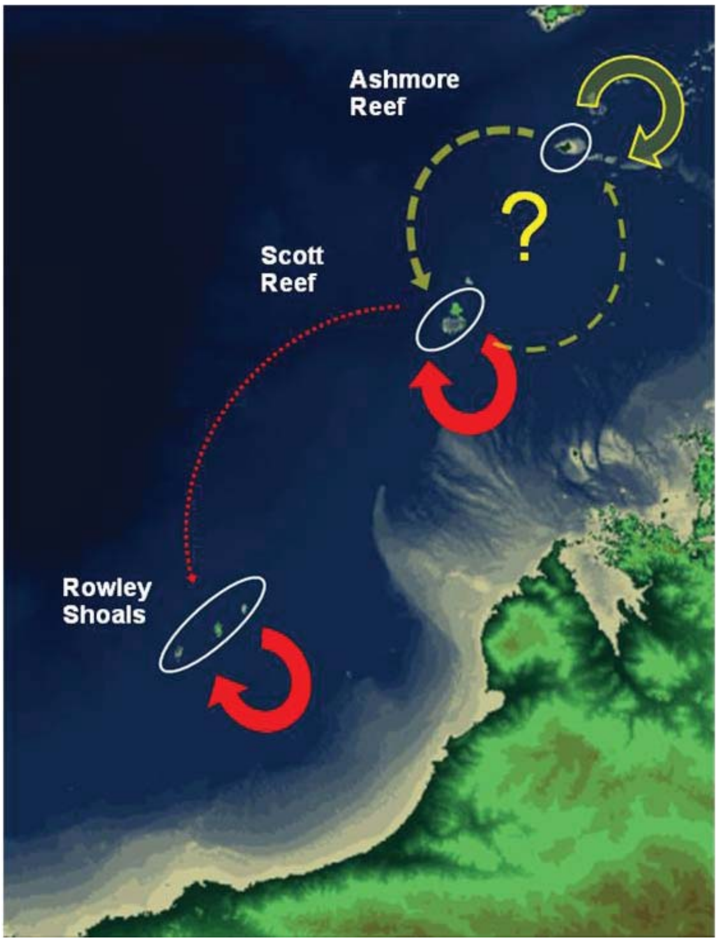


Figure 5.1.23 Hypothetical patterns of connectivity among atoll systems off north-west Australia for populations of coral and fish. Each system is largely self seeded, with only a limited supply of larvae from outside. Dispersal distances and the degree of connectivity among systems will be greater for populations of fish, than for corals. Connectivity between populations at Scott and Ashmore Reef will be greater than for Rowley Shoals, although the degree of connectivity is uncertain until genetic analyses of populations at Ashmore Reef are conducted (uncertainty indicated by yellow arrows). Within each reef system, connectivity among distant population is greater for fish than for corals, and greater at the Rowley Shoals than for Scott Reef.

Based on a combination of data at Scott Reef, coral larvae routinely disperse among adjacent locations, and fish larvae among more distant locations. Dispersal within Scott Reef was consistently more restricted than within the Rowley Shoals, due to the structure and size of the south-lagoon at Scott Reef and its affect on current flow. There is little exchange of larvae among the atoll reef systems of north-west Australia over years to decades, with the possible exception of fish larvae between Ashmore and Scott Reef (Figure 5.1.23). Although there is limited dispersal of coral and fish between Scott Reef and Rowley Shoals, Scott Reef probably acts as a reservoir of higher genetic diversity that can be passed on to Rowley Shoals over longer time periods; Ashmore Reef could be a similar reservoir for Scott Reef. Higher genetic diversity of communities in warmer water could supply southern reefs with genotypes more resistant to future stressors arising from climate change, such as warm water and diseases. The lack of large and regular input of larvae from outside these isolated reef systems has important implications for their management. Following disturbance, the recovery of coral and fish communities at Scott Reef, and even some coral communities within parts of Scott Reef, will primarily rely on the production of recruits generated by the survivors. Thus, local stressors must be minimised and restricted to small spatial scales on the least significant parts of the reef for communities to persist. Whether parts of the reef are considered more or less significant will depend on a combination of community abundance and diversity, and then extent to which they contribute to the maintenance of other communities across the reef system. This is particularly relevant given habitat fragmentation and global increases in regional scale disturbances due to climate change and development activities (Ayre and Hughes 2004; Jones et al. 2007).

5.2 Coral communities at Scott Reef and their resilience to disturbances

Summary

Coral communities must be resilient to disturbances if they are to persist in a healthy state of moderate to high cover and diversity. The resilience of coral communities is determined by the:

- habitat and its ‘normal’ environmental conditions;
- extreme variation in conditions associated with periodic disturbances;
- abundance of corals of differing susceptibilities to disturbance and their life histories;
- rates of birth (recruitment), growth and survival, and the resulting cover and structure;
- degree of connectivity to similar communities.

Together, these factors produce complex cycles of changes in community structure over years to decades, through periods increasing coral cover and diversity following severe disturbances. Because all communities are in a constant state of flux, assessing their health to a combination of disturbances requires long-term studies integrating a range of complimentary data. The Scott Reef Research Project (SRRP) has been collecting biological, physical and genetic data at Scott Reef for up to 15 years. Here we integrate these data to draw inferences about the coral communities across different habitats at Scott Reef, and their exposure and resilience to disturbances in the future.

As with all coral reefs today, communities at Scott Reef will be exposed to a range of natural and anthropogenic disturbances, the impacts of which will be amplified by climate change. The disturbances most likely to impact communities at Scott Reef are elevated water temperature and coral-bleaching, cyclones, reduced water quality (turbidity, sedimentation) due to natural or anthropogenic sources, and outbreaks of coral diseases and predation. The exposure, susceptibility and resilience of communities to these disturbances vary among habitats at Scott Reef. The coral habitats at Scott Reef can be divided among those in shallow (<15 m), deeper (15-30 m) and deep (>30 m) water, within the lagoons (north- and south-reef) or on the outer-slope. These arbitrary habitat divisions are based on gross changes in environment and community structure at Scott Reef.

Of all the communities, those in the shallow-habitat (<15 m) are the best studied, and variation among locations in this habitat are discussed in greater detail below. In general, the shallow-communities have the highest coral cover and diversity, but also undergo extreme changes in community structure because they are exposed to severe regimes of disturbance. These communities are most susceptible to elevated water temperatures and cyclone disturbances, but probably least susceptible to short-term reductions in water quality given the high light penetration and current flow. High water temperatures and exposure to other disturbances probably mean the shallow-communities are most susceptible to outbreaks of disease and predators, particularly at times of high coral cover, but what drives these outbreaks is not well understood. Across the shallow-habitat, resilience to disturbances is probably aided by high rates of recruitment, growth and survival, and connectivity to similar communities across Scott Reef that are separated by distances of up to approximately 10 to 20 km. Additionally, resilience may be aided by the supply of recruits from some communities in the deeper-habitat (15-30 m), if they are not affected by the disturbance and they overlap in common species.

The deeper-communities (15-30 m) are not well studied, but probably have some overlap in structure and demography to those at similar locations in the shallow-habitat in depths greater than approximately 7 m. Compared with the shallow-communities, those in the deeper-habitat probably have moderate coral cover and diversity. They are less susceptible to elevated water temperatures, but extreme heating over a protracted period of time can extend throughout the entire deeper-habitat. Severe cyclones probably have little direct impact on the deeper-communities, but deposition of fragments and sediment suspended by the wave energy is likely to injure and bury some corals. Lower light penetration and current flow mean the deeper-communities are susceptible to prolonged increases in turbidity or sedimentation from developmental activities. Lower water temperatures and light penetration may mean communities are less susceptible to outbreaks of disease and predators than those in the shallow-habitat, but could also cause lower rates of recruitment and growth. However, rates of survival may be similar or higher than for corals in shallow-communities, given less severe regimes of disturbance in the deeper-habitat. Resilience to disturbance will be aided by connectivity among locations over similar spatial scales as for the shallow-habitat (< 10 -20 km), but realised connectivity is likely to be less in the deeper-habitat given a more patchy distribution of some communities, particularly in the north- or south-lagoon. In most instances, the resilience of deeper-communities is probably not aided by the supply of recruits from those in the shallow-habitat where the impacts from disturbance are usually more severe, or from the deep-habitat where there is probably little overlap in common species.

The deep-communities (>30 m) are found only in the south-lagoon or on the outer-slope, and are highly adapted to low light penetration. Compared to the shallow-habitat, deep-communities have low cover and diversity, with the exception of higher cover in some patches in the south-lagoon. Only the most severe and protracted temperature anomalies are likely to cause bleaching of corals in the deep-habitat, and communities are not susceptible to cyclone disturbances. However, deep-communities are highly susceptible to further reductions in light due to increased turbidity. The flat growth form of corals in the deep-habitat maximises light absorption, but means they are susceptible to sediment accumulation, and these species are probably not well adapted to actively removing sediment. Reductions in water quality that increase both turbidity and sedimentation are therefore likely to have severe impacts on deep communities. The deep-communities may not be susceptible to outbreaks of coral disease and predation, although this is uncertain. Rates of reproduction and growth are probably lowest in the deep-communities, but survival may be high due to a low exposure to disturbances. The patchy distribution of communities through the deep-habitat will reduce their connectivity and resilience following disturbances. Additionally, limited overlap in common species and the likelihood of more severe impacts from disturbances means the communities in shallower (< 30 m) habitats are unlikely to assist in the recovery of deep-communities following disturbances. The deep-communities are therefore highly susceptible to impacts from severe disturbances occurring over scales of greater than a few kilometres.

Within all of the coral habitats at Scott Reef, there is spatial variability in community structure, exposure and resilience to disturbances. This variability is best described for communities in the shallow-habitat, and is strongly influenced by their proximity to the north-lagoon, south-lagoon, deep-channel between north- and south-reef, and the outer-slopes. The community closest to the southern part of the south-lagoon (Location SL2) is characterised by the most unique conditions and habitat structure. In particular, very low current flow and high turbidity means the community has an abundance of fragile corals with branching or foliose growth form. Relatively low water quality and low current flow mean the community is susceptible to elevated water temperatures and bleaching, further reductions in water quality, and outbreaks of coral diseases and predation. In contrast, the sheltered position means the community has a low susceptibility to cyclone disturbance. The most similar conditions and community to that at Location SL2 is probably in the north-lagoon, although there have been few recent surveys in the north-lagoon. In contrast to these sheltered communities, those adjacent to the deep-channel (Locations SL3 & SL4) experience high current flow and a large range in water temperatures due to periodic cool-water intrusions, which can reduce their susceptibility to bleaching. The current flow and wider temperature range means these communities probably have a lower susceptibility to reductions in water quality and outbreaks of coral diseases and predation. However, these communities are susceptible to fragmentation by wave energy during cyclone disturbances, which also suspends course sediments that scour and smother colonies. The most similar conditions and communities to those adjacent to the deep-channel are those at the outer-slope (Location SS1 & SS2) on the eastern side of Scott Reef. The outer-slope communities are most susceptible to cyclone disturbances approaching from the east, given their exposure to the open ocean. However, their exposure to the open ocean probably means they are only moderately susceptible to bleaching, reductions in water quality and outbreaks of coral diseases and predators; the exception may be a higher susceptibility of the community at north-reef to bleaching due to the flow of warm water out of the lagoon and over the reef flat. The conditions and community inside east hook (Location SL1) is a diverse mixture of all the others. Consequently, the community is moderately susceptible to all of the possible disturbances.

The resilience of communities throughout the shallow-habitat to disturbances is due not only to their exposure to disturbances but also their connectivity to other communities and the resulting supply of coral recruits. The varying exposure of communities to all of the most likely disturbances and their rates of coral recruitment enable hypothetical patterns of resilience to be proposed. Assuming exposure to all disturbances, the community inside east hook (Location SL1) is probably most resilient, followed by that inside west hook and around the sandy islet (Location SL3). The community on the outer-slope adjacent to north-reef is then most resilient (Location SS2), followed by those on the outer-slope at east hook (Location SS1) and adjacent to the deep-channel on north-reef (Location SL4). The communities in the north-lagoon and in the southern part of the south-lagoon (Location SL2) are probably the least resilient to a combination of all possible disturbances.

Persistence of coral reefs exposed to varying regimes of disturbance

Coral communities must be resistant and resilient to disturbances if they are to persist in a healthy state of moderate to high cover and diversity. Resistance of coral communities can be described as their ability to persist undamaged in the face of disturbances (and stressors), such as cyclones, temperature increases or outbreaks of disease. Resilience of communities can be described as their ability to recover after being damaged by disturbances, through the process of birth, growth and survival. Commonly, resilience is used to describe both the resistance and resilience of communities to disturbances.

The resilience of coral communities and their persistence in a healthy state depends on the:

- normal habitat and environmental conditions;
- exposure to varying regimes of disturbance;
- relative abundance of corals with different life histories and susceptibility to disturbances;
- rates of birth (recruitment), growth and survival of corals, which determine the percentage cover and community structure;
- degree of connectivity to similar communities and their regimes of disturbance.

Even on 'healthy' coral reefs, the abundance of coral sizes and species (community structure) is in a constant state of flux, responding to changes in routine habitat conditions and recovering from natural regimes of disturbance. Healthy reefs may have low coral cover and diversity within particular habitats (e.g. deep-water), but their communities are able to recover to the previous structure following major disturbances and have a high proportion of new recruits and juvenile sized corals that underlie future cover and diversity.

Today, there is concern over an increasing number of coral reefs around the world, with an apparent long-term shift (phase-shift) to a more degraded state of low cover and diversity that is often preceded by a reduction in recruits and juveniles. A phase-shift by some coral reefs to a more degraded state results from their exposure to increasing combination of disturbances and scales of impact. Most commonly, this occurs due to a combination of local chronic stressors, such as overfishing or reduced water quality, and more regional acute disturbances, such as elevated water temperatures, or outbreaks of coral predators or disease. It is often the introduction of chronic stressors that cause the degradation of communities, because they shift the routine conditions beyond the limits of coral distribution. Whether coral communities can persist through their changing regimes of disturbance depends on their routine habitat conditions, the extreme variation in conditions associated with disturbances, the abundance of susceptible corals and the supply of recruits from similar communities.

Habitat conditions

Routine habitat conditions primarily determine the distribution, structure and resilience of coral communities. Routine habitat conditions are physical (e.g. temperature, light, wave energy, substrata type) and biological (e.g. abundance of herbivorous fish, coral predators, diseases and macro-algae). Habitats that provide ideal conditions are characterised by a high diversity, cover and resilience, due to high rates of recruitment, growth and survival. Habitats with less favourable conditions are characterised by lower diversity, cover and resilience, due to lower rates of recruitment, growth and survival.

Disturbance regimes

Routine habitat conditions determine the distribution of coral communities, but their persistence within a habitat is strongly influenced by the regimes of disturbance. As with routine conditions, different habitats experience different regimes of disturbance, depending on the types, frequencies and severities of disturbances. Some of the most common disturbances to coral reefs include elevated water temperatures, storms and cyclones, reduced water quality, outbreaks of disease and coral predators, and overfishing. All of these disturbances display some degree of selectivity, meaning they affect habitats, locations, species and size classes of corals differently. The degree of selectivity determines the impact on the community. For example, communities in deep-habitats with poor water circulation are more susceptible to reductions in water quality than those in shallow-habitats, which are more susceptible to cyclones and coral bleaching. Further selectivity exists among locations and communities within habitats. For example, within shallow-habitats the impacts of severe cyclones are generally more selective than for severe coral bleaching, as the cyclonic wave energy can be patchy over small spatial scales, fragile corals are worst affected and a higher proportion of colonies are injured rather than killed; elevated water temperatures and mass-bleaching tend to be more uniform across small spatial scales and kill rather than injure a high proportion of corals. In some instances, habitats with the most favourable background conditions also have the most severe regimes of disturbance. The persistence of communities within these habitats relies on high recruitment, growth and survival during years of calm conditions, so inferences about their health requires information about changes in community structure over many years. In contrast, communities existing in more marginal habitats may be able to persist with lower rates of recruitment and growth because they are exposed a less severe regime of disturbance.

Community structure

Inferences about the impacts and resilience of communities to disturbance must consider community structure. The relative abundance of susceptible species within the community determines the impact from disturbance. For example, a large absolute reduction in coral cover following a cyclone may be due to very high cover of branching corals, yet the community may quickly recover from such a disturbance. Some of the most abundant species within communities are most susceptible to disturbances but also can undergo rapid increases in cover, and changes in these groups of corals over less than a few years may provide less accurate insights into community resilience than changes in groups of corals (species and size classes) that make smaller contributions to percentage cover. *Acropora* corals characteristically have the highest rates of reproduction and growth, yet they are also among the most susceptible to many of the common disturbances to coral reefs. Conversely, massive and encrusting corals have lower rates of growth and survival but are also among the least susceptible to common disturbances. An understanding of community resilience through different regimes of disturbance therefore requires that changes in abundance and cover of groups of coral with differing susceptibilities and resilience be consider separately over several years.

Connectivity among communities

The resilience of communities following disturbance is influenced by the supply of new recruits. Communities with a high supply of recruits, produced locally or from outside, will recover more quickly than those with limited recruitment. Recovery facilitated by the local production of recruits is more likely to occur following selective disturbances, which kill or injure a smaller proportion of the community (e.g. cyclones). Recovery is likely to be far slower following severe and widespread disturbances that kill the majority of the community (e.g. mass-bleaching), unless there is a supply of recruits from other locations or habitats that were not affected by the disturbance. However, a supply of recruits from other locations or habitats to aid recovery also requires an overlap in abundant species between communities and that they are within the routine distances and directions of larval dispersal. For example, communities that were not affected by a disturbance will provide little assistance to the recovery of impacted communities if they are located more than tens of kilometres away or their larvae disperse in the opposite direction; they will also provide little assistance if the majority of recruits they supply are of species that are not well adapted to surviving within the impacted habitat. The degree of connectivity among communities and their ability to aid each other's recovery therefore depends on their spatial separation, current speeds and directions, and the degree of overlap in species abundances.

Future disturbances to coral communities at Scott Reef

Historically, some of the natural disturbances most likely to have impacted coral reefs are cyclones, terrestrial inputs of freshwater and sediments during the wet season, and periodic outbreaks of coral diseases and predation. Today, these disturbances are combined with impacts from human activities. The four major human impacts are climate change and the associated increases in water temperatures, ocean acidification, severity of cyclones, and outbreaks of coral diseases and predators; land- and marine-based pollution; habitat destruction and degradation; and overfishing (Hughes et al. 2003; Raymundo et al. 2008). The distance of Scott Reef and the other off-shore atoll systems of Western Australia means they are not exposed to some of these disturbances, particularly the local stressors, although they are exposed to the regional-scale disturbances associated with climate-change. Monitoring programs today must therefore be conducted over large spatial-scales to ensure impacts from regional disturbances are not inappropriately attributed to local activities. Further discussion about the resilience coral communities at Scott Reef will focus on the most likely disturbances in the future, which are:

1. elevated water temperatures;
2. severe storms and cyclones;
3. reductions in water quality;
4. outbreaks of disease or coral predators;
5. overfishing.

Elevated water temperatures and coral bleaching

Coral bleaching is a consequence of a range of stressors (e.g. freshwater, sedimentation, cold water), but is most commonly a consequence of elevated water temperatures. The temperature tolerances of coral communities vary widely among reefs and habitats. Relative increases of more than 1 to 2°C above the mean monthly temperatures during the warmest months will cause bleaching and mortality in many coral communities. However, the impacts of increased temperature depends on both the magnitude and duration of change, so if small increases persist for more than weeks to months the impacts may be more severe. Bleaching 'Hotspots' are identified globally by the National Oceanic Atmospheric Administration (NOAA) when surface temperatures exceed the monthly mean values, and the duration of heating is measured as the Degree Heating Weeks (DHW) and bleaching is likely when Hotspots persist for several weeks (Liu et al. 2003). Different combinations of heating and duration produce the same measure of DHW. Hotspots of 1°C for 12 weeks will produce the same measure as 2°C for 6 weeks. DHW of >4°C-weeks have been shown to cause significant coral bleaching and >8°C-weeks causes widespread bleaching and/or mortality (Liu et al. 2003). However, bleaching is not only a product of the duration of maximum water temperatures, but also the amount of light penetration, current flow and the range in water temperatures. High light penetration, low current flow and a smaller temperature range due to higher than average minimums, are all likely to increase the severity of a bleaching event. Additionally, the longer the period of heating the more likely that a surface layer of warm water will penetrate to deeper-habitats, which can also occur when currents or winds reduce stratification. If corals survive a bleaching event, they are severely stressed for several months and subsequent rates of growth and reproduction are compromised. In the worst instances, bleaching results in the widespread mortality of corals.

Mass-bleaching in 1998 was the most severe disturbance recorded at Scott Reef (Figure 5.2.1), but moderate bleaching again occurred in 2010 (Figure 5.2.2) and more severe bleaching events are predicted due to ongoing climate change (see Chapter 3, Disturbances at Scott Reef). During the 1998 bleaching, heating began at the end of February and rapidly increased after the first week of March, when the warm surface layer was mixed down to 20 m by strong winds. Modelled data from mid-February through to the end of April (Steinberg et al. 2003) indicated surface temperatures of around 34°C. Through March and April temperatures at 16 m depth remained at between 30 and 32°C, where they rarely exceed 31°C, and exceeded 30°C at 35 m depth (Smith et al. 2003; Steinberg et al. 2003). The extreme water temperatures penetrated further down the water column as the period of heating exceeded two months (Figure 5.2.1). Coral bleaching thresholds of between >8°C-weeks and >14°C-weeks were exceeded in the shallow-habitat, and >4°C-weeks exceeded through the deeper-habitat down to a depth of 30 m (Steinberg et al. 2003).

As a result of the elevated water temperatures in 1998, there was a catastrophic mortality of corals at all locations across Scott Reef (Figure 5.2.1). Widespread bleaching and mortality was evident throughout the shallow depths. Observations by divers restricted to depths of around 20 m indicated this was the limit of mass-bleaching and -mortality. Throughout these depths, there was little selectivity in the disturbance, which killed most hard and soft corals at all monitoring locations (including Seringapatam Reef). Because so few corals survived, and Scott Reef is so isolated from the other reefs in the region, initial rates of coral recruitment and recovery were slow. The impacts to the coral community was so severe that they caused major changes to the fish communities (Halford and Caley 2009) and the effects of the bleaching event are evident more than a decade later.

Temperature ranges at Scott Reef vary among the different habitats, becoming progressively cooler with increasing depth (Figure 5.2.2). The maximum temperatures in the shallow-habitat occur in late December, become cooler through summer due to increased storm activity, and peak again in autumn. In contrast, the maximum temperatures in the deeper-habitats occur in autumn (Steinberg et al. 2003). Among locations within the shallow-habitat, temperature variation among locations and through time is more complex. There is little variation in average temperatures among shallow-locations, ranging between 29.5°C and 30.5°C in summer and 27.5°C and 28.5°C in winter. Finer-scale variation among locations exists over periods of days to weeks, but there are few consistent patterns to this variation. The exception is a larger temperature range over periods of days (tides) to months (seasons) at some locations close to cooler water intrusions emerging from the deep-water channel, or warm water flowing over the reef from the north-lagoon. Local variation in water temperatures are due to a complex interaction between temperature range, light penetration, and current flow, and the resulting patterns of bleaching within communities depends on the abundance of susceptible species (Loya et al. 2001, Smith et al. 2008).

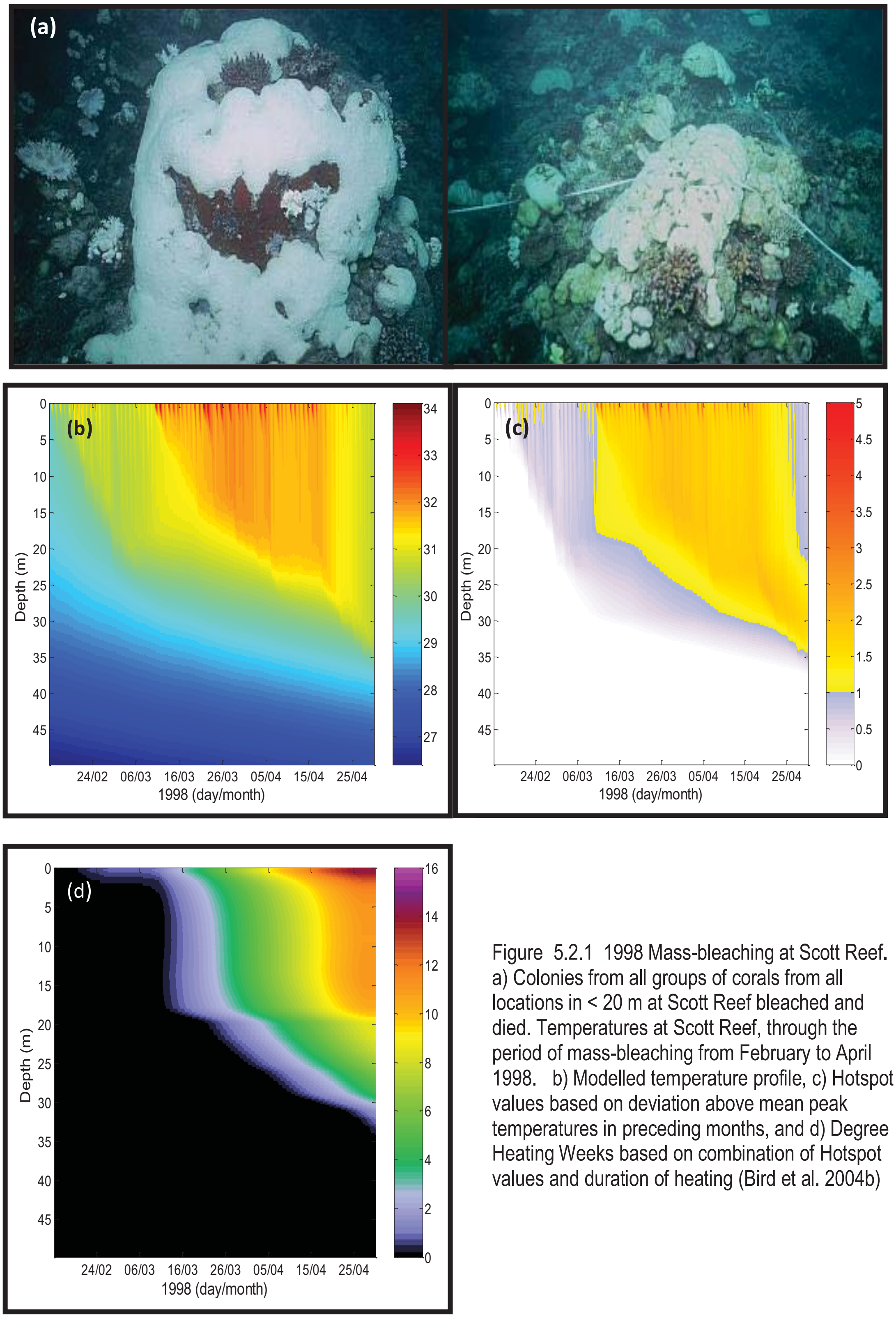


Figure 5.2.1 1998 Mass-bleaching at Scott Reef. a) Colonies from all groups of corals from all locations in < 20 m at Scott Reef bleached and died. Temperatures at Scott Reef, through the period of mass-bleaching from February to April 1998. b) Modelled temperature profile, c) Hotspot values based on deviation above mean peak temperatures in preceding months, and d) Degree Heating Weeks based on combination of Hotspot values and duration of heating (Bird et al. 2004b)

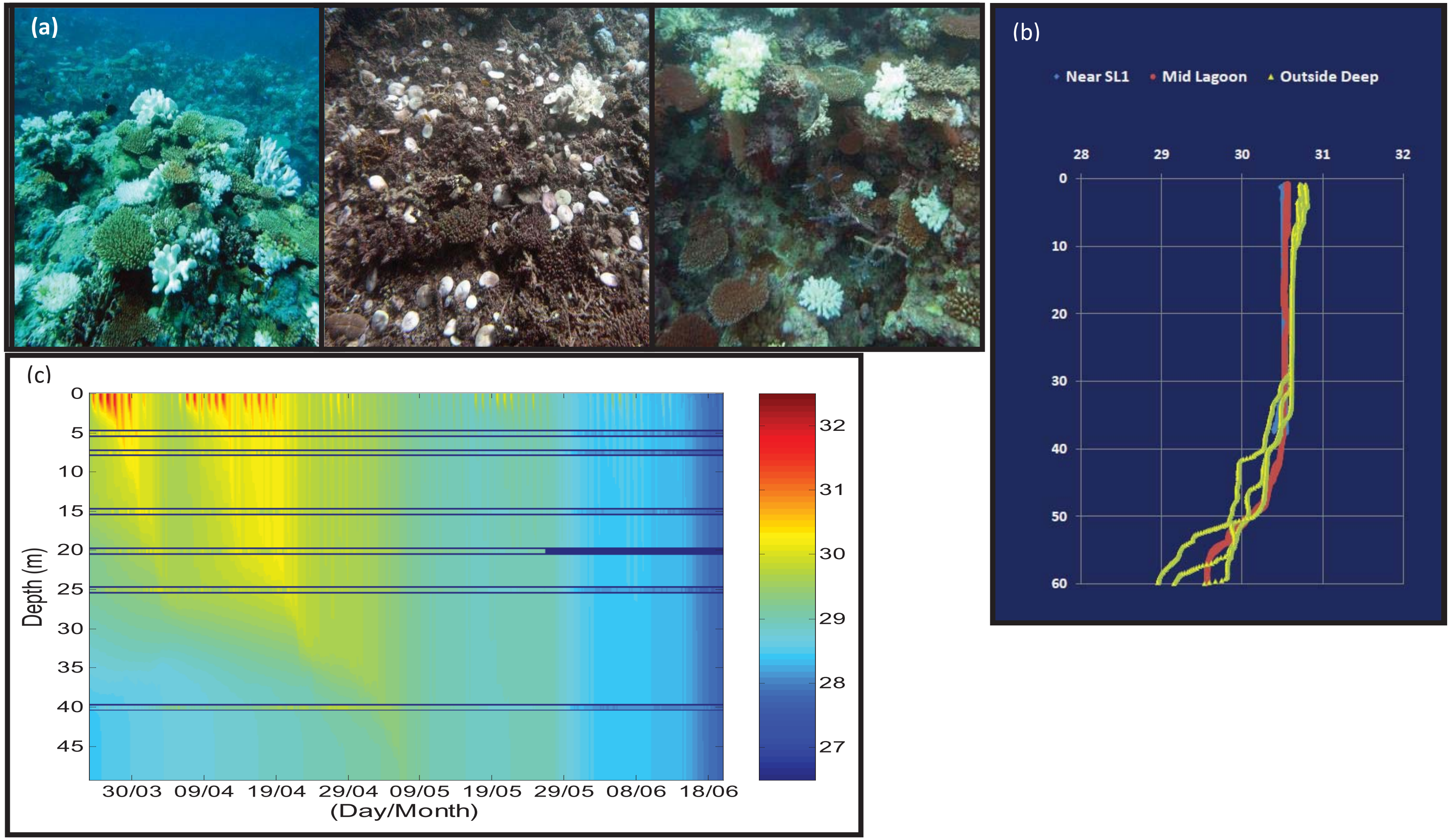


Figure 5.2.2 Bleaching at Scott Reef in 2010. Bleaching was more selective in the shallow-habitat than in 1998, affecting a smaller number of locations at Scott Reef and particular groups of corals. a) Bleached corals in the families, *Pocilloporidae* and Fungiidae at Locations SL1, SL2 and SS2. b) Temperature profiles (not monthly averages) at Scott Reef in April 2010. Water temperatures exceeded 30°C at 30 m adjacent to Scott Reef, near Locations SL1 at east hook, and down to 50 m in the south-lagoon (AIMS Cruise 5010). The impact of the deep-water communities is unknown. c) Temperature profile during ‘normal’ conditions in south-lagoon from March to June 2003.

Severe storms and cyclones

Historically, coral reef communities have been resilient to cycles of impact and recovery from cyclones over periods of years to decades (Connell 1997). Cyclone disturbances characteristically have more selective impacts than mass-bleaching; impacts can be patchy even within the most exposed locations, robust corals are less susceptible and many colonies may be injured rather than killed. Impacts from cyclones are primarily a consequence of extreme wave energy that fragments corals and moves the substrata on which communities grow (Figure 5.2.3). In these instances, branching and table corals with fragile growth forms are most susceptible to the impacts, but severe cyclones can fragment even massive corals and soft corals (Figure 5.2.3 b). Secondary impacts from cyclones include the scouring of coral tissue by suspended sediments and fragments during high wave energy (Figure 5.2.3 c). Additionally, suspended sediments and fragments can then be deposited on surviving corals, either burying colonies or causing further injury to tissues (Figure 5.2.3 c). Colonies with flat or massive growth forms, and those at the bottom of the reef slope, tend to be most susceptible to burial. Recovery from the selective impacts of cyclone disturbances can usually occur within years, following the growth and production of recruits from surviving colonies within the community or adjacent locations.

Extreme storms and cyclones are probably the most common disturbance to have affected coral communities at Scott Reef, with approximately 2.5 cyclones per year passing within 50 km in the last 90 years (Figure 5.2.4). Of these cyclones, one every five to ten years probably had a moderate to severe impact on at least some coral communities; these impacts tend to decrease with depth. Since long-term monitoring (9 m depth) commenced in 1994, there have been major impacts to coral communities from Cyclone Fay and two other cyclones have passed within 50 km of Scott Reef (Figures 5.2.3, 5.2.4). Category 5 Cyclone Fay passed directly over Scott Reef in March 2004, at which time it had a central pressure of 905 HPa and wind speeds of over 300 km per hour. Category 1 Cyclone Raymond developed close to Scott Reef in January 2005, with maximum winds speeds of < 60 km h^{-1} and Category 2 Cyclone George passed Scott Reef on 6th March 2007, with maximum wind speed of 92 km h^{-1}. Cyclones Fay and George both had noticeable impacts on the coral communities within the shallow-habitat at Scott Reef. The worst affected monitoring locations were on the outer eastern slope of Scott Reef or adjacent to the western edge of the deep-channel. Within these locations, impacts from the cyclone were most obvious in communities that had most rapidly recovered from the bleaching in 1998 and had a relatively high cover of fragile species.

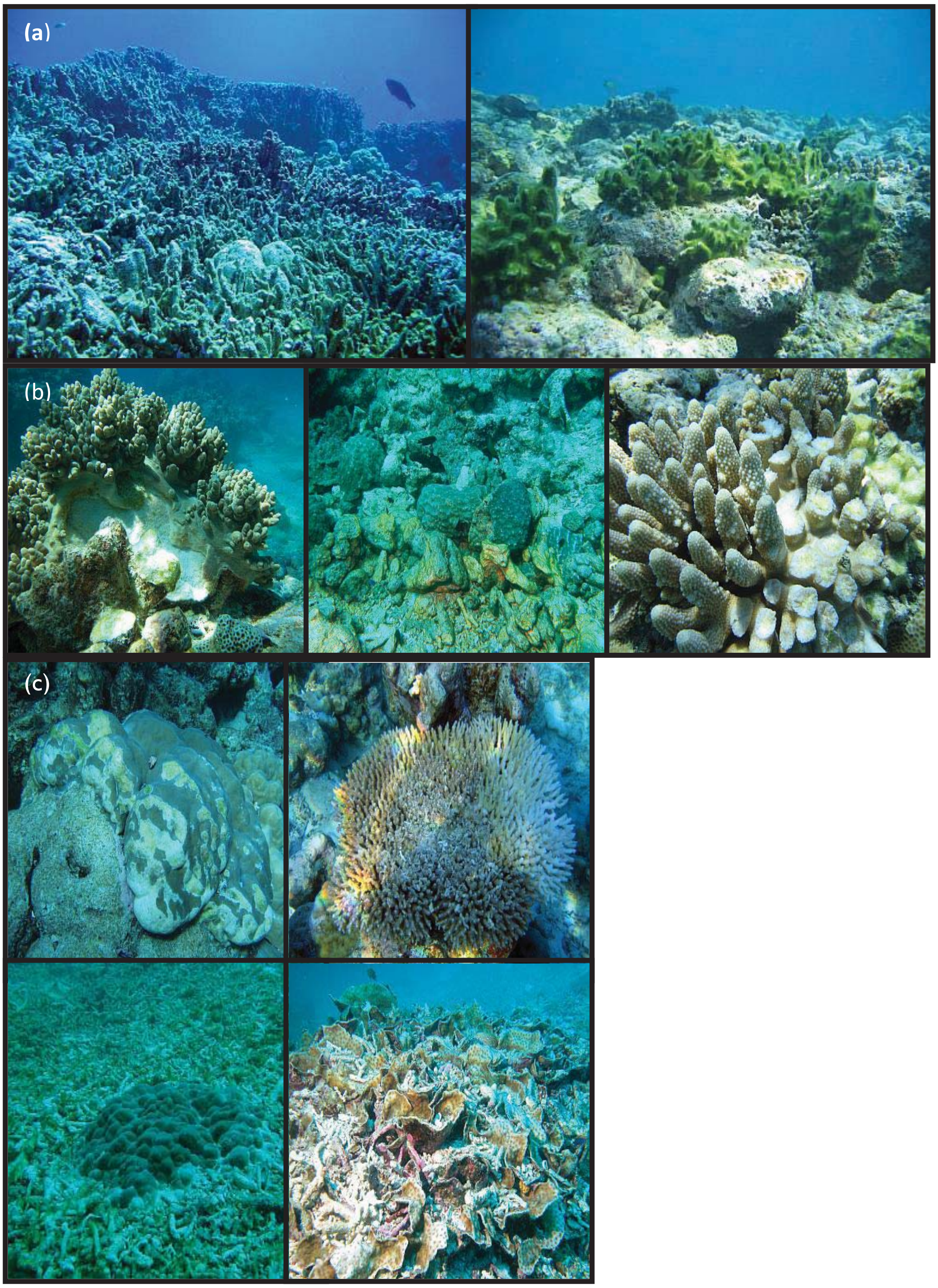


Figure 5.2.3 Impacts from Category 5 Cyclone Fay at Scott Reef. a) Cyclone Fay caused wide-spread destruction of corals and habitats at Scott Reef; the resulting reductions in percentage cover were less than would be expected because coral cover had not yet recovered from mass-bleaching in 2008. b) Even coral less susceptible to cyclones were impacted by Cyclone Fay, including soft corals that lack a rigid skeleton and hard corals with robust skeletons. c) Sediments and fragments suspended by wave energy during Cyclone Fay scoured colony tissue and were deposited onto surviving corals.

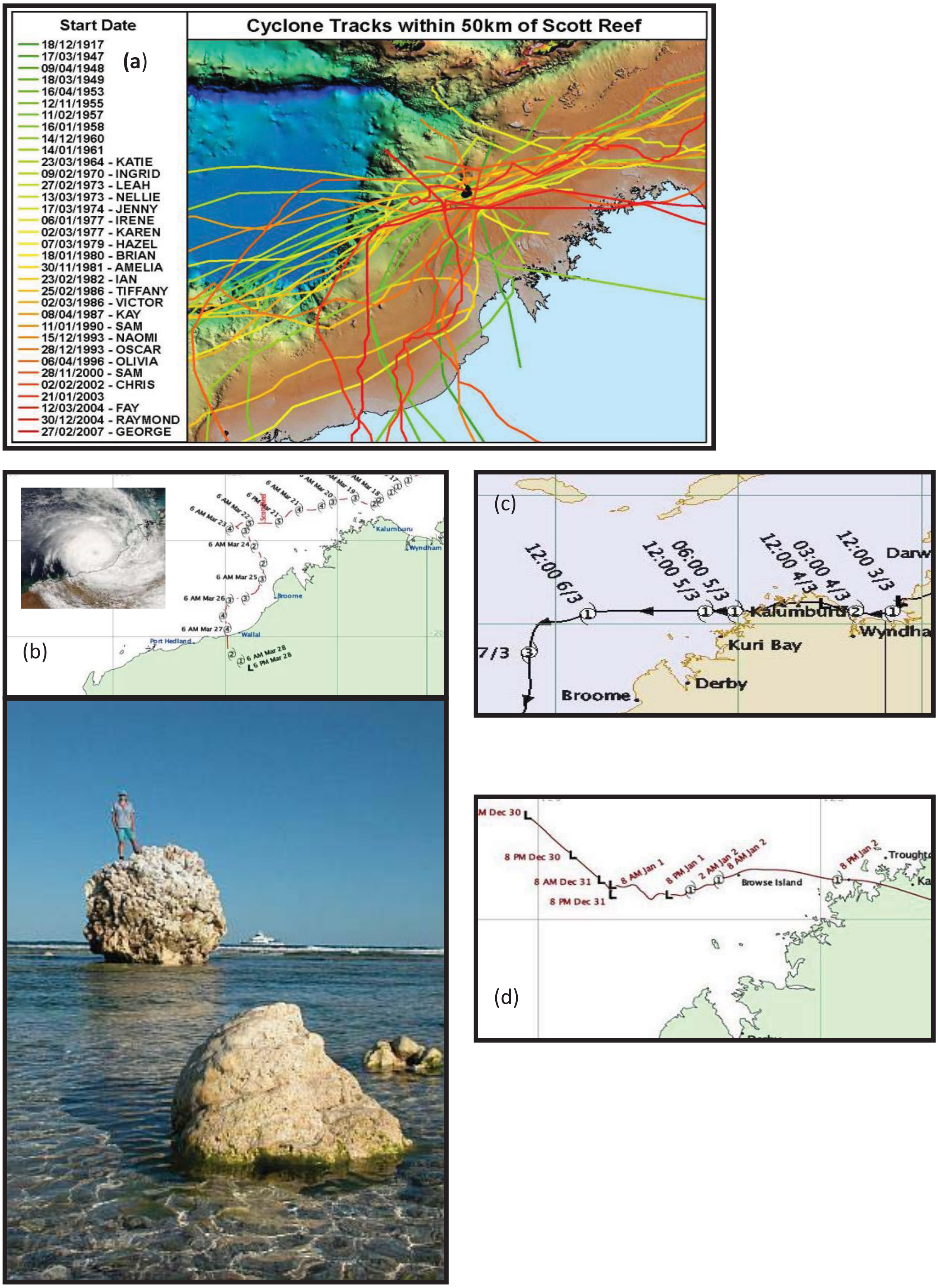


Figure 5.2.4 Cyclone disturbance at Scott Reef. a) Historic exposure of Scott Reef to storms and cyclones. b) Of these most recent cyclones, impacts from Cyclone Fay in 2004 were by far the worst, which fragmented corals and substrata, pushing massive boulders up onto the reef flat. Tracks of Cyclone c) Raymond in 2005 and d) George in 2007.

Reductions in water quality

Reductions in water quality are most commonly associated with increased turbidity, sedimentation and nutrients. Turbidity generally refers to the amount of dissolved and particulate matter suspended in the water column and its affect on light attenuation (Te 1997; Fabricius 2005) and sedimentation is the deposition of this material (Rogers 1990). Increased turbidity primarily stresses corals by reducing the amount of nutrition supplied by their zooxanthellae, due to reduced rates of photosynthesis. Over days to weeks, some corals can photoacclimate to small changes in light levels by adjusting the concentration of photosynthetic pigments and zooxanthellae. However, if photoacclimation cannot fully compensate for the decreased light availability, the stress will result in reduced rates of coral growth, and/or fecundity, competitive ability, resistance to disease, and survival. Additionally, lower energy reserves mean corals are less able to remove deposited sediments that are often associated with turbidity. Sedimentation represents a stress to corals because the prolonged accumulation of sediment on coral tissue results injury, so energy must be invested into mechanisms of sediment rejection. The susceptibility of corals to sedimentation depends on their growth form and their ability to remove sediment using a variety of mechanisms.

The location of Scott Reef on the shelf-edge means it is naturally free of local stressors associated with poor water quality, such as elevated nutrients, turbidity and sedimentation from terrestrial runoff. Levels of sedimentation and turbidity at Scott Reef are similar to other clear-water coral atolls (Dodge et al. 1974; Kojis and Quinn 1984; Rogers 1990). Periodic reductions in water quality at Scott Reef are due to tidal movements, storms and cyclones. Other potential sources of reduced water quality include future offshore development proposed in proximity to Scott Reef, which could temporarily increase turbidity in the vicinity of some development related activities. Good water quality and high rates of growth and survival of coral communities at Scott Reef probably underlie their recovery following the mass-bleaching in 1998. Additionally, high water quality and light penetration means some coral communities are found in habitats down to 70 m depth. Natural levels of turbidity and sedimentation at Scott Reef are strongly influenced by habitat conditions (e.g. wind, waves, tides) and the physical characteristics on and around a reef (e.g. depth, location, amount of sediment on the substrata). Turbidity and sedimentation are usually highest in sheltered locations, such as the lagoon or deeper reef slopes, during spring tides or periods of storms and cyclones, and lowest in shallow wave-exposed areas during periods of neap tides and calm conditions (Wolanski et al. 2005).

At Scott Reef, levels of turbidity and sedimentation tend to be higher and more variable in the shallow- than the deep-habitats. In the shallow-habitat, sedimentation varies seasonally and with exposure to storms and cyclones (Figure 5.2.5), but is also highest in locations adjacent to the deep-channel which have a sandy substrata and high current flow. In contrast, locations in the southern part of south-lagoon have low current flow and sedimentation, characterised by silt fractions and higher levels of turbidity. Mean sedimentation rates within months of sediment-trap deployment ranged widely, from a minimum of 0.8 mg cm^{-2} d^{-1} to a maximum of 6.9 mg cm^{-2} d^{-1} following periods of storms and cyclones, but there are no consistent patterns among locations (Gilmour et al. 2009b). Mean sedimentation during most periods was consistently < 2 mg cm^{-2} d^{-1}. In comparison, rates of sedimentation in the deeper-habitats were lower and less variable than in the shallow-habitat, being less influenced by storms and cyclones. In depths of between 20 m and 60 m in the south-lagoon, means sedimentation rates usually ranged between 0.2 and 0.5 mg cm^{-2} d^{-1}. Compared with rates of sedimentation, levels of turbidity at Scott Reef in depths of between 10-50 cm^{-2} are more consistent through time and among locations, usually being < 0.2 NTU during months around summer and $<$ 0.1 NTU during months around winter; the exception was much higher summer (0.88 NTU) and winter (0.52 NTU) levels near the southern part of south-reef.

Because the coral communities at Scott Reef have not evolved to cope with terrestrial inputs, they are probably highly susceptible to prolonged increases in turbidity and sedimentation. The impacts of turbidity and particularly sedimentation on coral communities also vary dramatically according to the types of sediments that are produced. A given weight of silt in suspension is more likely to reduce light penetration and stress corals when deposited than the same weight of sand sized particles. Although course particles are more difficult to remove that fine sediment, the accumulation of fine silt and clay over the same period of time is more likely to injure corals than are larger grain sizes, particularly with increasing organic content and bacterial activity (Hodgson 1990; Stafford-smith 1993 (Hodgson 1990; Weber et al. 2004). Even low levels of sedimentation combined with polysaccharides exuded by bacteria and diatoms (marine snow) can kill coral recruits (Fabricius et al. 2003). Additionally, mechanisms of sediment removal by corals have not evolved to cope with the coagulation of clay sized particles on their tissue. The interaction among the rates, types, and durations of sedimentation, and their effects on corals is still poorly understood (Fabricius and Wolanski 2000). The highest rates of sedimentation at Scott Reef occur after sand is suspended during cyclones, and the deposited sediment is characterised by a high fraction of course sand particles. A high fraction of fine silt characterised deposition at locations at the southern part of south-lagoon, but the total weights of deposition were consistently low, at below 2 mg cm^{-2} d^{-1} (Gilmour et al. 2009b).

Figure 5.2.5 Natural reductions in water quality at Scott Reef. Increased levels of turbidity and sedimentation at Scott Reef are a consequence of re-suspension during spring tides, storms and cyclones. a) High levels of turbidity and sedimentation were observed at Scott Reef following Cyclone Fay in 2004. b) Sediment accumulation injures coral tissues and facilitates the settlement of algae that can cause further injury over time.

Outbreaks of coral diseases and predators

Outbreaks of diseases and predators among coral communities are a part of their natural dynamics and a means of regulating a high abundance of a few dominant species. However, in recent decades there is increasing concern that outbreaks of coral diseases and predators on coral reefs are becoming more frequent and severe, due to a range of human activities. Coral diseases have emerged recently as a major threat to the world’s coral reefs (Garrett and Ducklow 1975; Antonius 1985; Richardson et al. 1998; Al-Jufaili et al. 1999; Garzon-Ferreira et al. 2001; Nugues 2002). There are currently approximately 20 diseases known to infect more than 100 species of corals (Sutherland et al. 2004), of which some are species-specific and others infect a wide range of species (Figure 5.2.6(a)). Most diseases are transmitted by pathogens such as bacteria, cyanobacteria and fungi, which are passively dispersed through the water column or transmitted by biological vectors. Outbreaks of coral predators most commonly involve the crown-of-thorns starfish *Acanthaster* and the marine snail *Drupella* (Figure 5.2.6(b)). Outbreaks of coral diseases and crown-of-thorns are often linked to a range of disturbances and anthropogenic stressors on the Great Barrier Reef (De'ath and Moran 1998; Bruno et al. 2003; Brodie et al. 2005) and outbreaks of *Drupella* have been recorded at Ningaloo Reef (Black and Johnston 1994; Holborn et al. 1994).

Susceptibility to most coral diseases and possibly predators is much greater when a coral is stressed. In particular, outbreaks seem to increase when corals are stressed by elevated water temperatures, cyclones or reduced water quality (Baird 1999; Bruno et al. 2003; Sutherland et al. 2004; Heron et al. 2010). Elevated water temperatures in both winter and summer months increase the growth and virulence of disease pathogens, in addition to reducing the immune response in corals. Increases in sedimentation following cyclones or anthropogenic activities have also been linked to an increased prevalence of disease (Green and Bruckner 2000; Sutherland et al. 2004). Outbreaks of *Drupella* have been reported following coral bleaching (Baird 1999) and outbreaks of crown-of-thorn starfish have been linked to increased nutrient levels and overfishing of predatory reef fish (De'ath and Moran 1998; Brodie et al. 2005). In addition to these physical conditions, the abundance of susceptible species within a community also determines the likelihood of outbreaks of coral diseases or predators, which are more likely to occur when there is a high abundance of *Acropora* corals; outbreaks of diseases can also occur in degraded communities with low coral cover.

Through 15 years of monitoring, a low incidence of coral disease is usually observed at Scott Reef, in addition to a low abundance of crown of thorns starfish and *Drupella* (Figure 5.2.6). However, in the last year disease has caused widespread mortality of some *Acropora* corals in at least one location near the *southern part of south*-lagoon, with concern that this could spread to other locations following the bleaching in May 2010. Associated with the recent bleaching and outbreak of diseases were increases in the number of crown-of-thorns and particularly *Drupella* observed feeding on colonies, although the predators were in relatively low abundance and were probably opportunistically feeding on coral already affected by the other stressors.

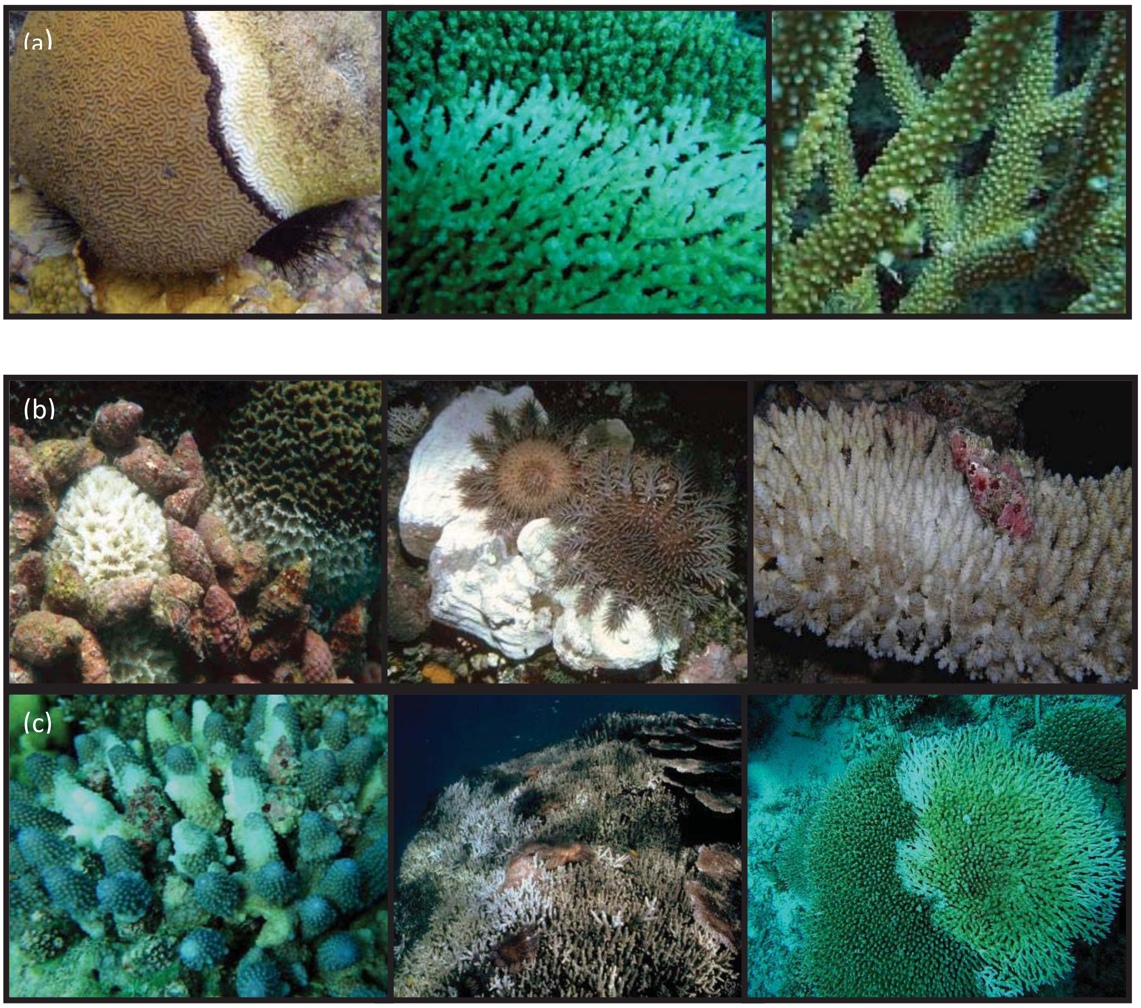


Figure 5.2.6 Outbreaks of coral diseases and predators. a) There are more than 20 known coral diseases, including black-band and white-band diseases, in addition to a range of growth anomalies for which the causes are not well known. b) Outbreaks of coral predators are commonly include the snail *Drupella* and the crown-of-thorns starfish *Acanthastrea.* c) Fast growing *Acropora* corals are often among the most susceptible to disease and predation, particularly when they reach high densities.

Overfishing

Scott Reef has comparatively little pressure from commercial and recreational fishing, but has been exposed to traditional fishing pressures for more than 300 years. Fishing by Indonesians at Scott Reef continues in traditional perahus (Figure 5.2.7) from which they collect a range of animals, including sea cucumbers (bêche-de- mer), trochus (topshell), reef fish and shark fin (Figure 5.2.7). Traditional fishing pressure at Scott Reef today is high, with close to 100 vessel visits per year in recent years (ERM 2008; ERM 2009). Many target species are probably over-exploited (Skewes et al. 2005; Meekan et al. 2006) with a lack of sea-cucumbers and trochus in shallow depths (Skewes et al. 2005; Bryce 2007; SKM 2008). Shark populations are also severely depleted at Scott Reef, compared to the Rowley Shoals, with the most plausible reason being overfishing (Meekan et al. 2006). The consequences of the overfishing these target stocks for the reef ecosystem at Scott Reef is uncertain, so the implications for the persistence of coral communities will not be discussed further. However, there is currently clear selectivity of some stocks, which are depleted throughout the shallow-water habitats at Scott Reef (see Chapter 3, Disturbances at Scott Reef).

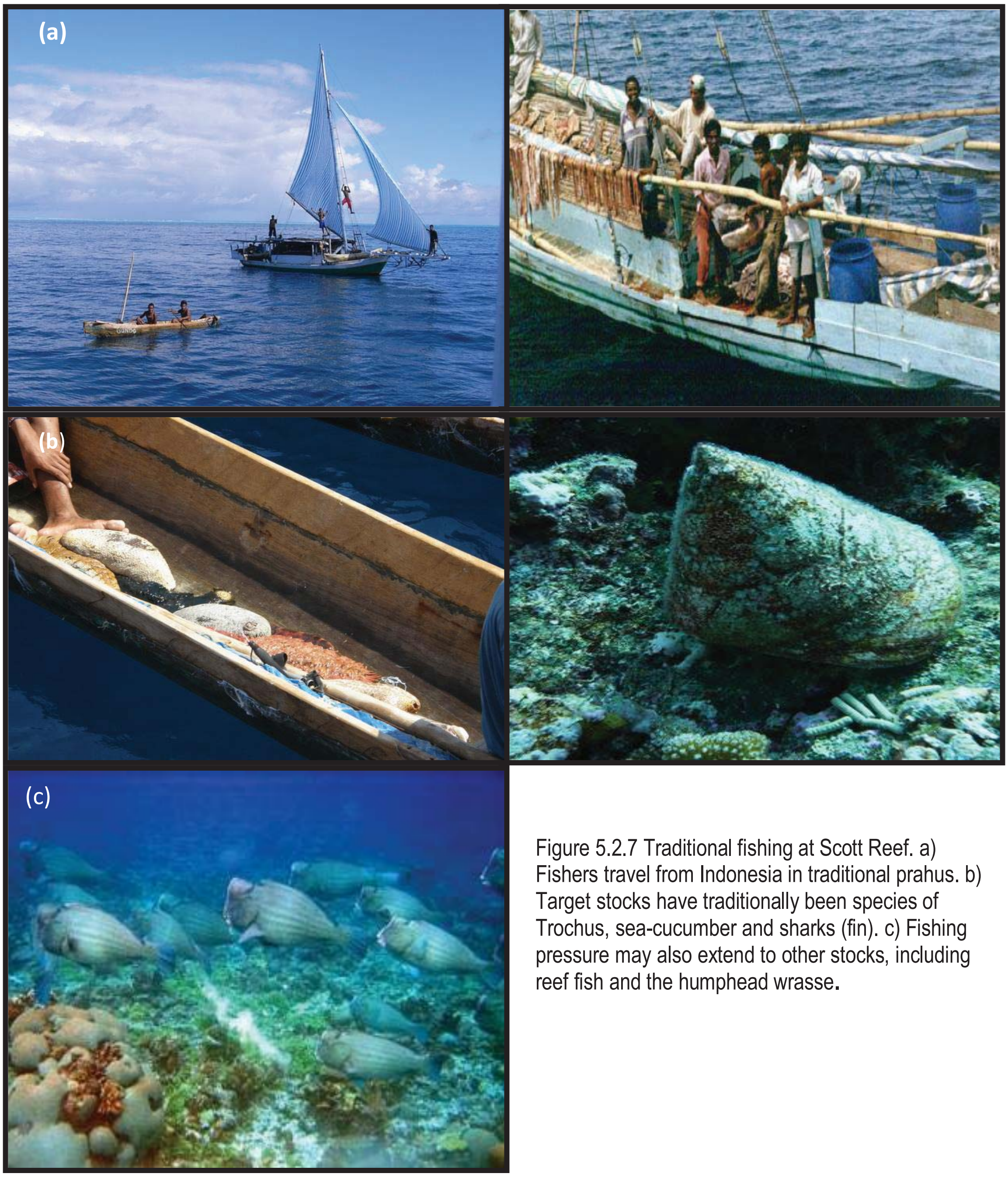


Figure 5.2.7 Traditional fishing at Scott Reef. a) Fishers travel from Indonesia in traditional prahus. b) Target stocks have traditionally been species of Trochus, sea-cucumber and sharks (fin). c) Fishing pressure may also extend to other stocks, including reef fish and the humphead wrasse.

Coral habitats at Scott Reef and the exposure, susceptibility and resilience of their communities to disturbance

Scott Reef is similar to other oceanic atolls off north-west Australia, having lagoonal, reef flat, reef crest and reef slope habitats (Done et al. 1994). However, the unique feature of Scott Reef is the extensive (>200 km^2) deeper-water lagoon (30 - 70m) in the sheltered waters of south Reef. The clear waters of Scott Reef provide sufficient light penetration to these depths to allow significant algal and coral communities to survive and grow in the south-lagoon. In February 2006, a survey of the benthic communities at Scott Reef was conducted by the Australian Institute of Marine Science (AIMS) to produce a map categorising fourteen habitat types (Figure 5.2.8; Smith et al. 2006a). These categories have been further grouped into six general habitats types here (Figure 5.2.8) to discuss variation in their physical conditions, community structure, exposure and resilience to disturbances. The six habitats vary according to their depth range and proximity to lagoons and the outer-slopes at Scott Reef, and are:

1. Shallow water (<15 m) lagoon
2. Shallow water (<15 m) outer-slope;
3. Deeper-water (15-30 m) lagoon;
4. Deeper-water (15-30 m) outer-slope;
5. Deep-water (>30 m) lagoon;
6. Deep-water (>30 m) outer-slope.

Biological and physical data from up to 15 years of monitoring is considered in an attempt to describe the susceptibility of coral communities at the six habitats to future regimes of disturbance at Scott Reef. A highly variable amount of information exists for these different habitats and their communities, on which inferences about susceptibility to disturbances is based; in some instances, inferences are based on a range of quantitative data, in other instances they are hypothetical. Nonetheless, this represents an attempt to integrate a range of data to summarise our current knowledge of coral communities at Scott Reef. Of the six habitat categories (Figure 5.2.9), by far the largest amount of data exist for the shallow water habitat. Among the locations and communities within the shallow-water habitat, there are differences in physical conditions, exposure to disturbances, community structure and demography; similar spatial variation probably exists for the other habitats. A more detailed discussion of variation within the shallow-water habitat follows the general comparisons among habitats.

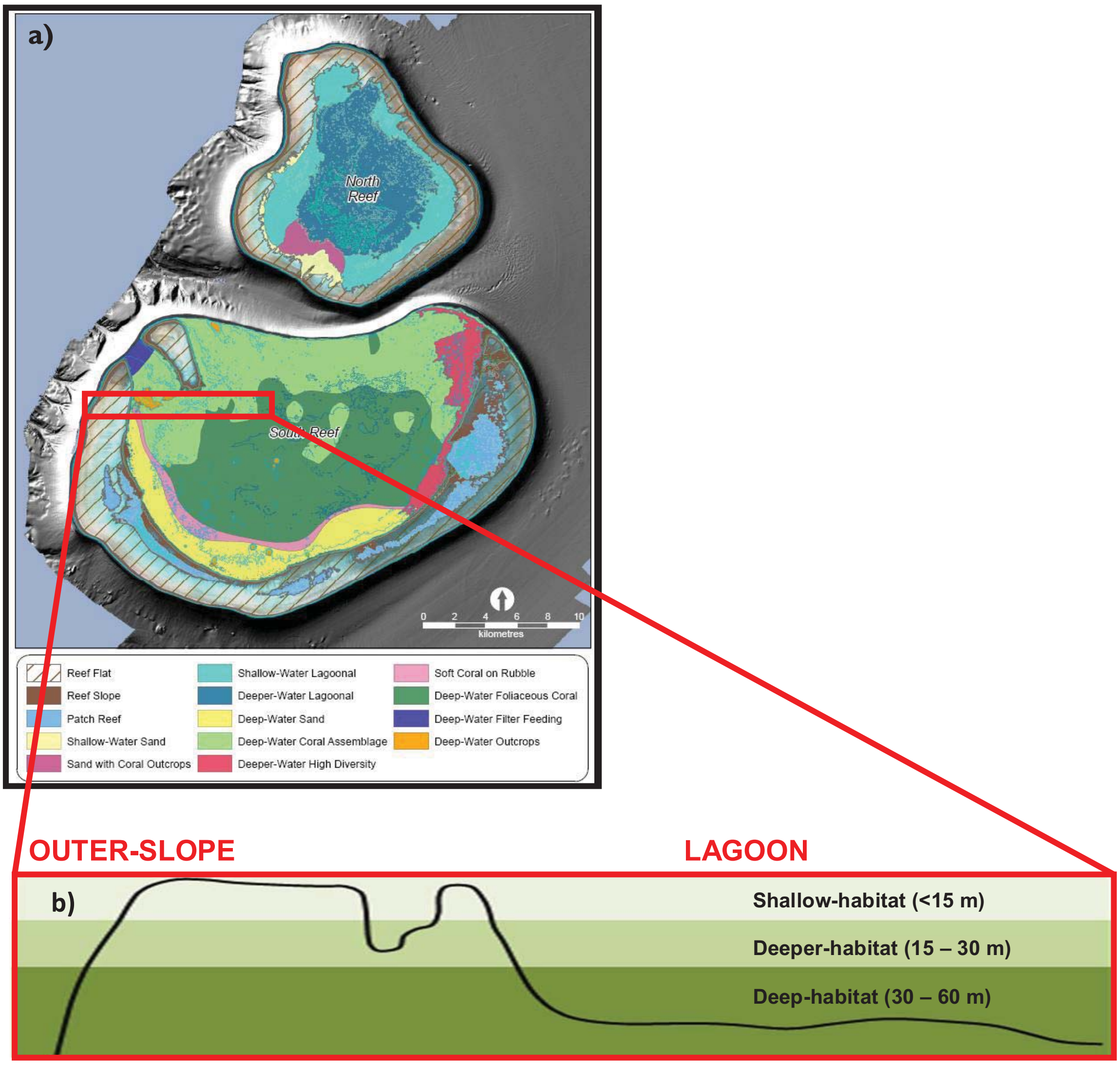


Figure 5.2.8 Coral reef habitats at Scott Reef. a) Habitat map for Scott Reef describing 14 habitat types. b) More general classification of six habitat types according to three depths and location within the north-lagoon, south-lagoon or outer-slope. Habitats of increasing depth are distinguished by darked shades of green, here and in subsequent figures.

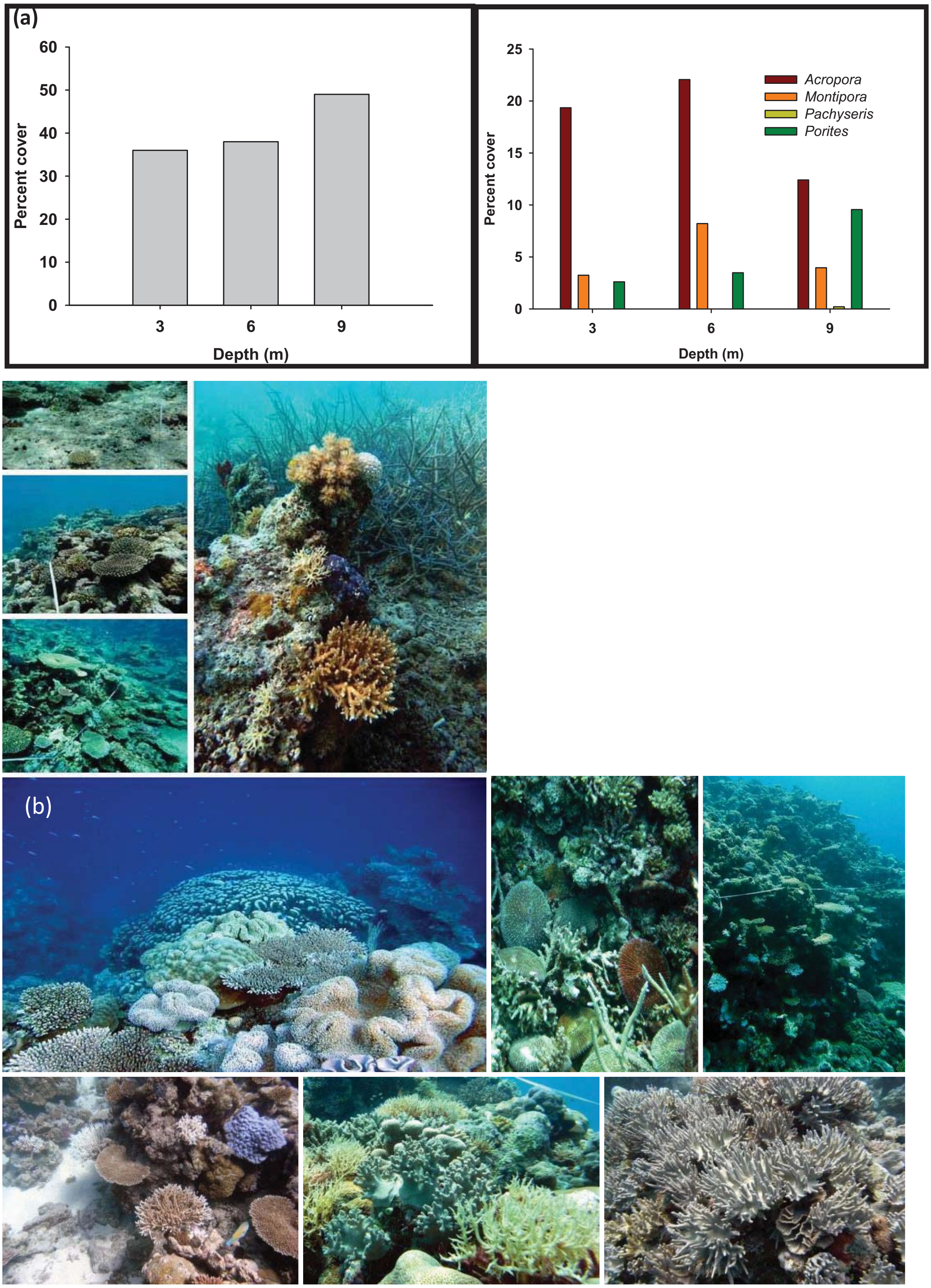


Figure 5.2.9 Coral communities at the Shallow-habitat at Scott Reef. Communities are best described within the south-lagoon and the outer-slope on the eastern side of Scott Reef. a) Coral cover was between 30-70% in 2008, but varies with disturbance. Corals in the genus *Acropora* are most abundant. b) Example of shallow- communities at Scott Reef.

Shallow-water habitats (<15 m)

Within the shallow-water habitat, the reef flat lies in depths less than three metres and extends from the lagoon to outer-slope habitats. Corals on the reef flat are regularly exposed during spring low tides and experience high water temperatures and extreme wave energy during storms and cyclones. The communities closest to the outer-slope are most exposed to wave energy. As a result, coral cover (< 5%) and diversity (< 40 spp.) is low and communities are dominated by robust corals from the families Faviidae, Poritidae and *Acroporidae*. These communities are extremely patchy and dynamic, and are not discussed further.

Habitat conditions and disturbances

The shallow-habitat below the reef flat (<3m) is probably the most favourable for coral growth, largely due to the abundance of light for photosynthesis and nutrition. Within this habitat is a diverse array of micro-habitats in the north and south reef lagoons, and the outer-slopes. Consequently, coral cover and diversity is highest in this habitat (Figure 5.2.9, 5.2.10), but can vary among locations through time because of exposure to disturbances. Almost 300 species from 58 genera of hard coral have been identified in the shallow-habitat, and coral cover is generally between 20 and 50%, but can fall below 10% at some locations following disturbances and can approach 100% following periods of calm.

The shallow-communities experience extreme variation in water temperatures and wave energy during cyclones. (Figure 5.2.10, 5.2.11) Extreme water temperatures and mass-bleaching in 1998 killed around 80% of corals in this habitat, with the most severe increases in temperature occurring in <20 m depth (Figure 5.2.1). In May 2010, increases in water temperature caused bleaching and mortality in some species and locations, but the disturbance was less severe and more selective in its impact than the 1998 event (Figure 5.2.2). Shallow-water communities on the outer-slope may be less susceptible to elevated water temperatures than those in the lagoons, particularly the north-lagoon, although proximity to the deep-water channel between north and south reef also reduces susceptibility to bleaching.

Wave energy from storms and cyclones are also most extreme within the shallow-water habitat (Figure 5.2.10, 5.2.11). In the last decade, category 5 Cyclone Fay crossed directly over Scott Reef in 2004 and category 2 Cyclone George passed to the south in 2007 (Figure 5.2.3, 5.2.4). Both cyclones impacted some of the shallow-communities, but the impacts were selective and varied according to their exposure and the abundance of fragile corals. The outer-slope communities are generally more susceptible to the impacts from cyclones than those in the lagoons.

Good water quality and high light penetration means the shallow-communities may be comparatively resistant to reductions in water quality (Figure 5.2.11). Although small reductions in light are unlikely to kill corals within the shallow-habitat, prolonged exposure to reduced light will probably reduce growth and reproduction, and reduce community resilience to a range of other disturbances. If reductions in water quality are also associated with increased rates of sedimentation, then communities are likely to be more significantly affected than for reductions in light alone. The lower rate of current movement and flushing in some lagoon communities means they are probably more susceptible to increased turbidity, and particularly sedimentation, than communities on the outer-slope. Impacts to communities will also depend on the relative abundances of susceptible species, their growth form, and their ability to photoacclimate and remove sediments.

There has been a low incidence of coral diseases and predators at Scott Reef through the period of monitoring, with the exception of an outbreak of disease in the southern part of south-lagoon in 2010. Of all the habitats at Scott Reef, communities at the shallow-habitat are possibly most susceptible to outbreaks of coral diseases and predators (Figure 5.2.10, 5.2.11), because of higher light penetration and water temperatures, and higher exposure to other stressors. However, little is known about the background distribution of coral diseases and predators at Scott Reef and what conditions would drive outbreaks. Some of the lagoon communities are likely to be more susceptible to coral diseases than those on the outer-slope, because of reduced flushing with the open ocean and lower water quality. Communities are most at risk of outbreaks when communities have very high cover dominated by a few susceptible corals species.

Demography and connectivity

Among all the habitats, background rates of reproduction, recruitment, growth and survival are probably highest for communities in the shallow-water habitat, but also most variable because of their exposure to disturbances. The most common species are widely distributed across the habitat, but variation among locations is often due to the dominance or absence of a few groups of corals. These species characteristically have very high rates of reproduction and growth, but are also most susceptible to common disturbances. For example, some branching and table corals are able to outcompete other corals because of their rates of growth and reproduction, but are also most susceptible to disturbances such as elevated water temperatures, cyclones or outbreaks of predators and disease. The life histories of these species means they have the potential for a wide distribution across Scott Reef, but at any one time their distribution may be patchy and change dramatically under different disturbance regimes. In addition to these species with a more 'boom-bust' life history, communities within the shallow-habitat are also distinguished by corals with only moderate cover at some locations with suitable conditions. These groups of corals tend to have lower rates of growth and survival and lower susceptibility to disturbances, with some exceptions. In particular, some hard and soft corals that distinguish communities in the south-lagoon and adjacent to the deep-channel at north reef have only moderate rates of growth and survival, but are susceptible to disturbance. The life histories of these corals and the limited distribution across Scott Reef means their communities may be less resilient to disturbances, particular those that cause severe and widespread impacts. These differences in coral life histories, community structure, distribution, and disturbance regimes, drive the differences in resilience of communities within the lagoon or slope communities in the shallow-habitat.

Connectivity among locations in the shallow-habitat is largely restricted to less than 10-20 km for the most corals and less than a few kilometres for the brooding corals (Gilmour et al. 2008; Gilmour et al. 2009b). Consequently, recovery from disturbance requires a sufficient number of adult colonies across these spatial scales to supply new recruits to restock the community (Figure 5.2.12). Additionally, the direction of larval dispersal will also influence recovery from disturbances. Communities receiving larvae from several other locations will recover faster than those from which larvae are transported. Regardless of the direction of larval dispersal, if disturbances cause widespread mortality over distances greater than a few tens of kilometres, as with the bleaching in 1998, the supply of recruits is initially low and the communities are slow to recover. In the worst instances, abundant corals that were most susceptible to the bleaching are still comparatively rare ten years later at some locations, which include groups of soft corals and brooding corals.

If disturbances to the shallow-communities are so severe that they cause widespread mortality across the entire habitat, then there is limited opportunity for recovery to be aided by the supply of recruits from other locations within the habitat. However, recovery may also be aided by the supply of recruits from deeper-habitats (>15 m) if they overlap in common species and were sheltered from the disturbance (Figure 5.2.12). In the case of mass-bleaching in 1998, the most extreme increases in water temperature were restricted to the shallow-habitat (Figure 5.2.1). There are clear differences in community structure between the shallow-habitats (<15 m) and deeper-habitats (15-30 m), but a degree of overlap in common species probably exists between the two habitats in depths of greater than approximately 7 m. Thus, communities in the deeper-water habitat that are far less affected by extreme water temperatures and cyclones may supply recruits to aid the recovery of some shallow-communities (Figure 5.2.12). Observations during the coral bleaching indicated that widespread mortality was restricted to depths of less than 20 m, and that local recovery for at least some groups of corals was assisted by the growth and reproduction of survivors in depths of around 20 m; this was particularly true for some brooding corals whose larvae disperse locally (see Chapter 5.1). However, the degree of connectivity between the shallow and deep (>30 m) communities is likely to be far less than is required for these communities to aid each other's recovery following disturbance (Figure 5.2.12).

HABITAT	DEPTH	TEMPERATURE	LIGHT (% surface)	TURBIDITY (NTU)	SEDIMENTATION (mg/cm/d)	CURRENT FLOW	WAVE ENERGY	HARD CORAL SPECIES	HARD CORAL GENERA	HARD CORAL COVER (%)
SHALLOW	0-15 m	High	High (38)		Medium (2)	High	High	High (295)	High (58)	High (20-60%) temporally variable
DEEPER	15-30 m	Medium	Medium (17)		Medium (2)	Medium	Medium	Medium (150?)	High (40?)	Medium (20-40%?)
DEEP	30-60 m	Low	Low (4)	0.15	Low (0.5)	Low	Low	Low (51)	Medium (21)	Medium - Low (10-30%) spatially variable

Figure 5.2.10 Habitat conditions and susceptibility of scleractinian coral communities to potential disturbances at Scott Reef. Approximate habitat conditions and community characteristics, generalised through time and across depths and locations, for the different habitats. Inferences about habitat conditions are based on a combination of quantitative and qualitiave information.

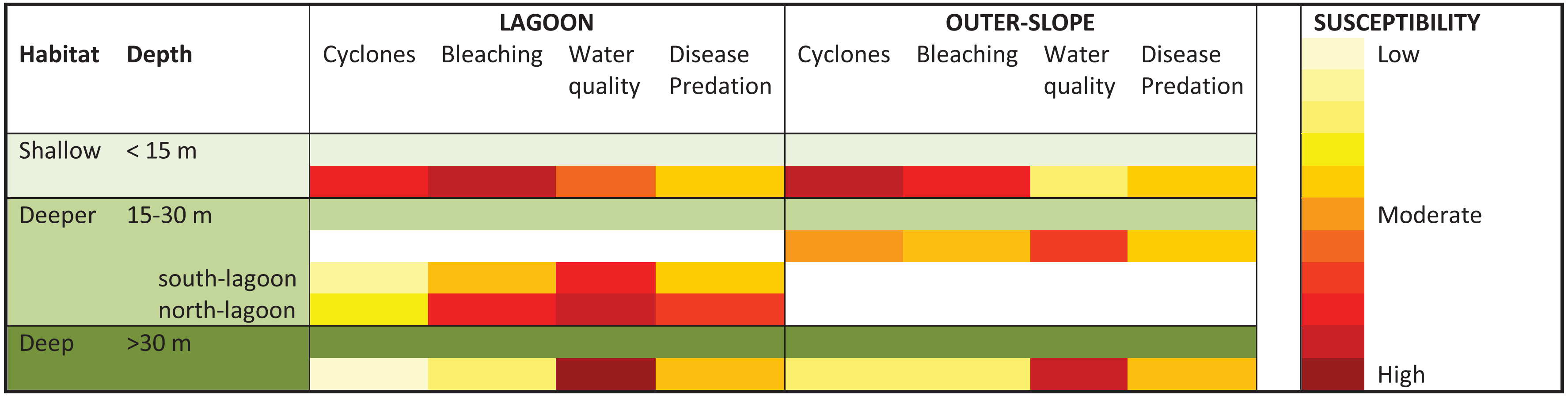
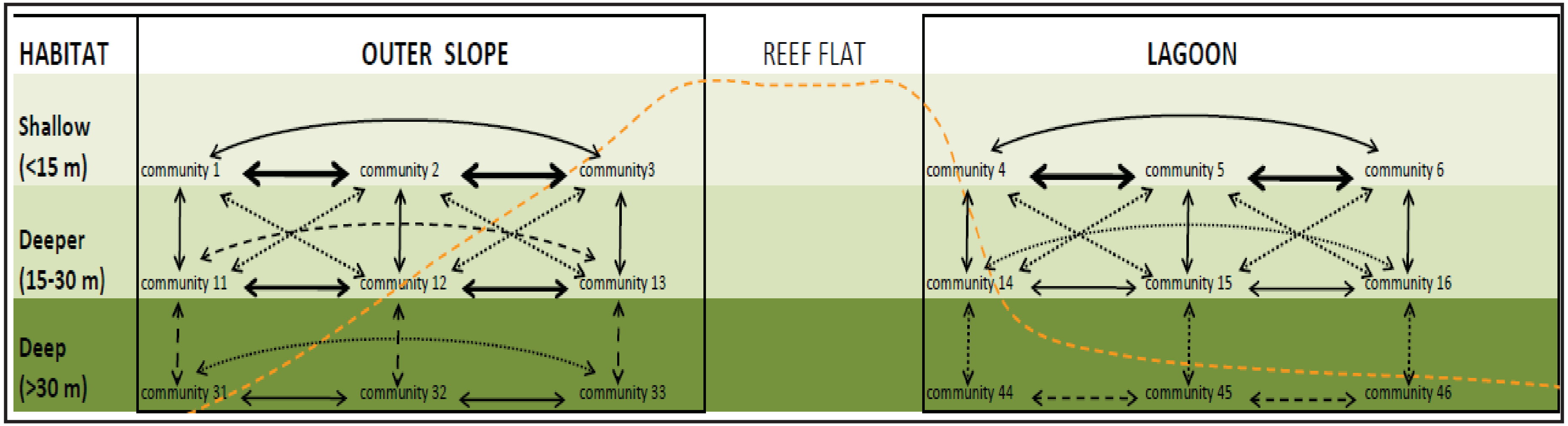


Figure 5.2.11 Hypothetical susceptibilities of coral communities within different habitats to potential disturbances at Scott Reef. Lagoon communities are divided between those at north-reef and south-reef.



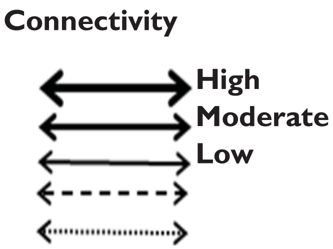


Figure 5.2.12. Hypothetical patterns of connectivity among communities at different locations within habitats (vertical arrows); the same location and different habitats (horizontal arrows); and different locations and different habitats (diagonal arrows). Weight of arrows represents strength of connectivity, based on overlap in abundances of common species and distances of larval dispersal (not direction of dispersal). Vertical arrows connecting adjacent communities within the same habitat represent routine distances of dispersal of 10 km.

Deeper-water habitats (15-30 m)

Habitat conditions

There is far less known about the communities in the deeper-water (15-30 m) habitat than in the shallow-habitat (<15 m), and perhaps even less known about variation in the structure of its communities than in the deep-habitat (> 30 m). There is a diverse array of micro-habitats and conditions among locations throughout the deeper-habitat, particular in the lagoons at north and south reef (Smith et al. 2006a), (Figure 5.2.8). However, the reef slope communities in the deeper-habitat probably have similar, but lower, cover and diversity than those in the shallow-habitat (Figure 5.2.10).

There is probably a degree of overlap in community structure and demography between the shallow- and deeper-water communities at similar locations on the reef, so some inferences about resilience are extrapolated from the shallow-communities. The differences in substrata type, habitat conditions and community structure between the shallow- and deeper-habitats at similar locations are probably greater in the south- and north-lagoon, than for the outer-slope. However, reductions in light and a steep-slope are also likely to alter demography with increasing depth on the outer-slope locations. Conditions in the deeper-water habitat in the north-lagoon are very different to those at the outer-slope, and communities prior to the bleaching in 1998 were characterised by a low diversity but high cover of a few branching corals. Most of these corals were killed during the bleaching and the available data indicate limited recovery of the most susceptible species and a low diversity and cover of corals in the deeper-lagoon at north reef. Some species in the deeper-communities are likely to be abundant in the shallow-habitat, but probably in depths greater than approximately 7 m.

Exposure to disturbances

The communities in the deeper-water habitat are less exposed to extreme changes in water temperature and wave energy from cyclones than those in the shallow-habitat (Figure 5.2.10, 5.2.11). The most extreme increases in water temperature associated with the 1998 bleaching event were restricted to less than 20 m depth (Figure 5.2.1), and observations by divers indicated the deeper-water communities did not suffer nearly the same level of bleaching. However, the diffusion of warm water to depths greater than 20 m and the warming of the entire deeper-habitat increased more rapidly after a month elevated temperatures (Figure 5.2.1). The habitat is therefore not a certain refuge from future mass-bleaching events, particularly following protracted periods of warming. Additionally, it is relative changes in water temperature that cause mass-bleaching and there were large relative increases in water temperature throughout the deeper-habitat during the recent (May 2010) bleaching at Scott Reef (Figure 5.2.2). Temperatures were over 30°C at a depth of 40m, but the impact on the deeper-water communities was unknown. Historically, the coral communities in the deeper-habitat have probably experienced only moderate fluctuations in temperature, and the most abundant corals are probably less resilient to relative changes in water temperature than those in the shallow-habitat.

Among locations within the deeper-habitat, communities near the southern part of south-lagoon, and particularly in the north-lagoon, are probably most susceptible to elevated water temperatures (Figure 5.2.3). Low current flow and the shallow depth of the lagoon mean the communities in the deeper-habitat are probably exposed to hot saline water for protracted periods of warming. Temperatures in the north-lagoon are probably higher than for similar depths at other locations at Scott Reef, and coral mortality following the 1998 bleaching was highest in the north-lagoon; this mortality was also due to the high abundance of susceptible species.

Communities in the deeper-habitat are less exposed to wave energy from cyclones than those in the shallow-habitat (Figure 5.2.10, 5.2.11). Although not as likely to be fragmented from extreme wave energy, the deeper-communities are susceptible to smothering by sand and coral fragments suspended by storms and cyclones (Figure 5.2.3). As with their susceptibility to bleaching, the outer-slope and lagoon communities probably have different susceptibility to cyclones, but the patterns of exposure and impact are difficult to infer and strongly depend on the abundance of fragile corals.

Light penetration to the deeper-habitat is less than half of that in the shallow (Figure 5.2.10), and probably restricts the distribution of many coral species. Consequently, reductions in water quality that also reduce light penetration will affect community structure. The magnitude of the impacts from reduced light penetration on the deeper-communities, and whether they are lethal or sub-lethal, will depend on the ability of common species to photoacclimate. Long-term reductions in light and photoacclimation probably have energetic consequences for the corals, reducing resilience of communities to a range of other disturbances. Additionally, reductions in light penetration are often also associated with other stressors, such as sedimentation. The impacts of sedimentation on deeper- communities will depend on the abundance of susceptible species and their ability to remove the deposited sediments. Periodic sedimentation may be common for some deeper-water communities following storms and cyclones, although the sediment fractions are likely to be course, the periods of deposition shorter, and the coral have more energy reserves for sediment removal, than would be expected from anthropogenic increases. Rates of sedimentation will also be influenced by hydrodynamics, and whether currents remove or deposit sediments locally. Among locations within the deeper-habitat, communities at the southern part of south-lagoon and in north-lagoon are again probably most susceptible to reductions in water quality, because of their limited flushing and/or lower water quality (Figure 5.2.11).

The susceptibility of deeper-water communities to outbreaks of disease and coral predators is unknown. The diverse, well flushed reef slope communities are probably less susceptible than those in the north-lagoon or bottom of the south-lagoon (Figure 5.2.11). Communities in the north-lagoon and bottom of south reef experience less flushing, higher temperatures, lower water quality, and can be dominated by a high abundance of susceptible species, all of which are likely to increase the incidence of outbreaks of disease or coral predators.

Demography and connectivity

Little is known about the demography of communities within the deeper-habitat and the degree of connectivity among locations. Communities with a similar structure and location to those in the shallow-water habitat may be expected to display similar patterns of demography and connectivity, particularly those on the outer-slope. However, a variety of micro-habitats and communities within this habitat is likely to produce a similar variation in patterns of demography and connectivity.

Patterns of reproduction and recruitment of corals in the deeper-communities are likely to be similar to that in the shallow-habitat, with the same proportion of spawning and brooding corals reproducing at similar times. The rates of reproduction, recruitment and growth may be lower than in the shallow-habitat, given lower water temperature and light availability. However, many species within the deeper-habitat may be well adapted to the conditions and some can proliferate under these conditions, such as the branching corals that dominated the north-lagoon before the bleaching. Survival of the corals well adapted to the deeper-water habitat may be similar or higher than those in the shallow-habitat, given they are exposed to less severe and more patchy disturbances; the exception is perhaps the susceptibility of some lagoon communities in the deeper-habitat that are highly susceptible to reductions in water quality and outbreaks of coral diseases or predators.

As with communities within the shallow-habitat, routine connectivity among locations within the deeper-habitat is probably restricted to distances less than 10-20km for the spawning corals and less than a few kilometres for the brooding corals (Figure 5.2.12). Given that impacts to the deeper-communities are likely to be less severe and more patchy than for the shallow-communities, there may be a greater opportunity for recovery from disturbances to be supplemented by the production of recruits locally, or from adjacent locations. However, the diverse habitat conditions and the patchy distribution of some deeper-communities (Figure 5.2.8) will also restrict connectivity and the supply of recruits to assist in recovery from disturbances.

Resilience of the deeper-communities following disturbances could be assisted by the production of recruits from the shallow- (<15 m) and/or deep- (>30 m) habitats, assuming some overlap in common species (Figure 5.2.12). The greatest degree of community overlap probably exists with the shallow-habitat, but for these communities to assist in recovery would require less severe impacts in the shallow-habitat than in the deeper-habitat, which is unlikely in many instances. Relative increases in water temperatures could result in mass-bleaching to deeper-communities and little impacts in shallow-communities that are better adapted to temperature fluctuations. In this instance, recruits from common species in the shallow-communities could supplement the recovery of those deeper, and subsequently increase the resistance of the deeper-communities to increasing water temperatures. However, in most instances shallow-communities are likely to be affected by disturbance worse than those in the deeper-habitat. Conversely, communities in the deep-habitat (>30m) that escaped disturbance impacts could provide recruits to supplement the recovery of deeper-communities, depending on the degree of community overlap (Figure 5.2.12). But, there is likely to be a limited overlap in abundant species with deep-communities (Figure 5.2.13), given conditions in depths beyond 30 m are becoming far more marginal for coral growth and require a high degree of adaptation, although little is known about species abundances throughout these habitats.

a)

Acroporidae

Astreopora expansa
Montipora aequituberculata

Agariciidae

Leptoseris explanata
Leptoseris foliosa
Leptoseris mycetoseroides
Leptoseris papyracea
Leptoseris scabra
Leptoseris yabei
Pachyseris speciosa
Pavona cactus
Pavona varians

Euphylliidae

Euphyllia cristata

Faviidae

Caulastrea furcata
Cyphastrea chalcidicum
Cyphastrea microphthalma
Cyphastrea serailia
Echinopora lamellosa

Fungiidae

Ctenactis crassa
Ctenactis echinata
Fungia concinna
Fungia horrida
Fungia paumotensis
Fungia repanda
Herpolitha limax
Herpolitha weberi
Sandalolitha robusta

Merulinidae

Hydnophora exesa
Hydnophora rigida

Mussidae

Australomussa rowleyensis
Lobophyllia hemprichii

Pectiniidae

Echinophyllia aspera
Echinophyllia echinata
Mycedium elephantotus
Oxypora lacera

Pocilloporidae

Seriatopora hystrix
Stylophora pistillata

Poritidae

Porites vaughani

Siderastreidae

Psammocora haimeana
Psammocora profundacella

b)

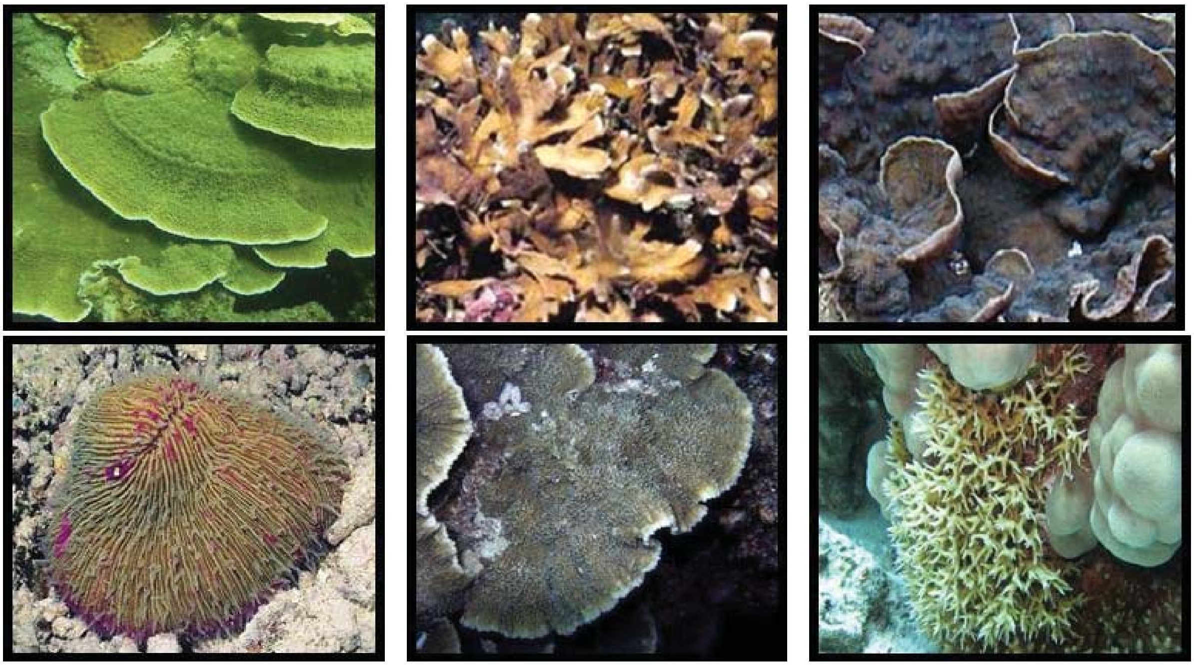


Figure 5.2.13 Overlap in community structure between shallow- and deep-communities at Scott Reef. a) Species of coral found in both the shallow and deep-habitats at Scott Reef in the south-lagoon. Of these species, probably only a few are common within both habitats and none are abundant in both habitats. A total of 295 species from 58 genera and 14 families were identified in the shallow-habitat, compared with 51 species from 27 genera and 11 families in the deep-habitat. Similar data do not exist for the deeper-habitat, although the degree of overlap in common species with the shallow-habitat is likely to be far greater. b) Example of coral species common in both shallow- and deep- communities, from left top to bottom rght: *Montipora crassituberculata, Pavona cactus, Echinopora lamellosa, Fungia repanda, Mycedium elephantotus* and *Seriatopora hystrix.*

Deep-water habitats (>30 m)

Habitat conditions

The coral communities in the deep-water habitat generally have lower cover and particularly lower diversity than those in the shallower-habitats (Figure 5.2.10, 5.2.14), but cover can vary widely among locations. The deep-habitat is restricted to the south-lagoon and the outer-slope, and is not found in the north-lagoon (Figure 5.2.8). The highest cover and diversity of corals in the deep-habitat is in the south-lagoon between 30 and 50 m (Figure 5.2.8), beyond which hard coral cover is low and communities are dominated be filter-feeding organisms such as sea-whips, sea-fans, sponges, and calcareous algae (Figure 5.2.14). Light penetration to the deep-habitat is roughly 10% of that in the shallow-habitat (Cooper et al 2009), and this is a primary reason for the lower diversity and cover of coral communities. The deep-communities are dominated by corals with highly adapted growth and physiology that maximises the energy obtained from the available light (Figure 5.2.14). The degree of adaptation required to live in this habitat excludes most hard coral species.

As with the other habitats, conditions vary dramatically among deep-communities in the south-lagoon and on the outer- slope. The substrata for coral growth on the outer-slope can be much steeper and locations can experience lower light and temperatures. This variation among locations has obvious implications for differences in community structure, but the implications for community demography and resilience are unknown. Within the south-lagoon, the deep-communities have highly variable coral cover and diversity (Figure 5.2.8; Smith et al. 2006a). The communities closest to the deep-channel and reef edge between 30 and 70 m depth characteristically have low to moderate cover and diversity, and an abundance of other benthic organisms such as calcareous algae, gorgonians and sponges. In some instances, these communities resemble those on the outer-slope in the same habitat. The communities towards the centre of the south-lagoon in 30-50 m depth are characterised by moderate to high cover of a few coral species with plate-like growth form, which can approach 100% cover (Figure 5.2.8, 5.2.14). The outer-slope communities have a very different structure to those in the more sheltered and less sloping substrata of the south-lagoon (Smith et al. 2006a). Communities of hard corals were found in this deep-water habitat to 50 m, but filter-feeding sponge and soft coral communities were most common at this depth and extended down the reef slope to 100 m; the deep-communities on the outer-slope are also very different those in the shallower (< 30 m) habitats on the outer-slope. Known patterns of variation in structure and demography of the shallow-communities are therefore unlikely to apply in the same way to these deep-communities.

Exposure to disturbances

Of all the coral habitats at Scott Reef, the deep-water communities are least likely to be exposed to elevated water temperatures and wave energy from cyclones. Elevated water temperatures during the 1998 bleaching were mostly restricted to less than 30 m, but began to penetrate to deeper than 30 m although after two months (Figure 5.2.1). During the recent (May 2010) bleaching at Scott Reef, water temperatures as high as 30°C reached 50m at the south-lagoon and outer-slope communities (Figure 5.2.2). It is the relative increases in water temperature that result in coral bleaching, and these deep-communities are unlikely to be as well adapted to changes in water temperatures as those in the shallow-habitat. Consequently, even small absolute increases in temperature of periods of weeks could cause widespread bleaching in the deep-habitat.

The deep-communities in both the lagoon and outer-slope at Scott Reef are unlikely to be susceptible to cyclone disturbance. Wave energy from even the most severe cyclones does not penetrate to these depths, and any impacts are probably restricted to the deposition of sediments and fragments following the cyclone, which is probably rare or unlikley. Corals are unlikely to be well adapted to removing any fragments or sediments and their flat growth form aimed at maximising light absorption makes them more susceptible to sediment accumulation.

Communities in the deep-water habitat are most susceptible to changes in water quality that reduce light penetration and increase sedimentation. Corals in the deep-water habitat obtain most of their nutrition from light absorption and photosynthesis through highly adapted growth forms and physiology (Cooper et al 2009). However, further reductions in light availability would probably limit their nutrition and reduce reproduction, growth and or survival. Some corals, particularly soft corals, are able to switch from autotrophic to heterotrophic nutrition, whereby they feed on particulate matter (URS 2007). However, it is not know whether deep-water corals at Scott reef have this ability, and the availability of a particularly food source may be low (Brinkman et al 2009). It is thought that much of the organic matter carried into the south reef lagoon from the deep-channel is consumed within the water column by microbial communities, and is not available to the benthic communities (Gilmour et al 2009b). The flat growth form of corals in the deep-habitat means they are susceptible to sediment accumulation, and these species are probably not well adapted to actively removing sediment. Reductions in water quality that increase both turbidity and sedimentation are therefore likely to have severe impacts on the deep-communities. Reduced energy reserves from light attenuation means even less energy for sediment removal, and the accumulation of sediments will quickly result in colony injury and probably mortality. A steeper gradient and higher current flow at outer-slope locations means corals in the deep-communities are less able to adopt a spreading growth form than those in the lagoon. Consequently, these communities may by more susceptible to light attenuation and turbidity, but less susceptible to sedimentation, than those in the deep lagoon.

The susceptibility of deep-water corals to outbreaks of coral disease and predators in unknown. Disease outbreaks most characteristically occur at locations with high water temperatures and poor water quality, a high abundance of a few susceptible coral species, or in communities stressed by disturbance. Throughout the deep-habitat, the low diversity and high cover communities in the south-lagoon are probably most susceptible to disease outbreaks or predators, but very little is known about the distribution of diseases and coral predators at these depths.

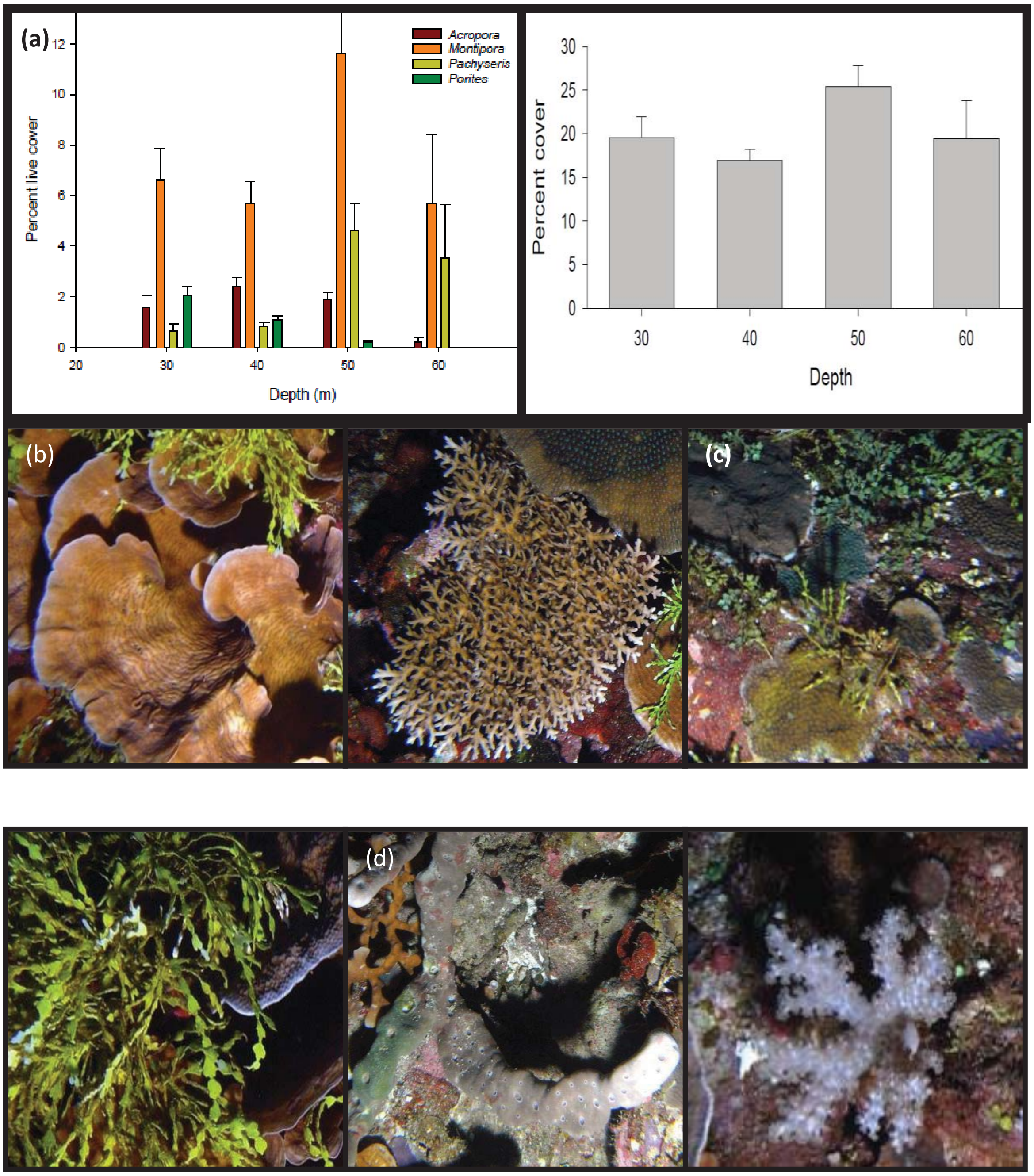


Figure 5.2.14 Coral communities at deep-water habitats at Scott Reef. Deep-water communities are best described within the south-lagoon. a) Coral cover is around 20%, but very patchy among locations, and communities corals in the Genera *Acropora* and *Porites* become less common with depth, and *Montipora* and *Pachyseris* more common. b) Coral communities with the highest cover are dominated by foliose species and c) coralline algae, and with increasing depth d) soft corals and sponges become more common.

Demography and connectivity

Very little is known about the demography of corals in the deep-communities. They are certainly close to the limit of their distribution, particularly for available light, and conditions are less than optimal for most of the community. Consequently, rates of reproduction, recruitment and growth are probably less than for corals in shallower-habitats. However, these lower demographic rates may be sufficient for the persistence of the communities because they are exposed to much less severe regimes of disturbance than those in the shallower-habitats.

The patterns of connectivity among the deep-communities are probably more restricted than those for the shallow-communities (Figure 5.2.13). Connectivity depends on the distribution of similar communities through the habitat, and on the spatial patterns of reproduction and recruitment. The degree of connectivity and the potential for communities to facilitate each other's recovery throughout the deep-habitat is probably reduced by their sparse and patchy distribution, particularly the different lagoon communities. Corals within the deep-habitat are known to reproduce by both spawning gametes and brooding larvae (Gilmour et al 2008; Cooper et al 2009), although the proportion of corals adopting each reproductive strategy is unknown. The brooding corals are likely to have patterns of dispersal restricted to less than a few kilometres, as with those in the shallow-habitat (Gilmour et al 2008; Gilmour et al 2009; Cooper et al 2009). However, the distances of dispersal for the spawning corals is less certain. Most spawning corals have buoyant egg-sperm bundles that float to the surface after spawning and then disperse for several days until the larvae are ready to settle. However, some spawning corals, such as the mushroom corals common in the deep-habitat, spawn much smaller eggs that are less buoyant; larval dispersal is therefore much more localised (Gilmour 2004). The proportion of corals in the deep-habitat that spawn buoyant eggs and sperm is unknown, as is the implications of this reproductive mode for dispersal and recruitment. The likelihood of recruiting successfully back into a patchy distribution of deep-communities is possibly reduced by a longer period of dispersal in shallow-waters. If so, corals in deep-communities may display reproductive traits that reduce the dispersal through the water column and maximise local recruitment, such as less buoyant gametes or brooding larvae. Regardless of their reproductive strategies, the patchy distribution of deep-water communities is likely to reduce their patterns of connectivity and the ability of other communities to aid recovery following disturbances. There is also probably limited opportunity for communities in shallower-habitats to aid the recovery of deep-communities following disturbance, given the requirement for a high degree of overlap in abundant species (Figure 5.2.14) and the requirement for larvae produced in the shallow-habitats to recruit to the deep. Consequently, the recovery of communities in the deep-habitat following disturbances is likely to rely heavily on the survival of corals within each community, and not from the supply of larvae from outside, making them particularly susceptible to severe disturbances acting over scales of greater than a few kilometres.

Variation among locations within the Shallow-water habitat

Habitat conditions

Among all the habitats at Scott Reef, by far the most information exists for the reef-slope (9 m) communities within the shallow-habitat (Figure 5.2.15). For these reef-slope communities, the differences in habitat conditions, exposure to disturbances, community structure and demography, largely depend on whether they are located on the outer-slope or in the lagoons; further differentiation depends on whether they are located in the north- and south-reef lagoons, and their proximity to the deep-channel between north- and south-reef.

Conditions at the outer-slope locations (SS1, SS2, SS3) are relatively similar, being characterised by a steep slope, a low cover of sand, and normally moderate water temperatures (Figure 5.2.16, 5.2.17). However, temperatures at Location SS2 can elevate with the flow of warm saline water over the reef from the north-lagoon. Communities normally experience moderate water flow and levels of turbidity and sedimentation, apart from times of exposure to cyclonic wave energy from the east.

The degree of similarity among the remaining locations is less than for the outer reef locations, and all vary in significant ways (Figure 5.2.16, 5.32.17). Among the remaining locations, SL3 on the inside of the west hook is most similar to the outer-slope locations, but also shares attributes with Location SL4 adjacent to the deep-channel on north-reef, and Location SL1 inside east hook. Location SL4 is characterised by a steep slope, a hard substrata and a high cover of rubble, but low cover of sand. In contrast, Location SL3 is characterised by a relatively flat substrata and a high cover of both rubble and sand, with patchy coral outcrops. Both locations experience a wide range of water temperatures, due to the flow of warm water out of the north-lagoon and cool water from the deep-channel. The high degree of mixing from these cool water intrusions reduces stratification and the likelihood of extreme heating during some summer months. The flow of warm saline water out of the north-lagoon exposes these locations to a moderate to high salinity range, and their proximity to the deep-channel means they experience high current flow, particularly during spring tides. Both locations are characterised by a moderate level of chlorophyll and turbidity, but high wave energy; the high cover of sand at SL3 is re-suspended by this wave energy, causing higher rates of sedimentation composed of courser fractions of sand than at Location SL4.

Conditions at Location SL1 on the inside of east hook fall between those characteristic of Location SL3 at the west hook and Location SL2 at the southern part of south-lagoon (Figure 5.2.16, 5.32.17). The east hook location has a moderate slope and moderate cover of rubble and sand. Water temperatures, salinity range, wave energy, current flow, chlorophyll, turbidity and sedimentation are all moderate, and sedimentation is characterised by fractions of fine sand and silt. There is probably a high degree of mixing of water from a range of different locations at east hook and there is evidence of strong eddy at this location.

Conditions at Location SL2 in the southern part of the south-lagoon are unique from all other locations (Figure 5.2.16, 5.32.17). The location is characterised by an extremely fragile and moderately sloping substrata, with a low cover of sand and low wave energy. Water temperatures can be high, due to the lack of mixing with oceanic water, low current flow and a high residence time. There is a low range of salinity, low sedimentation characterised by fine silt and clay, and high turbidity and chlorophyll content. The reasons for the low sedimentation and high turbidity at SL2 are uncertain, but possibly related to the low current flow and lack of mixing with the open ocean.

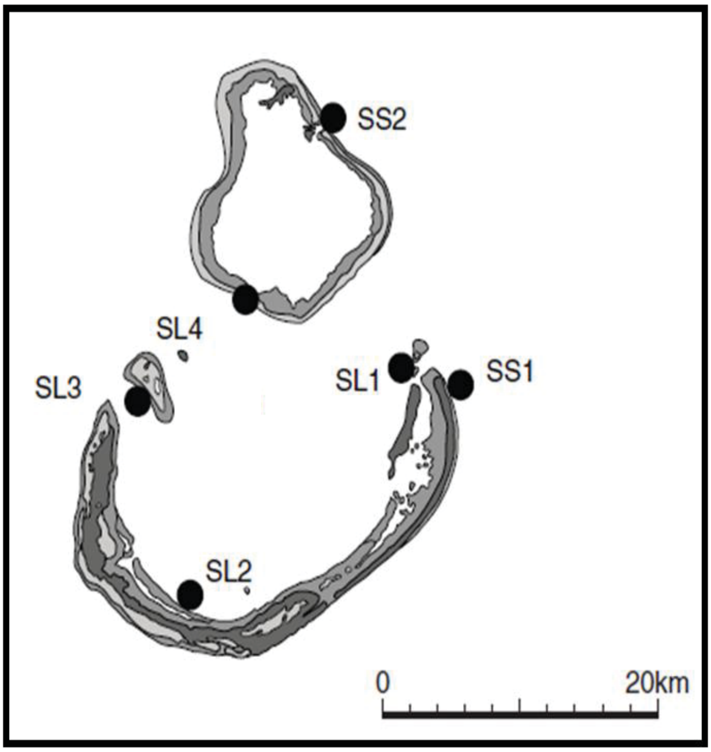


Figure 5.2.15 Study locations within the shallow-water habitat on the reef-slope (9m) at Scott Reef, at which some physical and most genetic and biological data have been collected for up to 15 years; this includes periodic surveys at Seringapatam Reef (SS3).

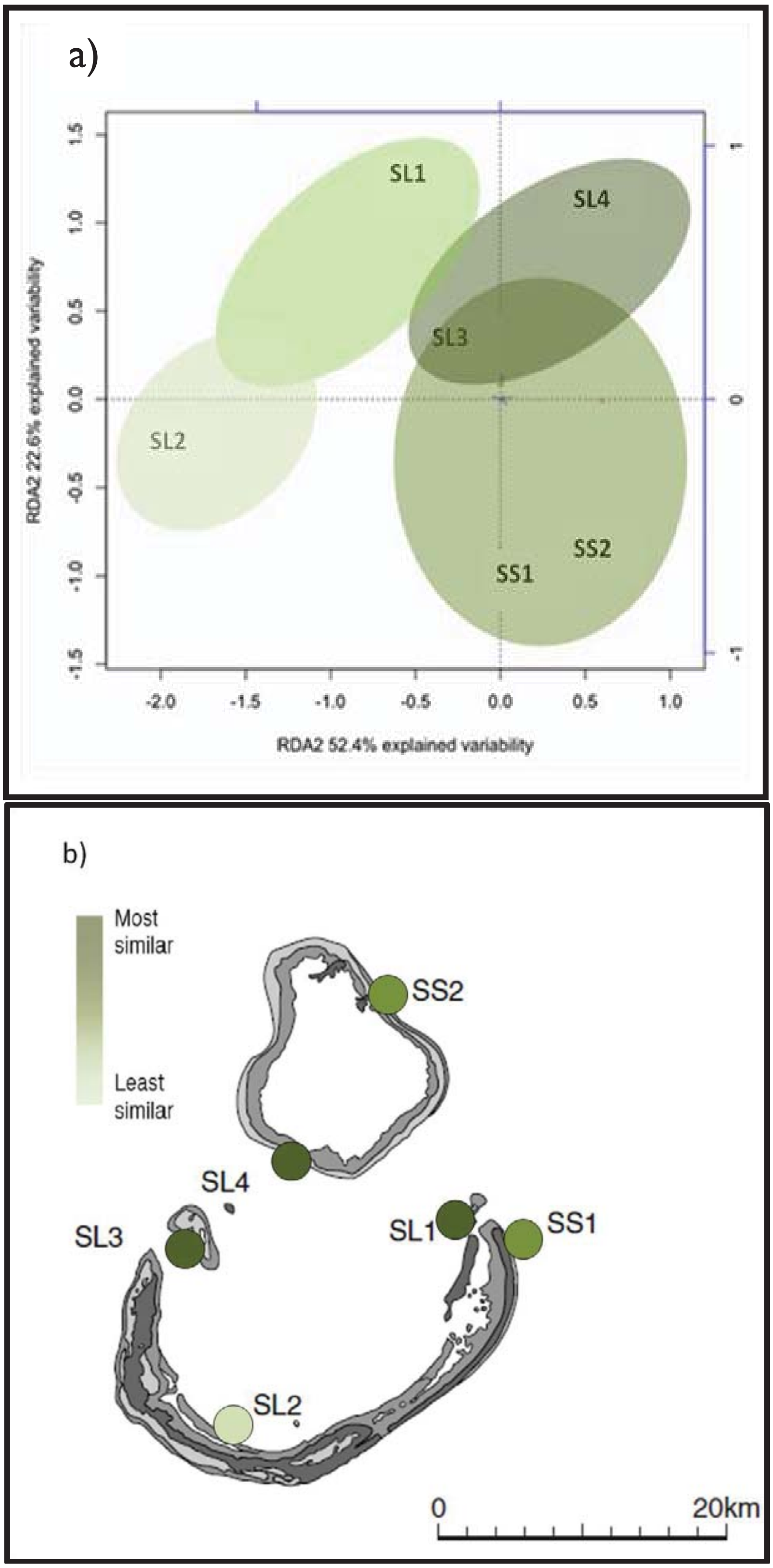


Figure 5.2.16 Variation in environmental conditions among locations at the shallow-water habitat. a) RDA analysis grouping locations according to physical conditions at six monitoring locations (see Figure 5.2.17), and b) hypothetical grouping of community conditions at monitoring locations at 9m depth, based on physical data and RDA analyses. The grouping of the north reef community with that in the southern part of south reef (SL2) is based only on qualitative comparisons and the larger relative differences to the other monitoring locations

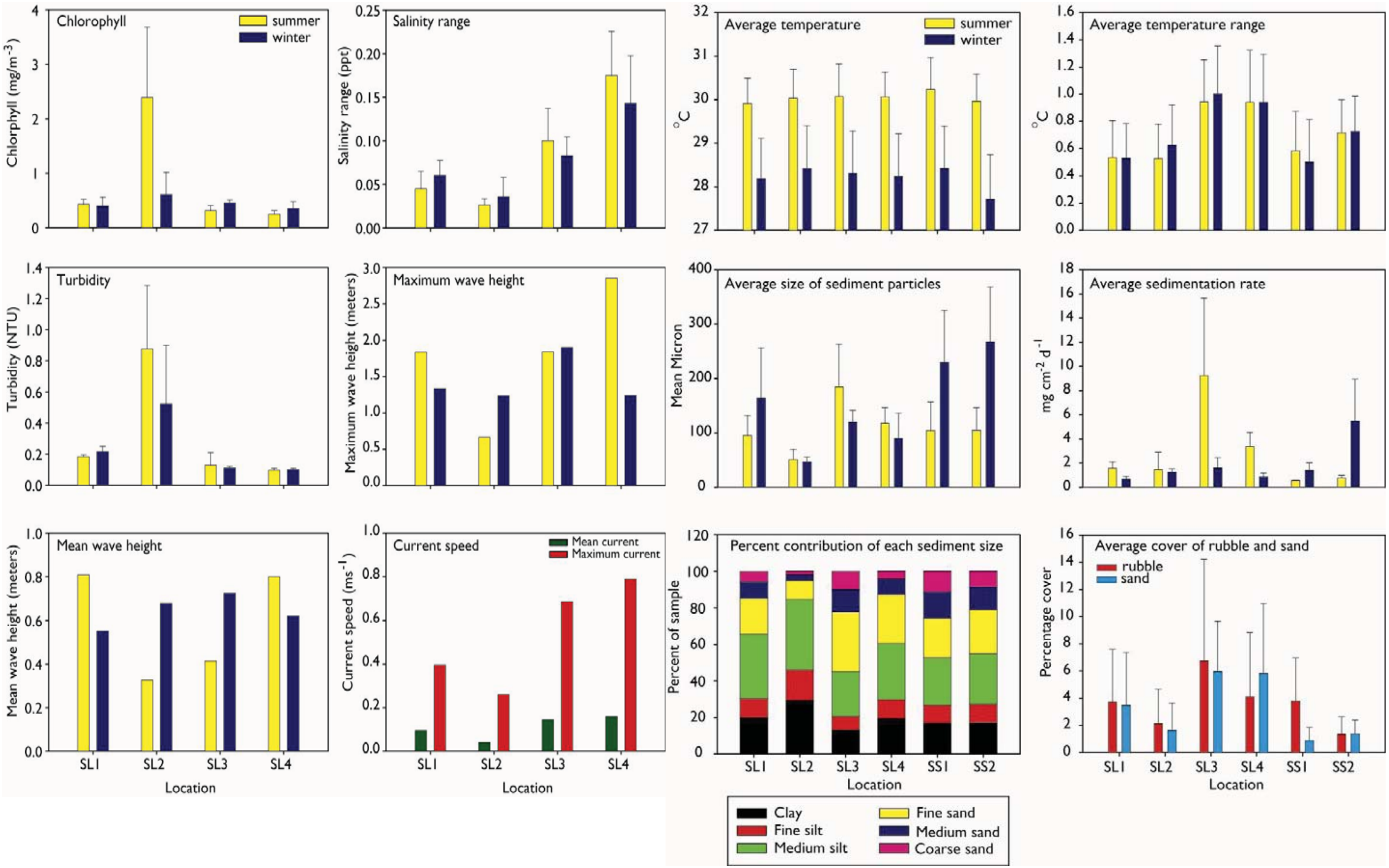


Figure 5.2.17. Variation in habitat conditions at locations across Scott Reef in the shallow-water habitat. Turbidity values are extrapolated from instrument arrays in the deeper-habitats, sediment values refer to deposited sediment in traps. Temperature and sedimentation data collected continuously from 2008 to 2010; remaining data collected periodically from instuments deployed in SRRP Project 3 (see Project 3 report for details).

Community structure

The structure of the reef slope communities in the shallow-water habitat has changed dramatically over the 15 years of monitoring, largely due to different disturbance regimes and the life cycle of some of the coral groups. The reef slope communities are among those most commonly exposed to disturbance, but are also most likely to recovery quickly from such impacts. These communities are therefore in various stages of recovery following different disturbances. The extent to which communities across different locations have similar structures depends largely on their stages of recovery and their previous disturbances. Following relatively calm conditions, communities can become dominated by different groups of corals such as staghorn corals and soft corals. Thus, inferences about grouping of communities are confounded by their variable regimes of disturbance and the boom-bust life cycle of various corals that can characterise these communities. Only with data spanning one or more decades can grouping of communities be considered.

Based on 15 years of monitoring the reef slope (9 m) communities at Scott Reef, general patterns of grouping in community structure among locations are evident. Four community types are evident; pre-bleaching (1994-1997), bleaching (1998-2001), recovery and Cyclone Fay (2002-2004), recovery and Cyclone George (2005-2008) (Figure 5.2.18, 5.2.19). The detailed grouping of locations vary among the periods, but generally following a similar pattern to the grouping of locations according to their habitat conditions. Thus, whether locations were on the outer reef slope, within the north or south reef lagoon, and adjacent to the deep-channel, had an overriding influence on the structure of their coral communities.

Locations SS1 and SS2 on the outer-slope consistently group together , with the differences between the two communities being most pronounced in the pre-bleaching years when there was a high abundance of the brooding coral *Isopora brueggemanni* at SS1 (Figure 5.2.18, 5.2.19). Both locations were severely affected by the bleaching and subsequent recovery has been slowed by their exposure to cyclones in 2004 and 2007; they are now dominated by massive and encrusting corals with only a low cover of *Acropora* corals (Figure 5.2.19).

Communities at locations SL3 at inner west hook and SL4 at the north Scott Reef, adjacent to the deep-channel, generally group together (Figure 5.2.18), but more because of their similar regimes of disturbance than their community structures. The major differences in community structure was the high abundance of soft corals at SL4 prior to the bleaching and the dominance of massive and encrusting corals, compared to a high abundance of *Acropora* and brooding *Isopora* at SL3 (Figure 5.2.18, 5.2.19); these communities have a similar cover of soft corals and massive and encrusting corals.

As with its diversity of habitat conditions, the community at Location SL1 is a mix of communities at all of the other locations, particularly the communities at SS2 and SL4 (Figure 5.2.18, 5.2.19). Communities at SL1 were moderately affected by the bleaching and subsequent cyclone disturbances. Additionally, communities here receive a large supply of larvae from other locations within the lagoon, adding diversity of the community structure and its recovery following the bleaching. This community is characterised by a mix of massive and encrusting corals, corymbose and branching *Acropora*, other corals and soft corals.

Location SL2 at the bottom of south reef consistently has the most unique habitat conditions and community structure (Figure 5.2.18, 5.2.19). The community at SL2 was severely affected by the bleaching, which caused a dramatic decline in the cover of branching corals, but the community has been relative sheltered from subsequent cyclone disturbances and is now dominated by an abundance of table corals. Additionally, this community is characterised by a suite of ‘other’ corals that are comparatively rare at all other locations, including foliose *Echinopora*, bottlebrush *Acropora* and fungiid corals.

Little is known about the changes in structure of coral communities within the north-lagoon over the duration of monitoring. There was a high abundance of staghorn corals within the lagoon, but most of these died following the mass-bleaching. Surveys conducted in 2009 suggest limited recovery of staghorn corals, but only a few sites were visited and surveys were restricted to the shallow depths; a high cover of staghorn corals was seen in the depths below 10 m at some locations. Communities today are probably dominated by patches of staghorn and a mixture of other corals in moderate to low abundance. Communities in the north-lagoon are also unique from all others at Scott Reef, but probably most similar to those at the southern part of south-lagoon.

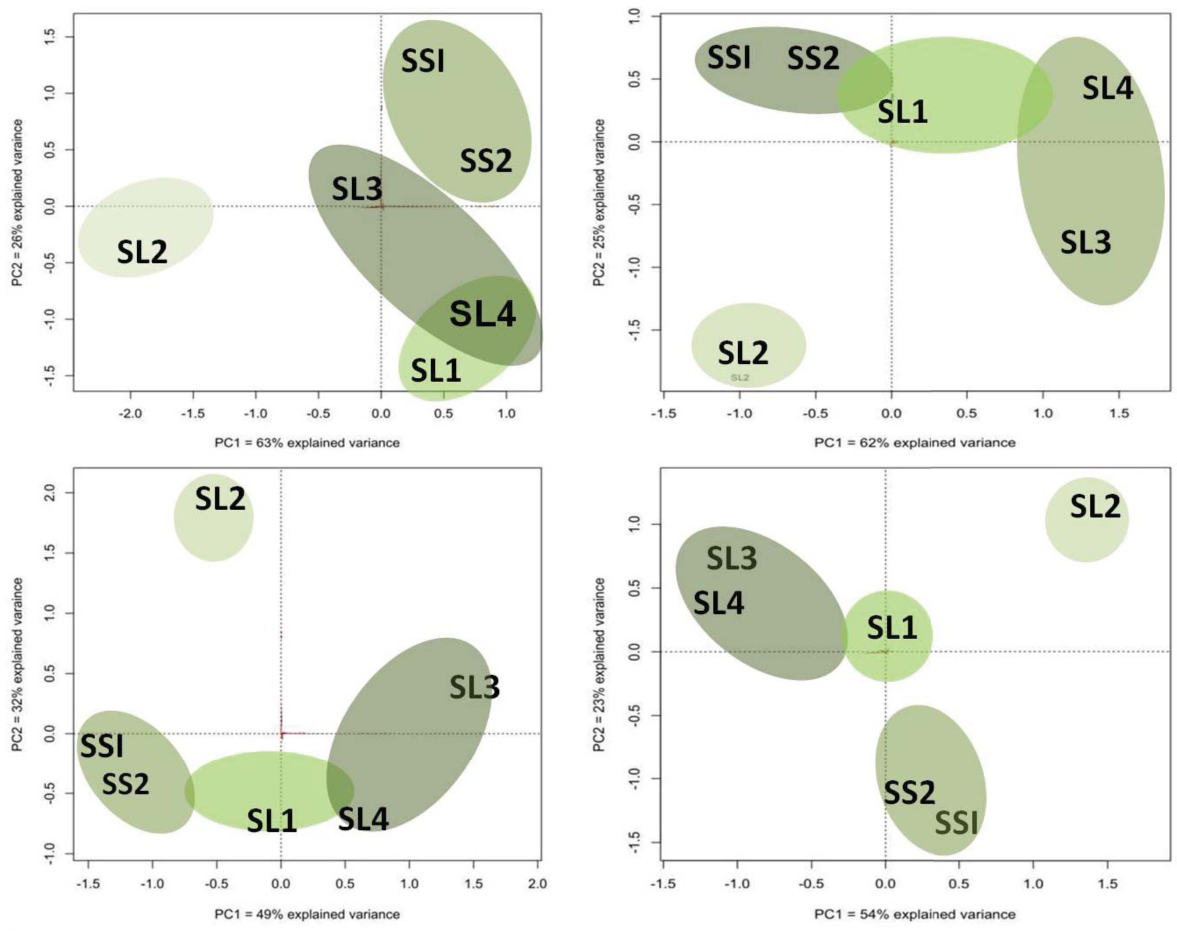


Figure 5.2.18 Structure of coral communities in the shallow-water habitat throughout the period of monitoring. Similarities in structure of coral communities, based on percentage cover of functional groups (a) over pre-bleaching years, (b) post-bleaching years (c) years of recovery and Cyclone Fay, and (d) years of recovery and Cyclone George. See Location Map Figure 1.2.1.

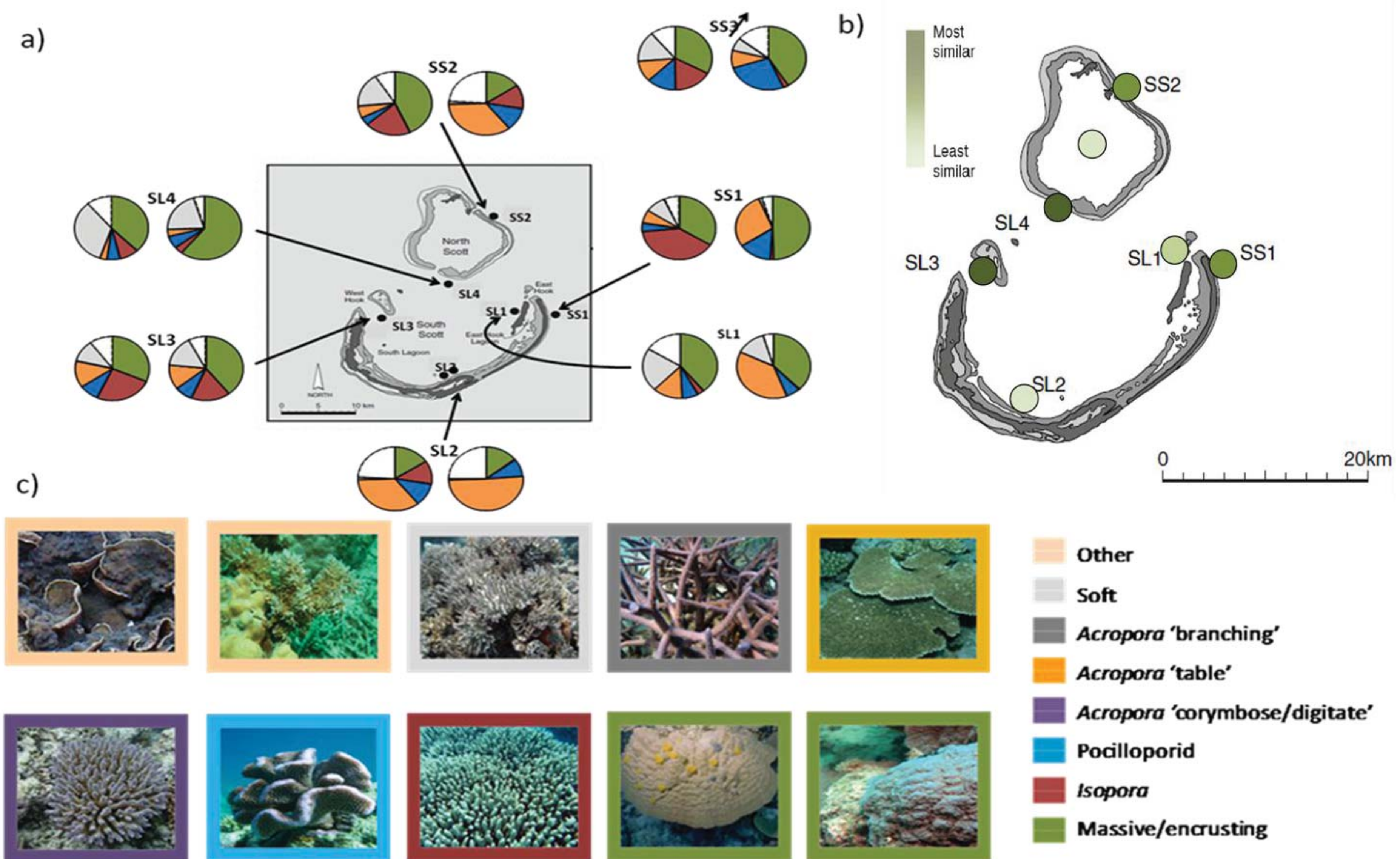


Figure 5.2.19 Coral communities in the shallow-water habitat at Scott Reef. a) Structure of coral communities at monitoring locations in 9 m depth before mass-bleaching (left pie graph) and ten years later in 2008 (right pie graph). b) Hypothetical grouping of communities at monitoring locations at 9 m depth based on cover of benthic organisms over 15 years of monitoring. The grouping of the north reef community with that in the southern part of south reef (SL2) is based only on qualitative comparisons and the larger relative differences to the communities at other monitoring locations. c) Examples of corals of different functional groups that contribute to community structure.

Susceptibility to bleaching

The shallow-water communities are most exposed to elevated water temperatures and the impacts of cyclones, but exposure to these stressors varies among locations. The susceptibility of coral communities to bleaching varies according to the duration of elevated water temperatures, the temperature range, current speeds the degree of mixing, and the abundance of susceptible species within the community. This complex interaction among parameters makes it difficult to predict the susceptibility of different communities in the shallow-habitat to bleaching, with some exceptions. The proximity of locations at SL3 and SL4 to the deep-channel means their communities experience a greater degree of mixing and current flow, a wider range of water temperatures, and periodic exposure to cool water intrusions during warmer months, all of which can reduce the likelihood of coral bleaching (Figure 5.2.16, 5.2.20, 5.2.21). Communities at SL3 and SL4 suffered a lower relative decrease in cover following the bleaching after adjusting for species susceptibilities, and this was probably a consequence of their proximity to the deep-channel. Conversely, the shallow-communities in the north-lagoon are probably most susceptible to coral bleaching (Figure 5.2.20), given their exposure to periods of consistently high temperatures and limited flushing with oceanic waters. The low current flow and limited mixing at the southern part of south-lagoon may also make the community at Location SL2 more susceptible to bleaching.

The structure of communities at all of the locations can change dramatically through time, and this includes the relative abundances of species most susceptible to bleaching. The branching and table corals that characterised communities in the north-lagoon and the southern part of south-lagoon during one or more periods are among the most susceptible to bleaching. Branching and brooding corals are also susceptible to bleaching, and may become abundant at any of the locations across Scott Reef. Conversely, the massive and encrusting corals are least susceptible to bleaching and are often most abundant at locations characterised by high current flow or on steep slopes.

Susceptibility to cyclones

The susceptibility of communities to storms and cyclones depends primarily on the severity and direction of the prevailing winds and waves, but also on the type of substrata and the community structure. In contrast to their lower susceptibility to bleaching, the communities at SL3 and SL4 appear to have a higher exposure to storms and cyclones than other lagoon locations (Figure 5.2.20, 5.2.21), based on reductions in cover and rates of injury and/or mortality following Cyclones Fay and George (Smith et al. 2004; Gilmour et al. 2008; Gilmour et al. 2009b).

Communities at SL3 and SL4 experienced greater degree of fragmentation due to wave energy, but also a high degree of scouring and deposition by sediments, given the high cover of sand at these locations (Figure 5.2.3). The outer-slope locations are also highly susceptible to cyclone damage, depending on the direction of the prevailing winds and waves, given their exposure to the open ocean (Figure 5.2.20, 5.2.21). Outer-slope communities in the eastern side of Scott Reef (Locations SS1, SS2) were severely affected by Cyclone Fay in 2004, but the impact from Cyclone George in 2007 is unknown; there is evidence of only minor cyclone impact at Locations SL1 inside east hook, or at SL2 at the southern part of south-lagoon (Gilmour et al. 2009b). Percentage cover data provide evidence of only major cyclone impacts unless surveys are conducted shortly before and after the disturbance, but rates of injury and survival to the coral *Acropora spicifera* indicated large impacts from Cyclone George at Locations SL3 and SL4 and a minor impact at Location SL1 (Gilmour et al. 2009b); study sites were not located on the outer-slope. The outer-slope communities on the western side of Scott Reef have not recently been surveyed, largely because of their exposure to winds and waves, and there is no information about how these have been affected by cyclone disturbances.

Locations SL1 and particularly SL2 are probably more sheltered from cyclone impacts that the other monitoring locations (Figure 5.2.20, 5.2.21). However, the substrata at Location SL2 is extremely fragile and the low current flow means the community is often dominated by corals with fragile growth forms, so the community is relatively susceptible to moderate wave energy. The communities at the north-lagoon are also relatively sheltered from the impacts of cyclone disturbances, although the sandy substrata and the previous dominance of branching corals means these communities may also be susceptible to moderate wave energy associated with cyclones (Figure 5.2.20, 5.2.21).

Susceptibility to reductions in water quality

Communities at all of the locations within the shallow-habitat probably will respond in similar ways to reductions in light due to turbidity, with perhaps a higher susceptibility of communities at SL2 where turbidity levels are already higher than at the other locations (Figure 5.2.17, 5.2.20, 5.2.21). However, if increases in turbidity are associated with increased sedimentation then the susceptibility of communities could vary more among locations. Sedimentation is likely to be higher at locations with low current flow and mixing, whereas suspended sediments are probably less likely to be deposited onto coral communities at locations with high current flow. Thus, coral communities in the north-lagoon and at location SL2 at the southern part of south-lagoon are likely to be more susceptible to reductions in water quality that could lead to sedimentation, and communities adjacent the deep-channel at locations SL3 and SL4 are likely to be least susceptible to sedimentation (Figure 5.2.20, 5.2.21). Communities at locations SS1 and SS2 on the outer-slope may also have a relatively low to moderate susceptibility to sedimentation given their proximity to the open ocean, whereas the community at Location SL1 at west hook is likely to have a moderate to high susceptibility (Figure 5.2.20, 5.2.21).

Susceptibility to coral diseases and predation

The susceptibility of coral communities to outbreaks of disease is related to the distribution of pathogens, water quality, the abundance of susceptible species and the extent to which individuals are already stressed. Reductions in water quality, low current flow and mixing, and elevated maximum and minimum water temperatures all increase the likelihood of disease outbreaks. Additionally, a high density of susceptible species increases the likelihood of diseases spreading though the community. Consequently, the most susceptible communities are probably those within the north-lagoon and the southern part of south-lagoon, particularly when the cover of branching or table corals reaches a very high level (Figure 5.2.20, 5.2.21). Indeed, poor water quality, the re-suspension of sediments following cyclone George, high turbidity, and the high cover of table corals at Location SL2 has seen an increasing incidence of disease and mortality at location in the last year (see Chapter 3 Disturbances at Scott Reef). Associated with this disease outbreak are increased observations of crown-of-thorn starfish and *Drupella*, often feeding on the stressed corals, although their abundances are low. A similar outbreak of disease is possible if communities in the north-lagoon were likely to reach high densities. For the remaining locations, variable susceptibility to outbreaks of disease and predators is probably more likely a consequence of differences in cover of susceptible species, in addition to a range of other secondary factors, such as the abundance of different fish species and previous exposure to cyclones.

Variable resilience of coral communities among locations

There are no clear patterns of variation in growth and survival of corals among locations in the shallow-habitat. Variation in reproduction, growth and survival is largely driven by the exposure of communities to different regimes of disturbance. However, there are clear differences in rates of recruitment among locations. Consistent differences in rates of recruitment, coupled with differences in habitat conditions and exposure to disturbances, can have important implications for the resilience of coral communities. Rates of recruitment to locations SL1 and SS2 are consistently higher than at the other locations, followed by Location SL3, SL2; locations SS1 and SL4 consistently have the lowest recruitment. Of all the disturbances considered, locations SL3 and SL4 are least susceptible to mass-bleaching and perhaps reductions in water quality, moderately susceptible to outbreaks of disease and coral predators, and highly susceptible to impacts from cyclone disturbance. Locations SS1 and SS2 are moderately susceptible to mass-bleaching, reductions in water quality, and outbreaks of coral diseases and predators, and highly susceptible to cyclones. Communities at Location SL2 and in the north-lagoon are highly susceptible to mass-bleaching, reductions in water quality, and outbreaks of coral diseases and predators, but probably least susceptible to cyclones. Location SL1 is moderately susceptible to all disturbances.

Based on their exposure to all possible disturbances, the community at Location SL1 is probably the most resilient of all locations, followed by the community at SL3; the communities at Location SL2 or in the north-lagoon are probably least resilient. Despite their moderate to low susceptibility to all but one disturbance, communities at locations SL4 and SS1 probably have a moderate to low resilience to disturbances because of the low rates of coral recruitment. Communities at Location SS2 probably have a moderate resilience, despite their moderate to high exposure to disturbances, because they periodically receive a supply of larvae from other locations. (Figure 5.2.21)

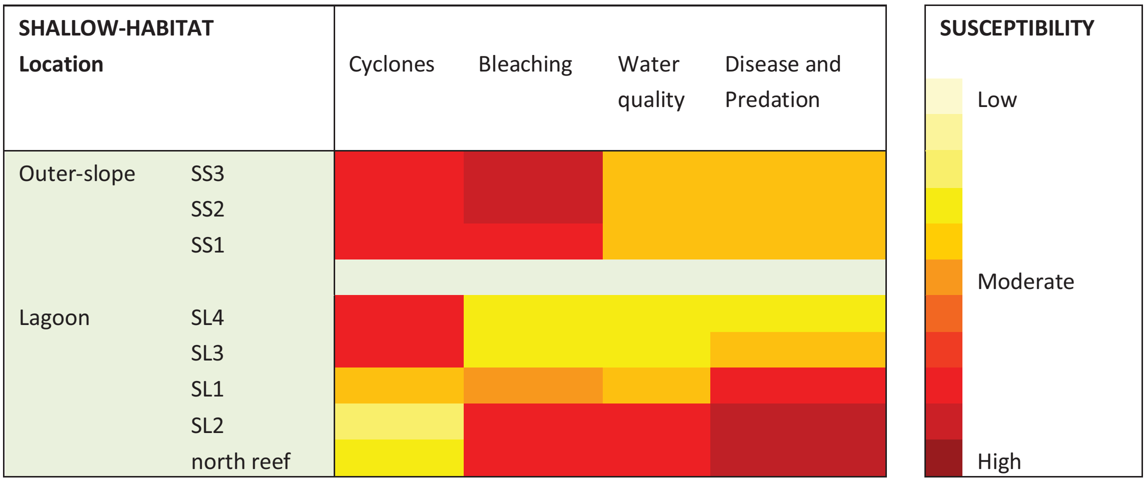


Figure 5.2.20 Susceptibility of shallow-water coral communities to potential disturbances at Scott Reef See Location Map Figure 5.2.15.

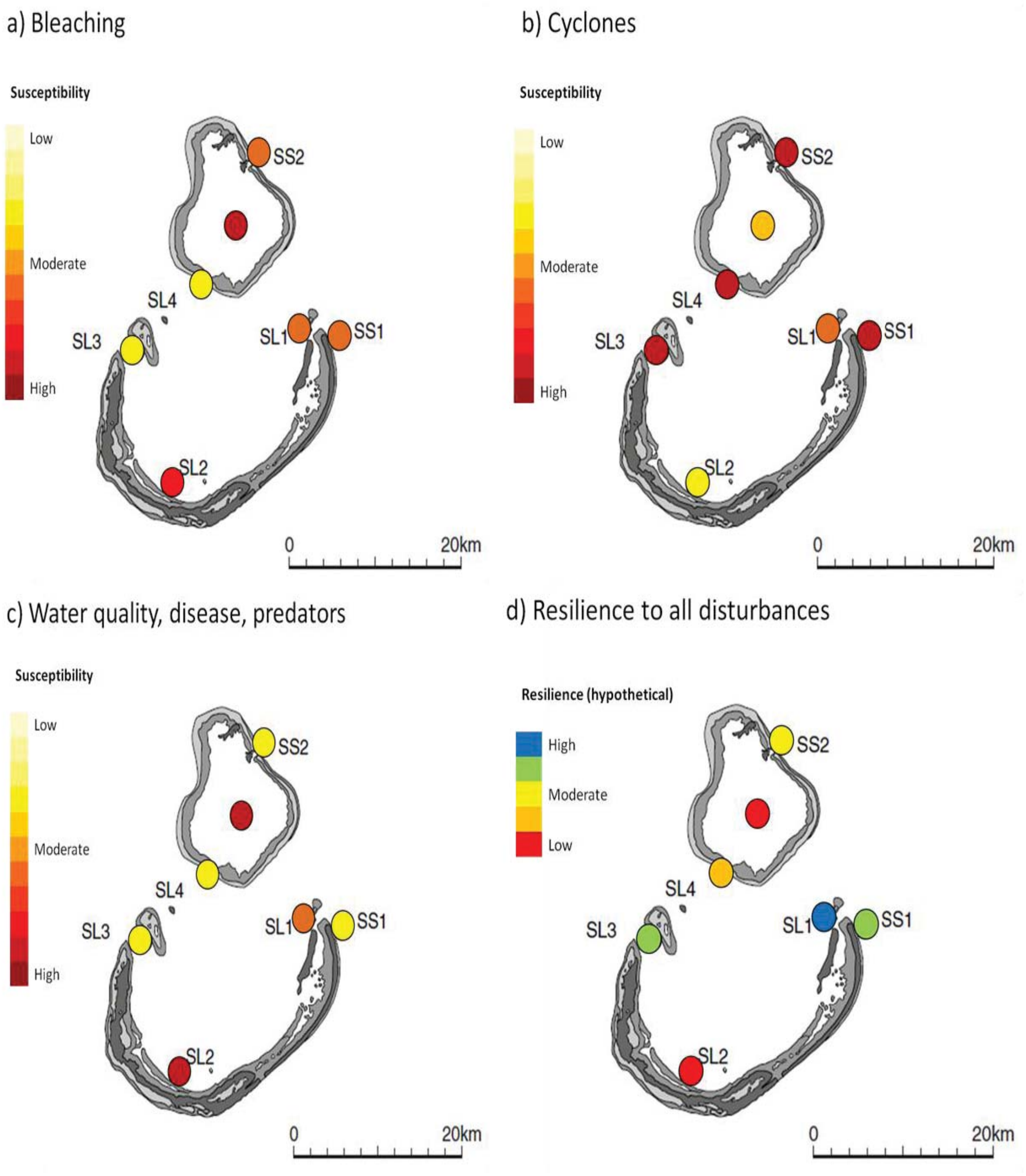


Figure 5.2.21 Hypothetical susceptibilities of coral communities at long-term monitoring locations to a) mass-bleaching, b) cyclones and c) reductions in water quality or outbreaks of diseases and predators. d) Resilience of coral communities based on their susceptibilities to all disturbances and their rates of recruitment. The resilience of communities, or their ability to recovery from disturbances, is decreased by a higher susceptibility to disturbances, but increased by higher rates of recruitment. These hypothetical susceptibilities are based on a combination of quantitative and qualitative biological and physical data, and have a high level of uncertainty. The grouping of the north reef community with that in the southern part of south reef (SL2) is based only on qualitative comparisons and the larger relative differences to the communities at other monitoring locations.

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Sub-Project Update

6. LONG-TERM MONITORING OF BENTHIC AND FISH COMMUNITIES

6.1 Percentage cover of benthic communities

Introduction

The current literature is full of reports of both sudden and insidious decline of coral reefs over large areas as a result of anthropogenic pressures, including overfishing, pollution and rising sea temperatures causing coral bleaching and diseases (Hoegh-Guldberg 2004; Hoegh-Guldberg et al. 2007; Sriver and Huber 2007). These anthropogenic changes compound natural pressures and impacts that have always been a part of the reef environment. The most severe manifestation of decline is a fundamental shift (phase shift) from dominance by reef-building corals to non-reef-building macro-algae (Done 1992; Hughes 1994), and often increased activity of reef-eroding taxa (e.g. sea-urchins and bio-eroding sponges). Hard coral communities that return to previous cover within years to decades after impacts may be considered as being 'resilient' (e.g. Smith et al. 2008; Done et al. 2010). However restoration of a prior percentage cover alone is a weak criterion for recovery. Of greater relevance to the restoration of reef building capacity, and biodiversity of coral-associated reef species, is the rate and degree to which the density, composition and size structures of the reef-building corals are restored; and, how the new spatial mosaic of coral communities (Ninio and Meekan 2002) compares to what was present prior to the reef's decline. The degree to which communities have returned to their prior state can be measured as both the composition of recovering patches, and their spatial heterogeneity through time. The underlying drivers that determine whether communities recover and the rate and extent to which the recovery trajectory converges towards a prior state, include the supply of new recruits (numbers and types), the prevailing conditions at the location (physical and biological), and the rates of growth and survival of the corals and their competitors.

Scott Reef has has provided an invaluable opportunity to investigate these issues: its oceanic setting insulates it from coastal influences (e.g. flood plumes, terrigenous sediments). Its remoteness from other reefs suggests that brood-stocks for coral recruitment are primarily located within the reef system. Genetic and oceanographic studies within the Scott Reef complex (Gilmour et al. 2009a; Underwood 2009) suggest that there is connectivity among coral and fish sub-populations within the reef system, that the strength of connections are variable, and the supply of coral recruits to different parts of the reef is also variable.

Scott Reef has been providing an invaluable ecological data set since the early 1990s. This has been made possible by Woodside and AIMS, supporting detailed multidisciplinary research programs on the regional significance of Scott Reef and its function as a biophysical system. The catastrophic coral bleaching of 1998 has provided invaluable insights into the functioning of atoll communities (Smith et al. 2008). The major coral monitoring program over the last fifteen years is a rich mine of information that allows us to not simply document basic issues of the rates and direction of change following the 1998 catastrophe, and also to gain a better understanding of underlying ecological and bio-physical processes that have broader relevance to coral reefs globally.

Methods

Surveys of coral communities at Scott Reef were conducted during most years since 1994. The long-term monitoring program focused on reef slope (9m) communities at seven locations at Scott and Seringapatam Reefs (Figure 6.1.1). Three of these locations (SS1, SS2, SS3) were situated at the outer-slope on the eastern side of south-reef, north-reef and Seringapatam Reef. The remaining locations (SL1-SL4) were inside the relatively sheltered south-lagoon, but two locations (SL3 and SL4) were moderately influenced by oceanic waters due to their proximity to deep-water passage between north- and south-reef. Each monitoring location consisted of three replicate locations separated by about 300 m, and five permanent transects (50 m) were surveyed at each location. These transects were surveyed in 1994-1999, 2003, 2004, 2005 and 2008 (see Smith et al. 2008; Gilmour et al. 2009b).

Analysis of transect data produced estimates of percentage cover of the dominant benthic groups (Gilmour et al 2009). Due to difficulties in consistently distinguishing among massive and encrusting genera in the family Faviidae these corals were grouped to the family level; *Montipora* corals were grouped with other encrusting corals, and corals with less than 3% cover were pooled into the category of ‘other corals’.

A range of physical data were also collected to describe conditions at the monitoring locations (Gilmour et al 2009; Brinkman et al 2009). These data included measures of temperature, chlorophyll turbidity, wave height, current speeds and sedimentation.

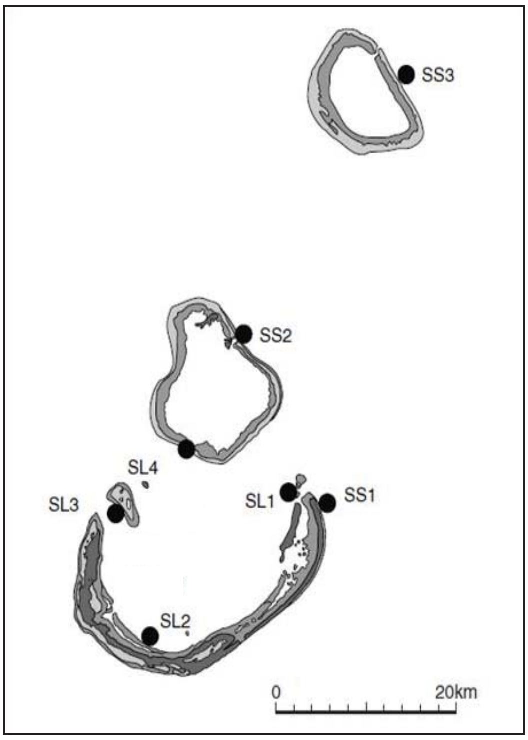


Figure 6.1.1 Location of survey sites at Scott Reef and Seringapatam.

Results

A total of 272 hard coral species were recorded in early surveys (Done et al. 1994) at Scott Reef, with broad affinities to reefs in neighbouring regions. Subsequent surveys extended this list to almost 300 species (Smith et al. 2004), (Gilmour et al. 2008), probably due to additional sampling effort and revisions of coral taxonomy in the intervening decade, rather than actual increases in numbers of species.

During the first years (1994-1997) of monitoring the reef-slope (9 m) locations, coral communities separated into three broad groups according to their community structure. The first group included the outer-slope locations (SS1 and SS2) and one lagoonal location (SL3) (Figure 6.1.1), at which the majority (> 80% cover) of the community was composed of *Isopora brueggemanni*, *Acropora*, *Porites*, *Pocilloporidae*, *Montipora* and Faviidae, in order of relative abundance (Figure 6.1.2). The second group included locations SL1 and SL4 (Figure 6.1.2), which were distinguished from the previous communities (SS1, SS2, SL3) by a lower cover of *Isopora brueggemanni* and a higher cover of soft corals (Figure 6.1.2). The third and most unique group consisted only of Location SL2 at the southern part of the south-lagoon (Figure 6.1.2); this community had a high cover of branching *Acropora* and an abundance of mushroom corals (*Fungiidae*) and foliose *Echinopora*, distinguishing it from all the other communities (Figure 6.1.2).

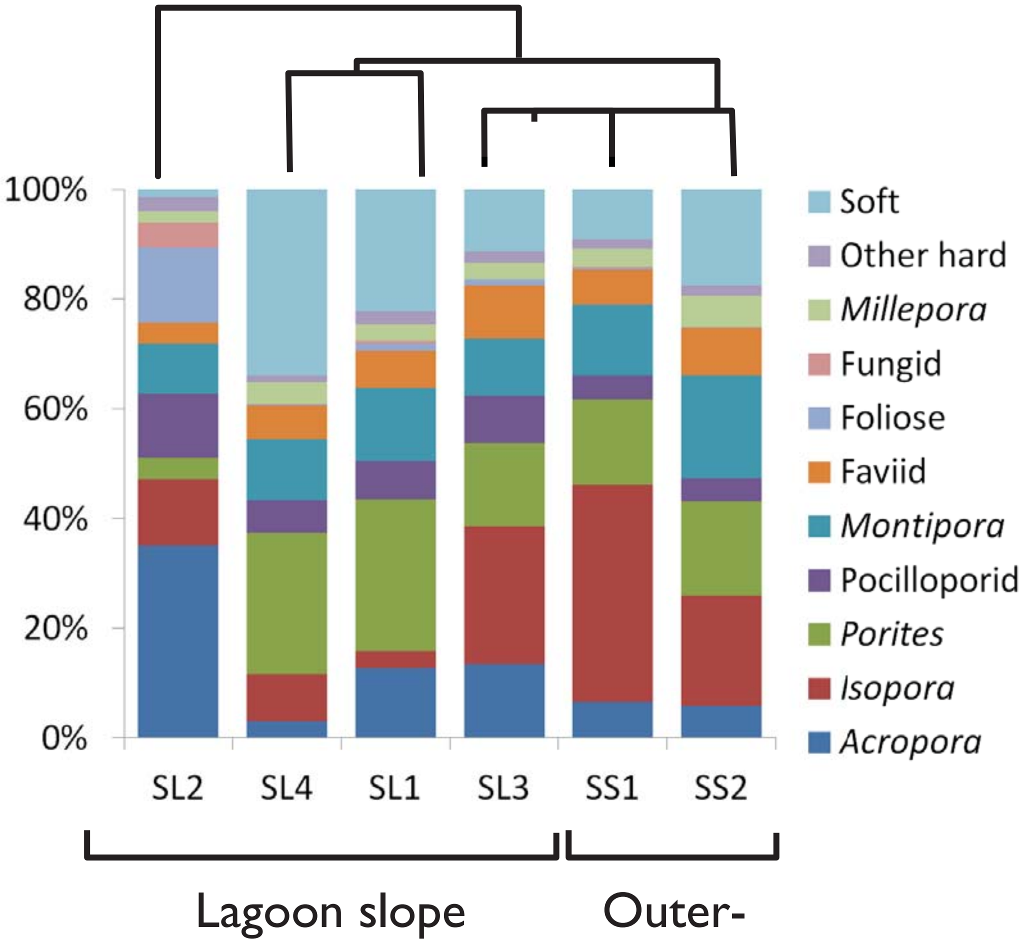


Figure 6.1.2 Cluster analysis of communities on Scott Reef, showing percentage cover of corals at each location. See Location map Figure 6.1.1.

During the first surveys of Scott Reef (Done et al. 1994; Heyward et al. 1995b), there was no evidence of major disturbance to the coral communities in recent years, and communities were structured according to their location on the reef and associated habitat conditions. In particular, a subset of physical conditions (Figure 6.1.3) characterised the different exposures of communities to the open ocean on the outer-slope locations, and their proximity to the deep-channel (SL1, SL3, SL4) or the southern part of south-lagoon (SL2) (see Fig. 5.2.17). In particular, the higher levels of chlorophyll and turbidity, and lower current speeds, at the bottom of south lagoon (SL2), the higher current speeds and temperature ranges adjacent to the deep-channel (SL3, SL4), and the higher sediment sizes associated with high current speeds and wave energy at exposed locations (SL3, SS1, SS2). A more detailed discussion of physical conditions at monitoring locations is in Section 5.2.

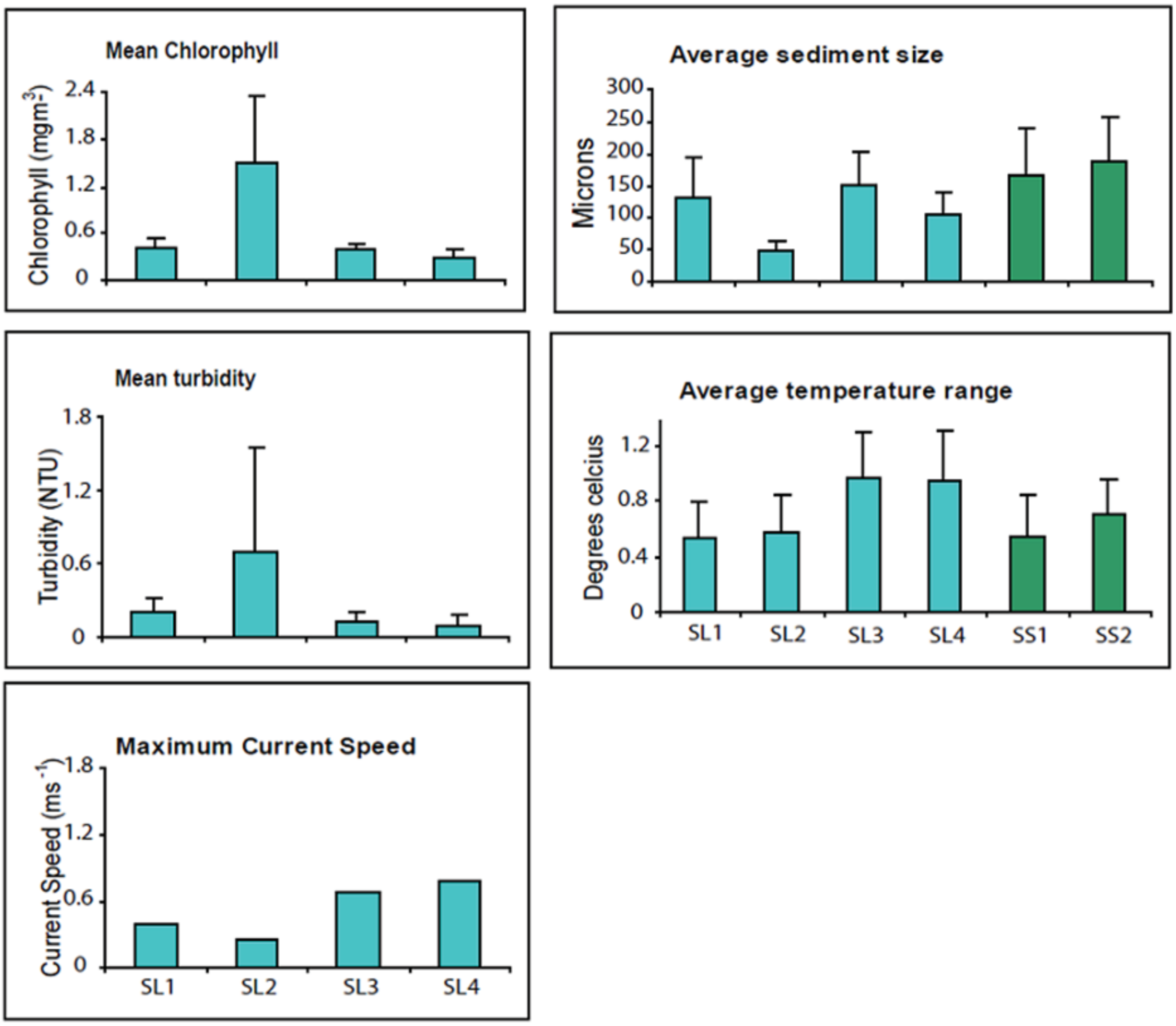


Figure 6.1.3 Summary of a selection of environmental variables collected at Scott Reef. See Location map Figure 6.1.1.

Disturbance and recovery in monitoring locations

As a result of lethal coral bleaching in 1998, both hard and soft coral communities lost ~80% of their cover (which had been tracking slowly upwards until that time) (Figure 6.1.4a). The number of genera in the monitoring samples also decreased from ~20 to ~10 per location (Figure 6.1.4b). Hard coral cover and number of genera per location then increased from the year 2000, but soft coral cover remained low. There was little evidence of slowing in the rates of increase in hard cover or number of genera following the cyclones in 2004 and 2007.

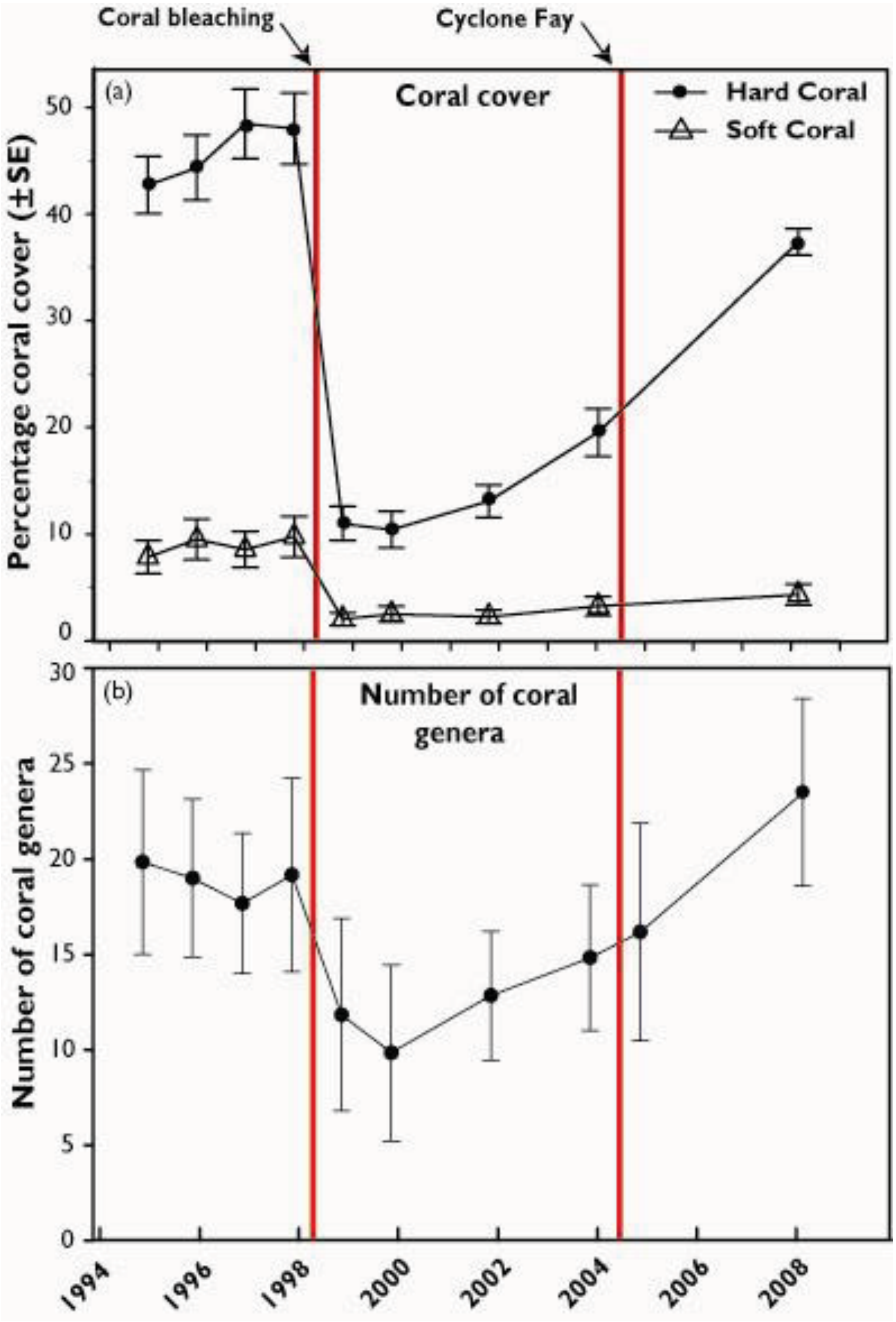


Figure 6.1.4 a) Change in cover of a) hard and soft corals (± 95% confidence bands). b) Change in the number of genera (± S.D.). Red lines reflect the time of mass-bleaching in 1998 and Cyclone Fay in 2004.

The mass-bleaching impacted coral communities at all locations, but there was some variation in the impacts according to their habitat conditions and their initial community structure. Among the lagoon locations (Figure 6.1. 5a–d), the greatest bleaching impacts were at the eastern (SL1) and southern (SL2) locations, where the declines occurred across all genera. The overall impact was particularly obvious in SL2 because of the high proportion of vulnerable *Acropora* in the pre-bleaching community. There was an increase in total coral cover in both locations from 2000 onwards, with the genus *Acropora* making the greatest contribution in both cases. In the remaining lagoon locations (SL3 and SL4), the bleaching caused much smaller declines in both total coral cover, but subsequent increases in coral cover were also slower than at the other lagoon communities. In the outer-slope locations (SS1 and SS2) (Figure. 6.1.5 e-f), there were major impacts from the bleaching and very slow recovery trajectories, particularly for the *Isopora* that had dominated the communities.

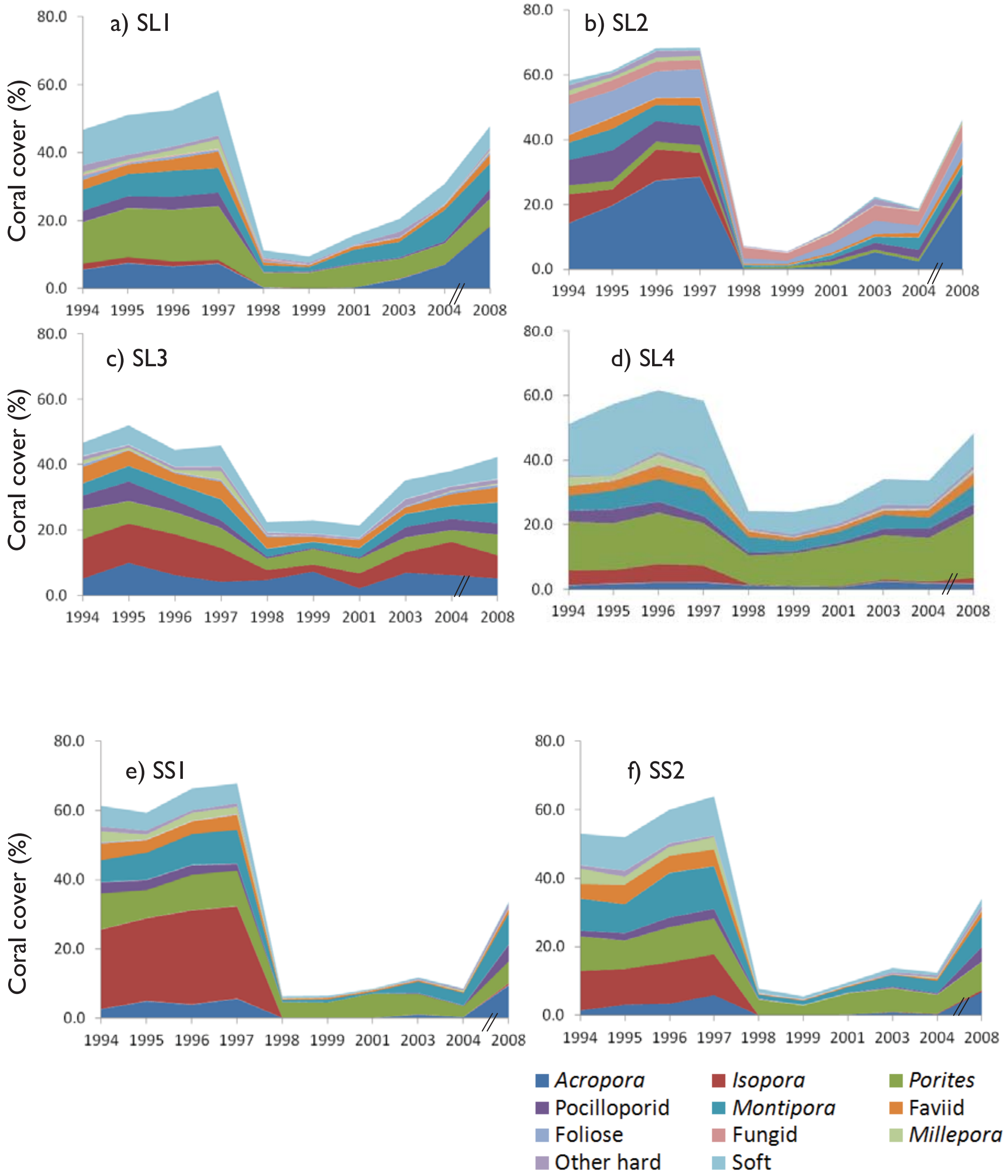


Figure 6.1.5 Changes in the cover of groups of hard and soft corals at different monitoring locations at Scott Reef. See Location Map Figure 1.2.1.

Based on the changes in coral communities at Scott Reef and within each monitoring location, bleaching impacts and recovery trajectories can be divided into four periods of change (Figure 6.1.6): pre-bleaching (1994 –1997); bleaching (1998 – 2001); recovery and Cyclone Fay (2003 – 2004); further recovery and Cyclone George (2008) (Figure 6.1.6). The reduction in cover of the most susceptible species of corals following the bleaching homogenized the communities through time. The pre-bleaching years combined at a dissimilarity level of ~0.25 (reflecting the high abundances and diversity among locations), whereas the immediate post-bleaching years grouped at ~ 0.03 (reflecting uniformly lower abundances across genera and little change through time). The subsequent period of recovery (2003 – 4) was also relatively homogenous across locations and years (~ 0.3), but in a different way to that immediately after the bleaching. By 2008, there were clear differences in community structure compared to the earlier periods, with the most recent community combining with the post-bleaching years at a dissimilarity level of ~0.45; there was also greater heterogeneity among locations than in the pre-bleaching years (end of the 2008 branch at dissimilarity level of ~0.35).

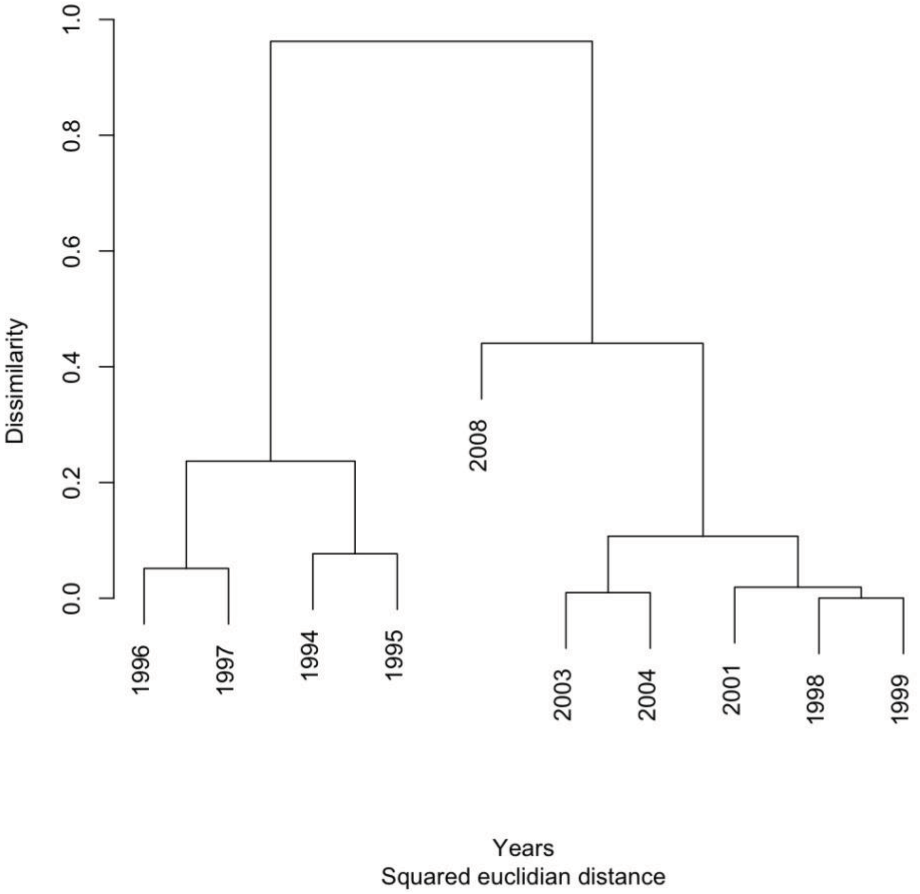


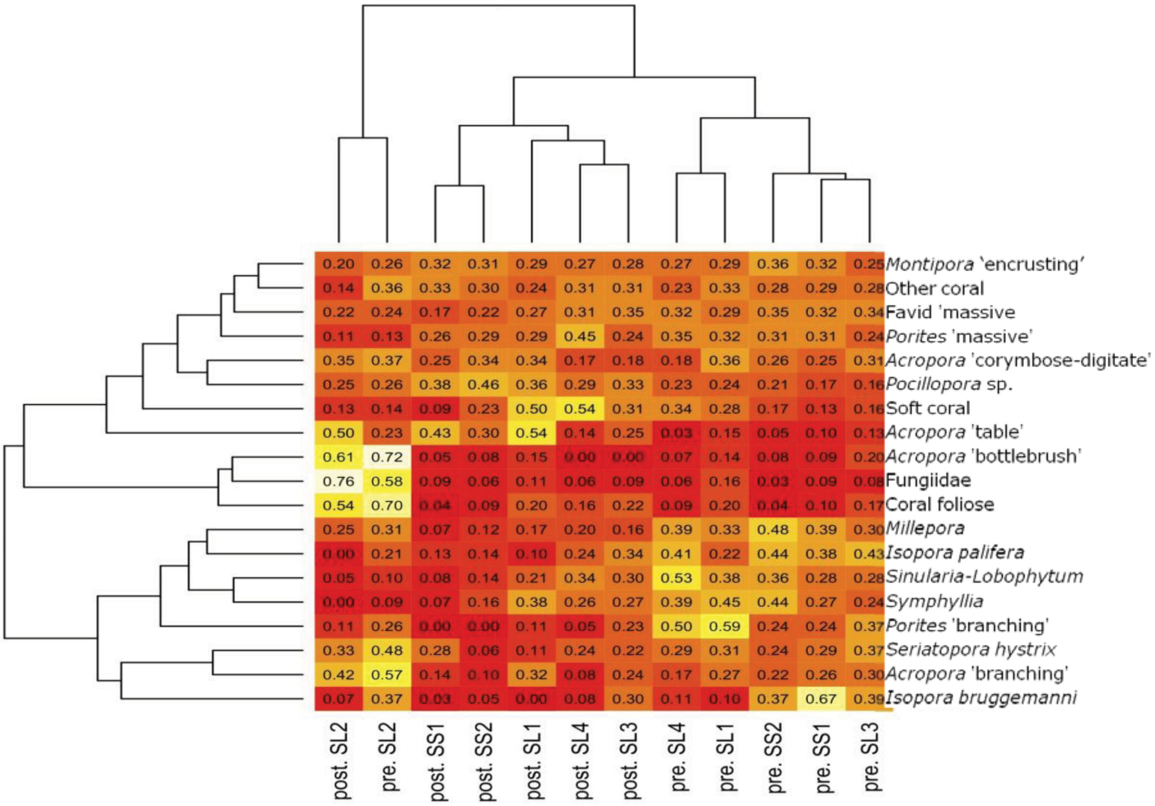
Figure 6.1.6 Cluster analysis grouping the changes in the structure of coral communities at Scott Reef among years.

Among the locations, there were both similarities and differences in the structure of communities prior to the bleaching and in the most recent survey in 2008 (Figure 6.1.7). For Location SL2 at the southern part of south-lagoon, community structure in 2008 was most similar to that prior to the bleaching. Five coral groups had similar cover in 2008 to pre-bleaching years: encrusting *Montipora*, bottlebrush *Acropora*, foliose corals, fungiids and branching *Acropora* (Figure 6.1.7). Three groups that were scarce or absent pre-bleaching were present at > 3% in 2008; corymbose-digitate *Acropora, Seriatopora hystrix* and *Isopora brueggemani.* The most notable difference in community assemblage was the increased cover of table *Acropora* in 2008.

For each of the other five monitoring locations, community structures were similar to that in the pre-bleaching years, but for some notable exceptions. These exceptions are largely a consequence of corals abundant in the pre-bleaching years having not recovered, or corals that were rare in pre-bleaching years becoming abundant in 2008. Corals that were abundant (3-16% cover) in the pre-bleaching years but which had not recovered (<3%) were primarily the soft corals and brooding

Isopora, but include: *Millepora; Sinularia-Lobophytum; Symphyllia;* branching *Porites*, *Isopora palifera*, *Acropora brueggemanni*. Corals that were in greater abundance (> 3%) in 2008 than in pre-bleaching years include *Pocillopora* and table *Acropora*.

The brooding corals *Isopora brueggemanni* and *I. palifera* were virtually eliminated from five of the six locations by the 1998 bleaching event, where they had previously been abundant (Figure 6.1.5). Only at Locations SL3, where some cover remained following the bleaching, has there been good recovery of the *Isopora*. By contrast, massive *Porites* were least impacted by the bleaching and had the most rapid initial rates of recovery at all locations, as did the massive Faviids at the locations within the lagoon where they had been abundant (Figure 6.1.5 a–d). However, the Faviids were severely impacted at the outer-slope locations where there was little sign of recovery (Figure 6.1.5 e–f). In summary, coral cover and diversity of genera was similar to pre-bleaching levels in 2008 at most locations, but recovery at other locations was slower and important differences remain in community structure between pre-bleaching years and the most recent survey.



	post. SL2	pre. SL2	post. SS1	post. SS2	post. SL1	post. SL4	post. SL3	pre. SL4	pre. SL1	pre. SS2	pre. SS1	pre. SL3
Montipora 'encrusting'	0.20	0.26	0.32	0.31	0.29	0.27	0.28	0.27	0.29	0.36	0.32	0.25
Other coral	0.14	0.36	0.33	0.30	0.24	0.31	0.31	0.23	0.33	0.28	0.29	0.28
Favid 'massive	0.22	0.24	0.17	0.22	0.27	0.31	0.35	0.32	0.29	0.35	0.32	0.34
Porites 'massive'	0.11	0.13	0.26	0.29	0.29	0.45	0.24	0.35	0.32	0.31	0.31	0.24
Acropora 'corymbose-digitate'	0.35	0.37	0.25	0.34	0.34	0.17	0.18	0.18	0.36	0.26	0.25	0.31
Pocillopora sp.	0.25	0.26	0.38	0.46	0.36	0.29	0.33	0.23	0.24	0.21	0.17	0.16
Soft coral	0.13	0.14	0.09	0.23	0.50	0.54	0.31	0.34	0.28	0.17	0.13	0.16
Acropora 'table'	0.50	0.23	0.43	0.30	0.54	0.14	0.25	0.03	0.15	0.05	0.10	0.13
Acropora 'bottlebrush'	0.61	0.72	0.05	0.08	0.15	0.00	0.00	0.07	0.14	0.08	0.09	0.20
Fungiidae	0.76	0.58	0.09	0.06	0.11	0.06	0.09	0.06	0.16	0.03	0.09	0.08
Coral foliose	0.54	0.70	0.04	0.09	0.20	0.16	0.22	0.09	0.20	0.04	0.10	0.17
Millepora	0.25	0.31	0.07	0.12	0.17	0.20	0.16	0.39	0.33	0.48	0.39	0.30
Isopora palifera	0.00	0.21	0.13	0.14	0.10	0.24	0.34	0.41	0.22	0.44	0.38	0.43
Sinularia-Lobophytum	0.05	0.10	0.08	0.14	0.21	0.34	0.30	0.53	0.38	0.36	0.28	0.28
Symphyllia	0.00	0.09	0.07	0.16	0.38	0.26	0.27	0.39	0.45	0.44	0.27	0.24
Porites 'branching'	0.11	0.26	0.00	0.00	0.11	0.05	0.23	0.50	0.59	0.24	0.24	0.37
Seriatopora hystrix	0.33	0.48	0.28	0.06	0.11	0.24	0.22	0.29	0.31	0.24	0.29	0.37
Acropora 'branching'	0.42	0.57	0.14	0.10	0.32	0.08	0.24	0.17	0.27	0.22	0.26	0.30
Isopora bruggemanni	0.07	0.37	0.03	0.05	0.00	0.08	0.30	0.11	0.10	0.37	0.67	0.39

Figure 6.1.7 Similarities and differences between community structure in 2008 and in pre-bleaching years at monitoring locations. Data are Hellinger transformed values of percentage cover, the largest values are light colours and the smallest values are dark colours. Cells of similar colour reflect the similarities between locations, pre- and post-bleaching (2008) periods, and/or coral groups. See Location Map Figure 1.2.1.

The state of the coral communities in 2008 reflected a combination of survival and regrowth of some corals following mass-bleaching, limited recovery in others, and a sequential change in abundance of others within the communities. Grouping of the corals into broad functional categories highlights their different contributions in the post-bleaching decade (1998 – 2008) (Figure 6.1.8). In all six locations, corals in the functional group massive and encrusting corals best survived the 1998 coral bleaching; their cover increased from 1998 to 2008, and they remained the dominant group at all locations until 2004.

Only in the least impacted location (SL3, Figure 6.1.8c) did other groups survive to contribute significantly to overall cover in the period 1998 to 2004. In other locations, the recruitment of new corals was evident as early as 2003 in the lagoon locations S L1 and SL2 (Figure 6.1.8), and as late as 2008 in the slope locations (Figures.6.1.8e, f). The new recruits were primarily *Pocilloporidae* (*Seriatopora* spp. and *Pocillopora* spp. in roughly equal measure) and *Acropora* (corymbose, digitate, table and branching forms).

At the locations with the most rapid increases in coral cover in recent years, there was a noticeable increase in the cover of corymbose and digitate colonies, followed by their replacement by an increased cover of table corals. The major increase in the table *Acropora* in 2008 probably reflected the increased number of species with this growth form and also the transformation of colonies from a more corymbose growth form when they are small (< 15cm) to a more recognisable table a larger size. The brooding *Isopora* and soft corals were noticeably absent from all locations, apart from those at which they had best survived the bleaching (SL3, SL4). In particular, *Isopora brueggemanni* and *I. palifera* at Location SL3 had doubled in cover from ~ 2% after the 1998 bleaching event to ~4% by 2008.

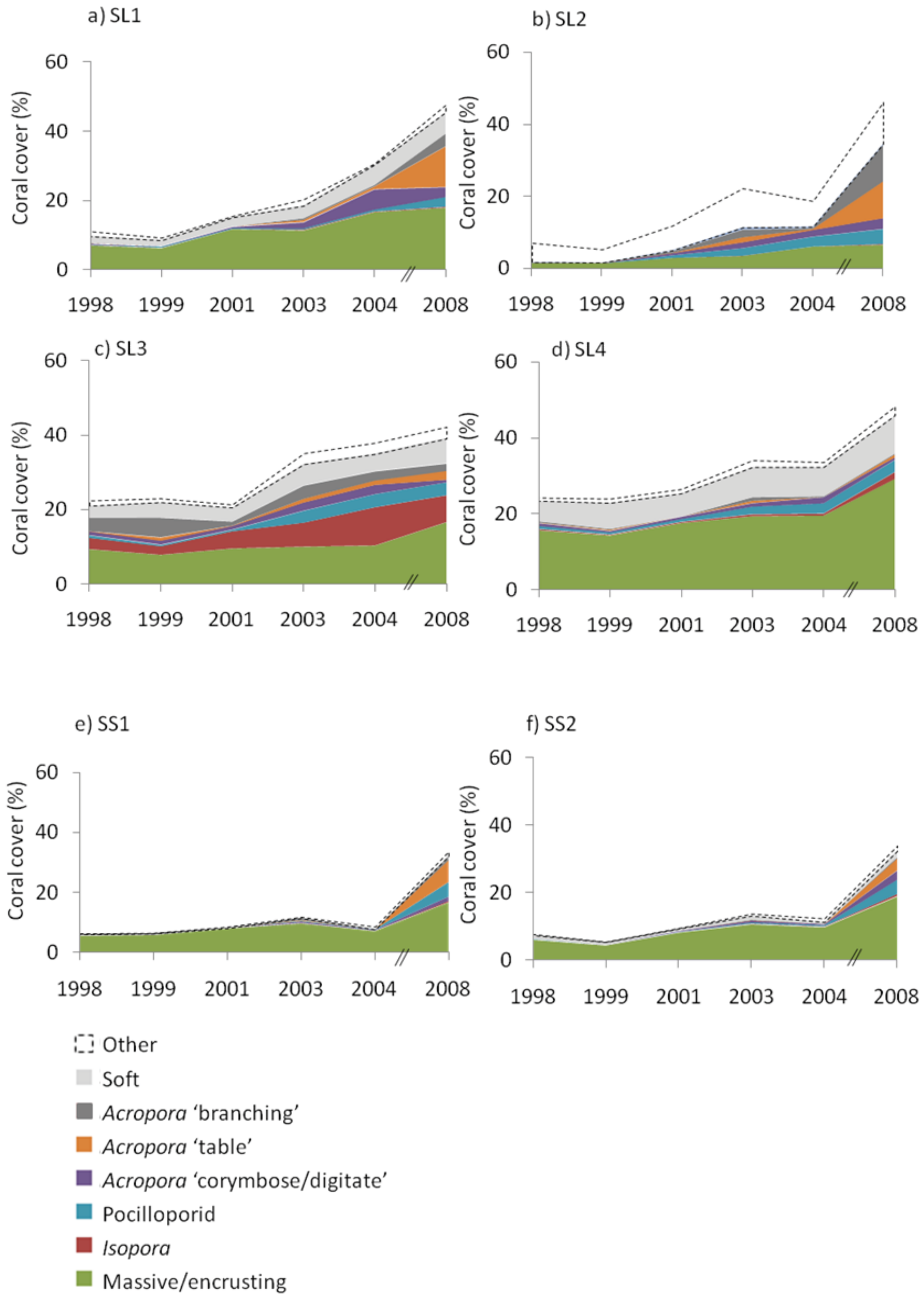


Figure 6.1.8 Successional changes in the structure of coral communities at Scott Reef following the bleaching. See Location Map Figure 1.2.1.

Discussion

Monitoring studies at Scott Reef illustrate how environmental and biological influences interact to affect spatial and temporal variation among local communities. Patterns in mortality and recovery from disturbance reflect combinations of factors such as local habitat conditions (e.g. temperature, currents, swell), existing community structure, and the life-history (e.g. brooders, spawners) of corals in these communities. Monitoring programs that span many years and large spatial scales are crucial to understanding how these factors impact coral abundance through time.

The role of environmental factors in structuring coral communities has been well documented in both hard and soft corals (Ninio and Meekan 2002). Environmental gradients at Scott Reef ranged from exposed reef slope environments, through to deep-channels and low energy lagoonal locations. Coral communities mirrored these gradients, suggesting that prior to bleaching, communities proliferated through their preferred environmental envelopes and that the differences in structure (species and sizes of corals) were an outcome of local conditions and stochastic settlement events. The best example of local habitat conditions structuring community structure throughout the monitoring period is the most protected lagoonal Location (SL2), which consistently had a distinct community with relatively high cover of foliose corals, fungiids and bottlebrush *Acropora.* This location was characterised by poor circulation, high turbidity and small sediment fractions, which are possible drivers for the relatively high abundance of foliose corals. These corals are characterised by their fragile laminar morphology and a relatively poor ability to shed larger size classes of sediment (Hubbard and Pocock 1972).

Community structure and life history traits of dominant corals also determined the impact and recovery from the bleaching event. Before bleaching in 1998, species that proliferated through asexual growth and propagation, such as the soft corals and branching *Acropora, Porites* and *Isopora,* were important drivers of community structure. Given that the recovery of these groups of corals is largely driven by local proliferation, either as asexual growth and division in soft corals or brooded larvae in the *Isopora,* there has been slow recovery at locations worst affected by the bleaching. The brooding coral *Isopora brueggemanni* releases planulae over several months in a year that are competent settle close to the parent, so the species can quickly occupy available space locally and exclude some other corals. However, the limited dispersal also means that brooded larvae do not recruit and recolonise more distant locations. Consequently, when some *I. brueggemanni* colonies survived the bleaching the larval they produced recolonised the local population, but not those worst affected. Although it is not a good direct competitor, this fast growing coral is able to out-compete other species once it has settled and become established, by overgrowing and overtopping (Lang 1973; Lang and Chornesky 1990; Tanner 1995). Thus, at locations such as SL3, fields of *I. brueggemanni* are again expected to dominate the community, in the absence of additional disturbances such as bleaching or cyclones.

In 1998, extreme sea-water temperatures caused widespread mortality of hard and soft corals across Scott Reef that reduced cover of hard coral and number of genera to less than 25% of their pre-bleaching levels. The impacts of bleaching were so severe that they caused major changes to the fish communities (Halford and Caley 2009). Bleaching impacted all locations, suggesting that the conditions responsible for bleaching operated across spatial scale of several kilometres (Smith et al. 2008), Location SL3 was the least effected, possibly due to cool water intrusions from the deep-channel (Steinberg et al. 2006).

Previously dominant, fast growing, coral such as the branching *Acropora* or brooding *Isopora brueggemanni* showed large reductions in average cover following the bleaching, and these coral have a fragile growth form that is susceptible to a range of disturbances (e.g. cyclones, temperature) (Knowlton et al. 1981; Highsmith 1982; Loya et al. 2001; Baird and Marshall 2002; Madin et al. 2008).

The soft corals were also dramatically affected by the bleaching and the massive and encrusting corals that were least affected became the dominant members of all communities.

In the years following the bleaching event, two cyclones impacted the coral communities at Scott Reef. The impact of these cyclones was greatest on fast growing *Acropora* species at some locations (SS1, SS2, SL3, SL4). These findings are consistent with other studies that found cyclone impacts to be less severe and spatially limited when compared to bleaching (Tanner et al. 1994; Connell et al. 1997). Coral reefs have evolved with cyclones over evolutionary time scales and infrequent impacts can even maintain species diversity (Connell 1997). In addition, injured colonies and sheltered locations can supply larvae to recolonise communities exposed to the cyclone's path. 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 (Emanuel 2005) and could have implications for the resilience of coral and fish communities at Scott Reef in the future.

Following these major disturbance events, our data show increases in both cover of coral and number of genera to pre-bleaching levels, but that the pattern is not consistent across all locations and that community structure is still different to that prior to the bleaching. These changes were largely driven by net decreases in cover of many less abundant corals, large declines in cover of soft corals and *Isopora brueggemanni*, and increases in cover of tabulate *Acropora*.

Bleaching is the most dramatic and widespread disturbance that has occurred at Scott Reef since the start of the monitoring program and the effects are still evident more than a decade later. Communities were subsequntly impacted by cyclone disturbances, although the impacts were less severe and more selective than for the bleaching. The communities least affected by the bleaching continued to recover despite their exposure to cyclones, whereas the recovery of those worst affected by the bleaching was delayed more significantly by exposure to cyclones. While community groupings generally remained consistent through time overall, communities generally shifted from a dominance of corals characterised by mechanisms of local proliferation (e.g. soft corals and *Isopora brueggemanni*) to fast-growing spawning corals that disperse more widely (e.g. tabulate *Acropora*). These dramatic changes in cover played an important role in homogenising communities across Scott Reef, whereas there was a greater degree of differentiation in community structure among locations prior to the bleaching.

6.2 Size-structure of coral communities

Summary

The size frequency distribution of three major groups of scleractinian corals, *Acroporidae*, *Pocilloporidae* and *Isopora* was measured at six reef slope locations at Scott Reef between 1996 and 2008. In 1998, a catastrophic bleaching event caused a decrease of between 75-96% in the number of colonies of the coral groups studied, at all locations surveyed, and across size classes. Recovery of small size classes of *Acroporidae* and *Pocilloporidae* was seen at most locations by 2003/2004, and by 2005 (six years after the bleaching event) the total number of colonies had reached pre-bleaching levels, although most of these colonies were still in small size classes. By 2008, the number and size frequency of colonies of *Acroporidae* and *Pocilloporidae* were similar or higher than that seen in pre-bleaching years at all locations. *Acroporidae* and *Pocilloporidae* are both coral families found to be quick to recolonise following disturbance, and this data shows that species within these families can quickly recolonise locations following disturbances provided a sufficient number of colonies survive across Scott Reef. The Genus *Isopora* was seen to recover at SL3 and SL4, the locations least affected by the bleaching, in all size classes except those larger than 50cm which were still between 0-43% of pre-bleaching levels in 2008. At all other locations however, *Isopora* was completely absent from the transects in 1998 – 2003, and in 2008 was still at less than 25% of its original colony number. The slow recovery of *Isopora* may be due to the lack of surviving adults in those locations to provide recruits given the localised dispersal of brooded larvae.

Introduction

Size frequency distributions provide more information on coral populations than coral cover alone, as coral cover data is biased by large colonies, and is not suited to pick up changes in numbers of recruits or juvenile corals. The use of size frequency data can illuminate more of the demographic processes behind the decline, recovery or stability of a coral reef in response to environmental conditions (Connell 1973; Meesters et al. 2001). For example it can show the life history strategies of species groups, indicate stages of recovery, identify periods of good or poor recruitment, and the increase or decrease of certain size classes through disturbance, partial or whole colony mortality and fragmentation (Ebert et al. 1993; Bak and Meesters 1999; Edmunds and Elahi 2007; McClanahan et al. 2008). Here we measure the size frequency of three major groups of scleractinian corals, *Acroporidae*, *Pocilloporidae* and *Isopora* at Scott Reef over 12 years, through three disturbance events at Scott Reef, the mass bleaching of 1998, Cyclone Fay in 2004 and Cyclone George in 2007.

Methods

The size frequency of three major groups of scleractinian corals, *Acroporidae*, *Pocilloporidae* and *Isopora* was measured at Scott Reef in 1996, 1998, 1999, 2003-2006, and 2008. The locations studied were the 6 Reef slope locations at Scott Reef SL1 - SL4, SS1 and SS2. Ten permanent transects were surveyed at each location. Coral colonies larger than 10cm were measured in belt transects 1m x 20m, and colonies smaller than 10cm were measured in belt transects of 25cm x 20m (Figure 6.2.1). Counts of colonies <10cm were standardised to 20m^2 to match the area in which the large colonies were measured. Measurements were made of the longest linear dimension, and have been grouped here into size classes: 0-2cm, 3-5, 6-10, 11-15, 16-20, 21-30, 31-50, 50-100, and >100cm. Not all locations were studied each year due to logistical constraints, therefore to compare the size frequency of coral families across "all Scott" locations, SL2 and SS2 were not included as they were not surveyed in every year.

Figure 6.2.1 Measuring the Size Frequency Distribution of corals along permanent belt transects on the reef slope locations of Scott Reef.

Results

In the first survey year 1996, highest numbers of colonies of the surveyed families were seen at Locations SL1 and SL2, with 2128 colonies measured within the transects at SL1 and 2284 at SL2, approximately twice the colony density seen at the other four locations (Figure 6.2.2 & 6.2.6). Following the 1998 bleaching event, the number of coral colonies decreased dramatically at all locations and for all coral family groups investigated. In 1998 (surveyed a few months after the bleaching event) coral numbers were between 4 – 25% of the 1996 counts at all locations. Some recovery is seen at most locations by 2003 and by 2008 (ten years after the bleaching event) total coral numbers were up to 104% of the pre-bleaching level, with a good spread across size classes. Some evidence may be seen of two smaller disturbance events which occurred during the recovery period, Cyclone Fay in 2004 and Cyclone George in 2007. Category 5 Cyclone Fay caused the movement of thousands of corals at Scott Reef, and may be responsible for the loss of medium sized corals and the sudden increase in small colonies seen at some locations in 2005 through fragmentation and partial mortality. The less severe Cyclone George may be responsible for a reduced rate of growth between 2006 and 2008 compared with the previous period, and a loss of medium to large colonies at SL3 and SL2.

Locations

At Location SL1, there were some survivors of all size classes following the bleaching in 1998. Heaviest losses (80-93%) were seen in the small size classes 0-15cm, approximately 50% of the medium to large colonies survived. By 2003 however, there were fewer medium to large colonies than counted in 1998, possibly indicating that many colonies that initially survived the bleaching, eventually died or reduced in size due to their injuries. In 2005, seven years after the bleaching event, all size classes were at or above pre-bleaching levels, and in 2008, although there are less recruits, there are up to 4 times as many 20-100cm colonies seen than in 1996 (Figure 6.2.2).

Location SL2 was hit heavily by the bleaching, and in 1998 shows a drop in all size classes of between 92-100%. By 2003 some recovery is seen in the small to medium size classes, up to approximately 50% of pre-bleaching levels. Between 2003 and 2005, there is a loss of approximately 20% of medium sized colonies (15-50cm) and a large increase in small colonies. This loss may be partly due to Cyclone Fay which passed through Scott Reef in 2004, causing most damage to the eastern facing reef slopes SL2 and SS1. The increase in small colonies may be a result of new sexual recruits, asexual recruits due to fragmentation, or reduction in size of larger colonies through partial mortality following the cyclone. Rapid growth is seen between 2005 and 2006. Relatively little growth is seen between 2006 and 2008 compared with the previous interval, which may reflect further disturbance by the 2007 Cyclone George (Figure 6.2.3).

Location SL3 was the site least affected by the 1998 bleaching. Size Frequency data were not collected at SL3 or SL4 in 1998, however coral cover data for this period show that SL3 retained the highest proportion of hard coral cover, and in the next Size Frequency survey in 2003, the number and size frequency of colonies at SL3 have already recovered to a state very similar to that seen in 1996. With the exception of coral colonies 50-100 cm and >100cm, due to the loss of large *Isopora*. Growth continues at SL3 until there is a higher cover of these three families (especially *Pocilloporidae*) in 2006 than seen pre-bleaching. Between 2006 and 2008 there is a 24-49% decrease in the medium size classes- 11-50cm, most likely due to Cyclone George, in 2007 that caused the most damage at this location (Figure 6.2.4 & 6.2.5).

Location SS1 has seen the greatest increase during the study period, after dropping to almost nothing in 1998 (Figure 6.2.6), and showing very little increase in colonies between 2003 and 2005 after being hit by the 2004 cyclone. Coral numbers of our studied families have increased to 317% of pre-bleaching levels by 2008 (from 746-2495 colonies), due to a large increase in *Pocilloporidae* and *Acroporidae*. The only size class not yet to recover at SS1 is the largest >100, previously seen in large *Isopora* stands.

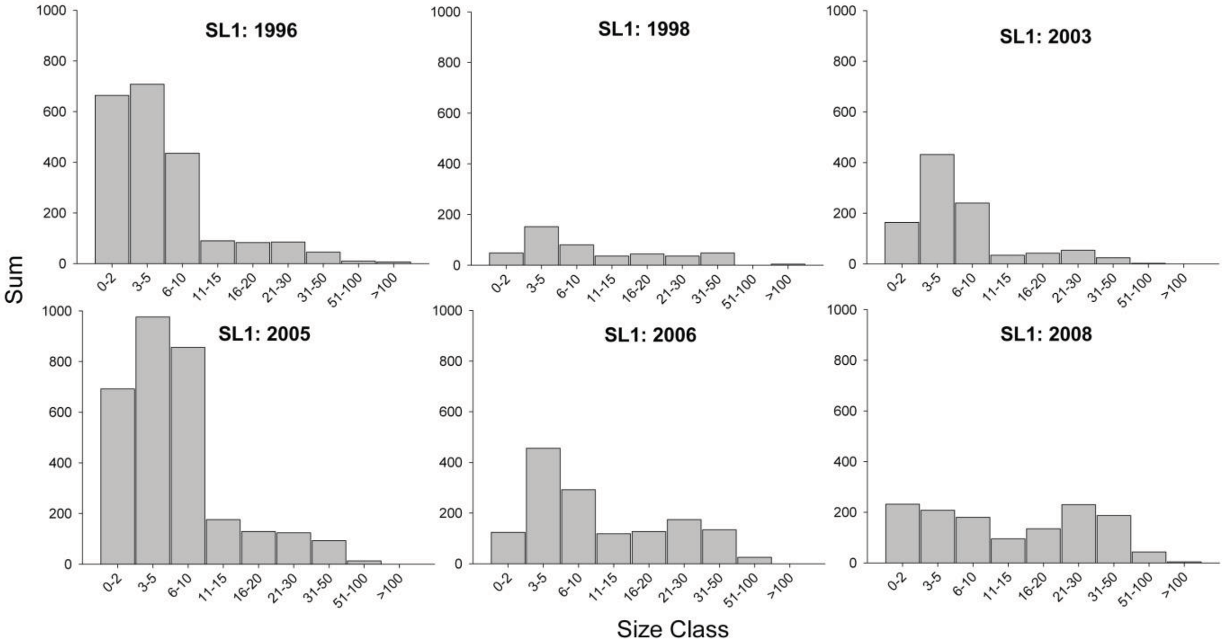


Figure 6.2.2 Size Frequency Distribution of all surveyed coral families at Reef slope Location SL1. Size classes are measured using the longest linear dimension (cm). See Location Map Figure 1.2.1.

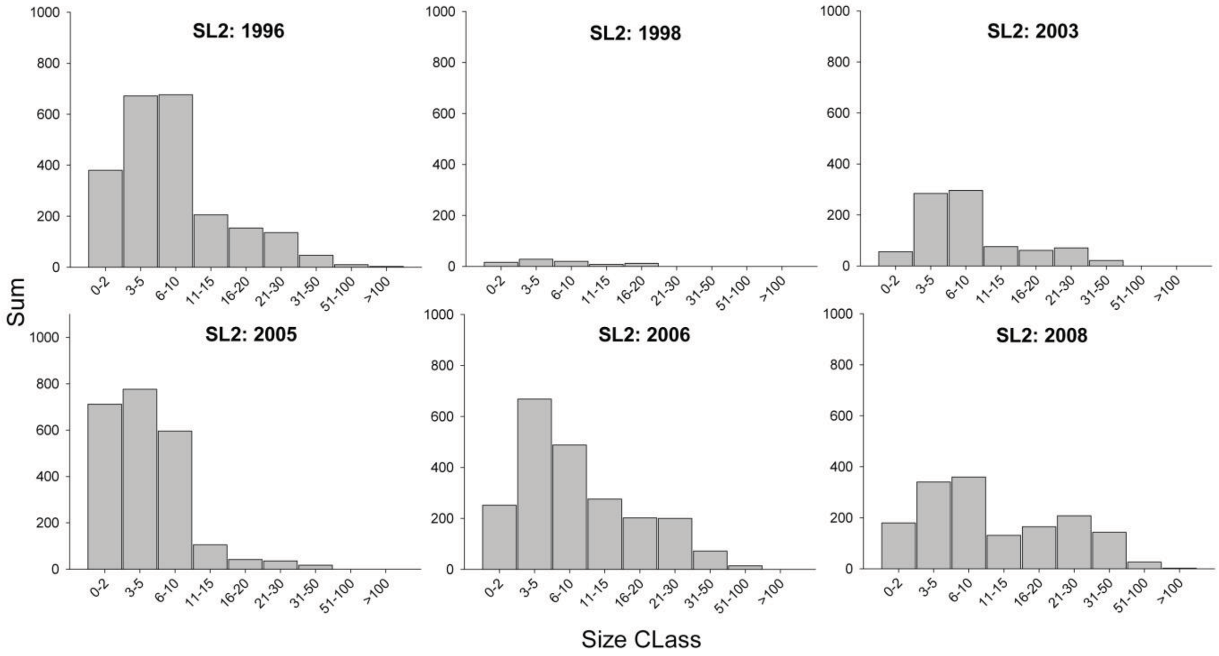


Figure 6.2.3 Size Frequency Distribution of all surveyed coral families at Reef slope location SL2. Size classes are measured using the longest linear dimension (cm). See Location Map Figure 1.2.1.

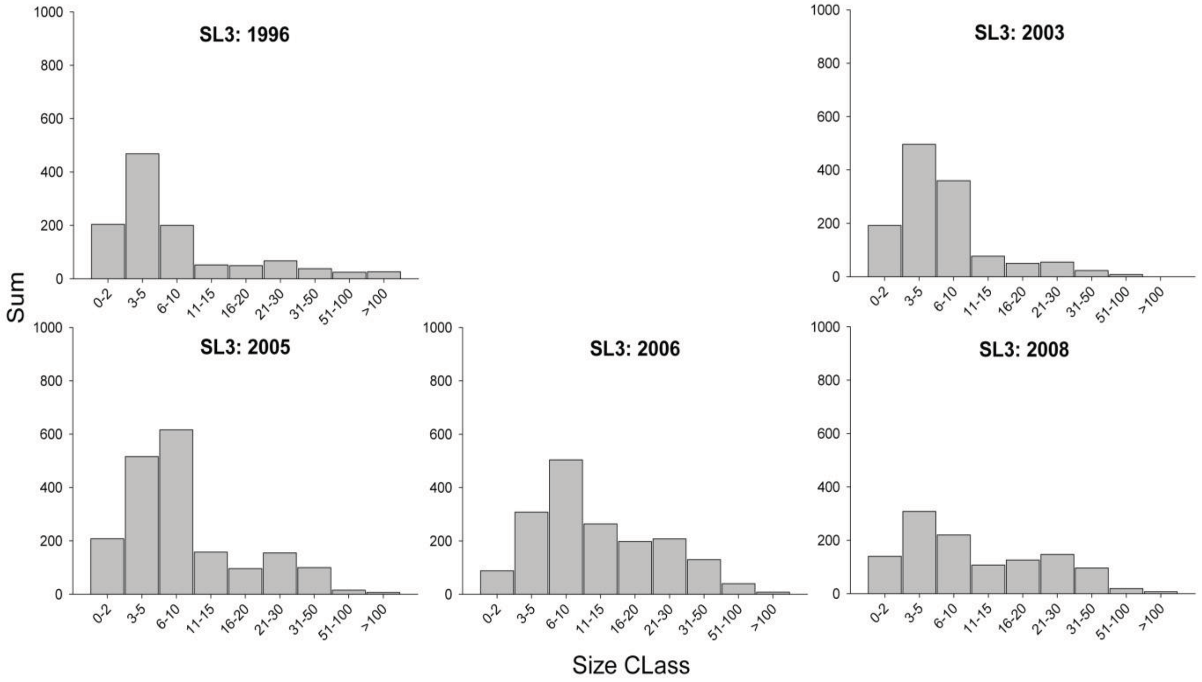


Figure 6.2.4 Size Frequency Distribution of all surveyed coral families at Reef slope Location SL3. Size classes are measured using the longest linear dimension (cm). See Location Map Figure 1.2.1.

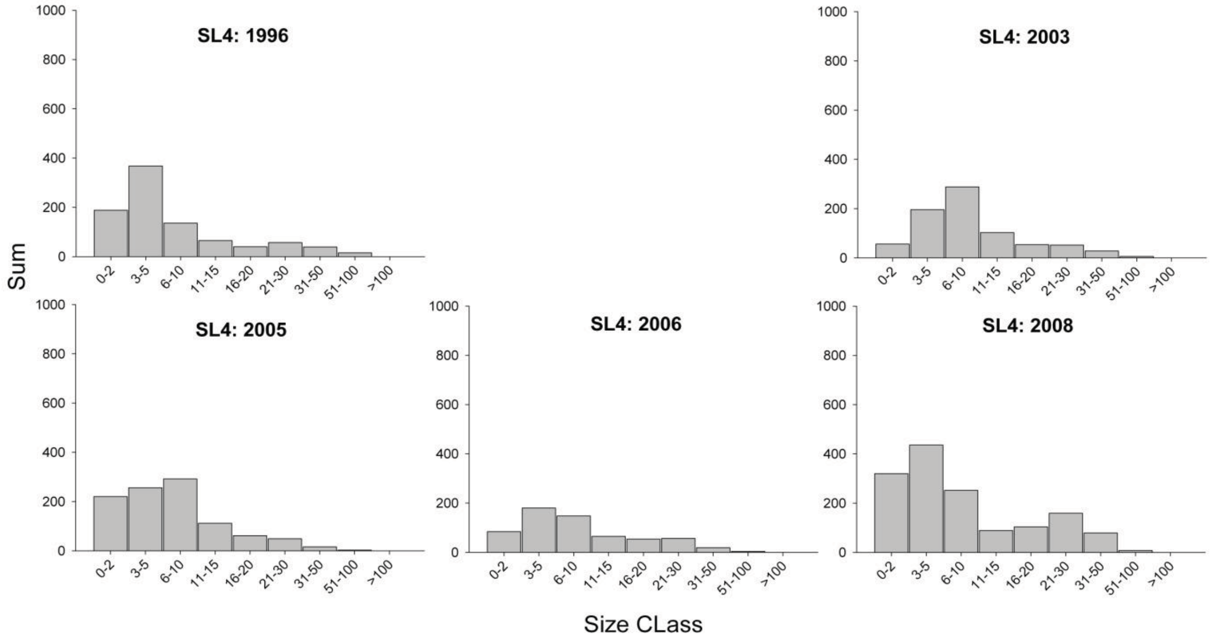


Figure 6.2.5 Size Frequency Distribution of all surveyed coral families at Reef slope Location SL4. Size classes are measured using the longest linear dimension (cm). See Location Map Figure 1.2.1.

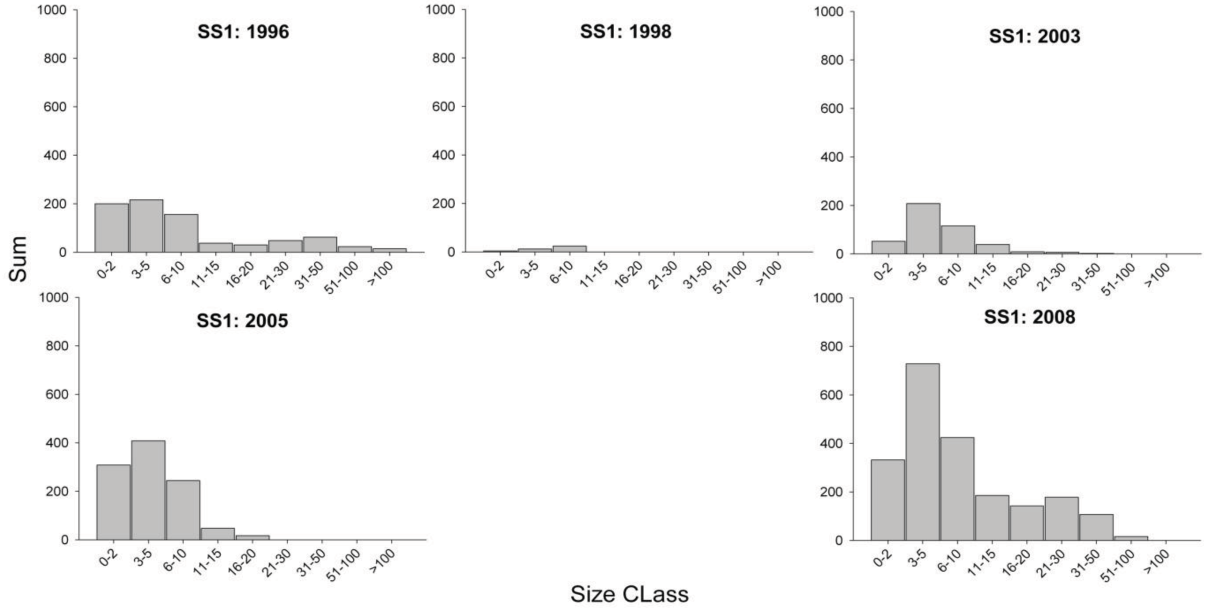


Figure 6.2.6 Size frequency distribution of all surveyed coral families at Outer Reef slope location SS1. Size classes are measured using the longest linear dimension (cm). See Location Map Figure 1.2.1.

Coral Family groups

In 1996, *Acroporidae* was the dominant of our three studied groups, with a total of 5341 colonies counted within the transects (Figure 3.1.6), followed by *Pocilloporidae* 1237 (Figure 6.2.8), then *Isopora* 884 (Figure 6.2.9). Although the large majority of corals >51cm were *Isopora,* which would have increased the overall cover of *Isopora.* The size frequency distribution of *Acroporidae* populations across locations is strongly skewed to the right (due to relatively high numbers in small size classes). Skew to the right is a general pattern seen for coral species groups with life history strategies characterised by relative small size, short lifespan and frequent and successful recruitment (Meesters et al. 2001). This pattern is less pronounced for *Pocillopora* and *Isopora.*

All three of these family groups were drastically reduced across all size classes following the 1998 bleaching. There were at least some colonies of *Acroporidae* and *Pocilloporidae* still present at all locations in 1998, and both families were well into recovery by 2003, *Acroporidae* slightly faster than *Pocilloporidae*. By 2008 both families had exceeded their pre-bleaching levels. The 2008 *Acroporidae* count was 105% of the 1996 count with 5615 colonies, *Pocillopora* was 104% of the 1996 count with 1281 colonies. In contrast, *Isopora* completely disappeared from the transects at all but two locations –SL3 and SL4 where it was at very low numbers. Recovery of *Isopora* to pre-bleaching levels has only occurred at these two locations. At the other locations, *Isopora* was not seen until 2004, and levels are still low in 2008, between 19 - 25% of pre-bleaching levels, with 0% of the largest colonies >100cm. The total count of *Isopora* across locations in 2008 was 680 colonies, 76% of the 1996 count. The slow recovery of *Isopora* may be due to the lack of surviving adults in those locations to provide recruits.

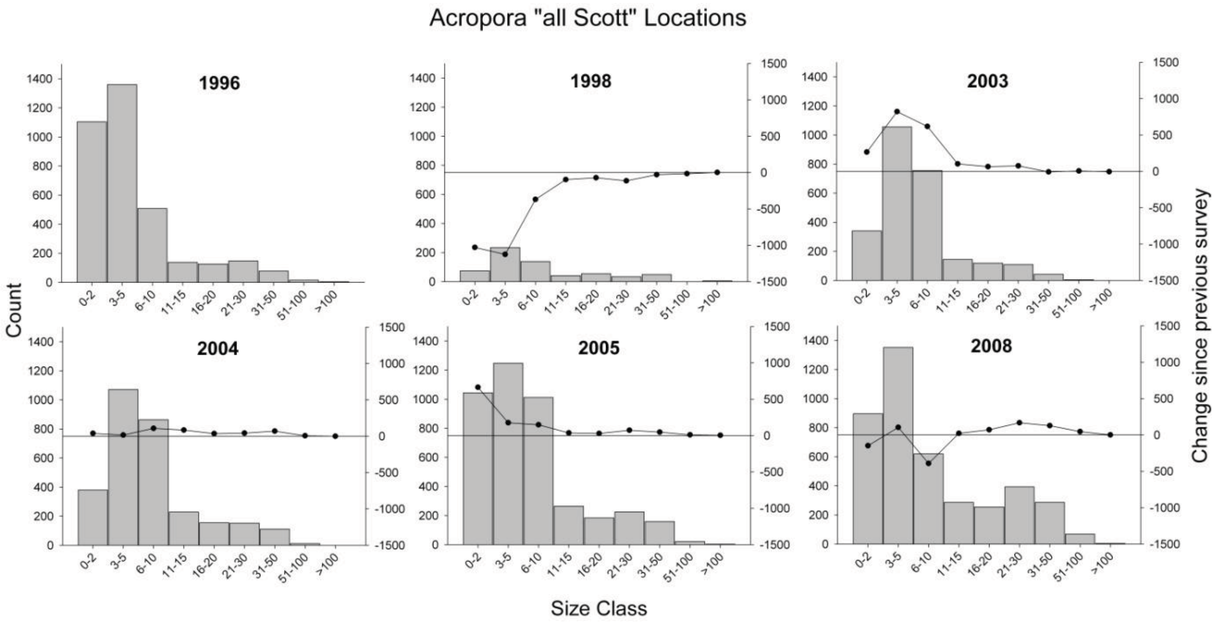


Figure 6.2.7: Size Frequency Distribution of Acropora (Locations SL1 SL3 SL4 SS1 combined). Size classes are measured using the longest linear dimension (cm). See Location Map Figure 1.2.1.

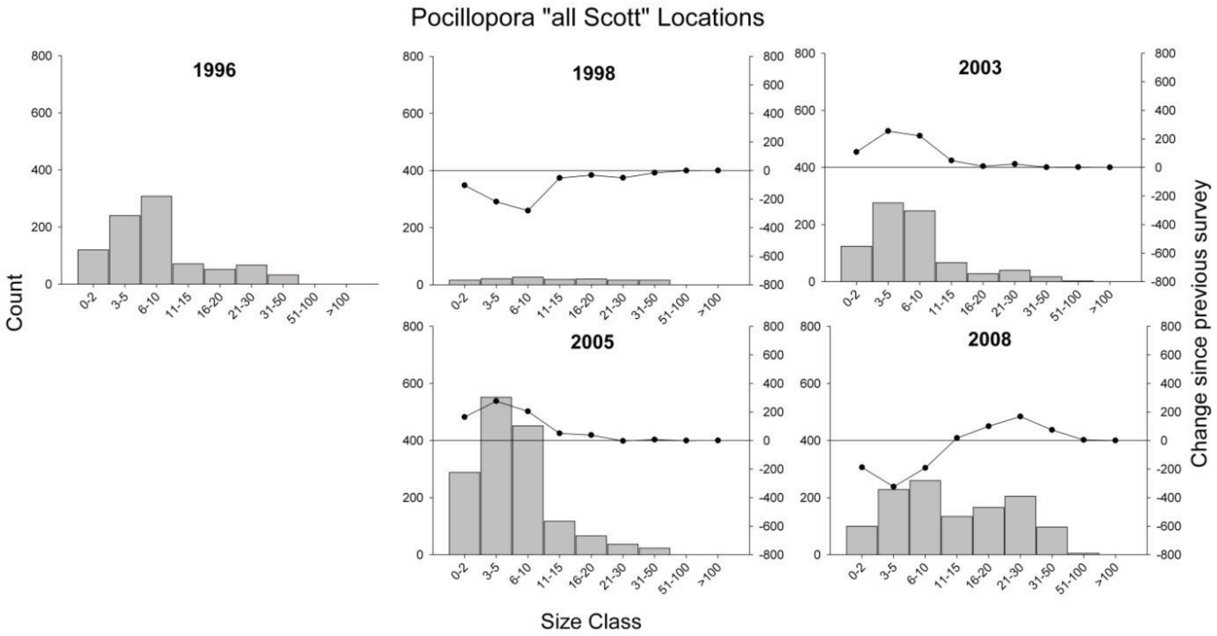


Figure 6.2.8 Size Frequency Distribution of *Pocillopora* (Locations SL1 SL3 SL4 SS1 combined). Size classes are measured using the longest linear dimension (cm). See Location Map Figure 1.2.1.

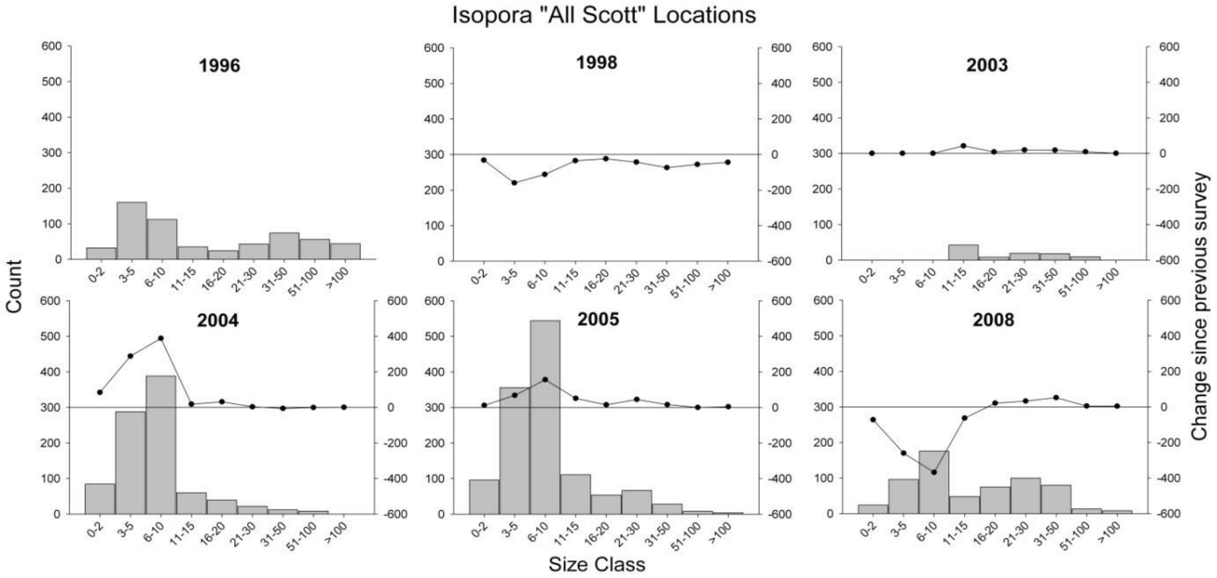


Figure 6.2.9 Size Frequency Distribution of *Isopora* (Locations SL1 SL3 SL4 SS1 combined). Size classes are measured using the longest linear dimension (cm). See Location Map Figure 1.2.1.

6.3 Abundance, diversity and composition of fish communities

Summary

Scott Reef is one of only three emergent oceanic atoll systems in the north-east Indian Ocean between Indonesia and the tropical north-west coast of Australia. Here we show that the fish community at this important reef system has undergone significant change in composition through a 15 year period, and is now quite different to the assemblage that occurred on the reef prior to a mass coral bleaching there in 1998. The effect of the bleaching event in 1998 was most striking on species that used coral either for food such as butterflyfishes or for protection such as many planktivorous damselfishes. Following death of the coral from bleaching and subsequent overgrowth by algae, abundances of herbivores increased, as did numbers of detritivores, which probably benefited from the trapping of detritus by rubble and algal turfs. Fish assemblages on the reef underwent three distinct phases during the study 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 more generalist diet and habitat requirements.

The passage of Cyclone Fay directly over Scott Reef in early 2004, is likely to have caused additional changes to the composition of the benthic community and stalled the recovery of the fish community. Unlike benthic communities, for which disturbance due to bleaching and cyclones are the principal and obvious drivers of change in patterns in abundance and structure, we detected significant trends in fish assemblages during the 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, particularly in the case of piscivorous and invertivore feeding species belonging to

the families Lethrinidae, Lutjanidae and Serranidae. This increase in abundance was accompanied by an increase in fish species richness, and both trends were apparently unaffected by the major bleaching event or the passage of cyclones across the reef. One possibility is that these patterns were the result of increasing fishing pressure on Scott Reef by Indonesian fishermen that have targeted large predatory reef fish and sharks over the last decade. Studies on other reef systems have shown that apex predator release can result in fundamental changes to the biomass and abundance of lower trophic levels in coral reef ecosystems, which might account for some of the changes recorded by our study. In particular, this might explain the increasing number of piscivore and invertivore species over the duration of the study.

Introduction

Coral reefs are the most diverse ecosystem within the marine environment and accommodate thousands of species, including up to one-third of all known marine fishes (Moberg and Folke 1999b). The reason that they are able to host so many species may be, in part, because they are dynamic environments that are subject to episodic disturbances that alter structural components of the environment to provide a diverse array of habitats (Connell 1978; Huston 1979; Huston 1985; Connell et al. 1997; Hughes and Connell 1999; McCulloch et al. 2003; Wilson et al. 2006; Mumby et al. 2007; Wilson et al. 2009). Two of the most common of these disturbances include coral bleaching associated with high sea temperatures, and frequent and intense tropical storms and cyclones (Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007; IPCC 2007).

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

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

The role of disturbance in coral reefs and the prediction of likely effects of climatic changes in the future can be difficult to assess due to the temporal scales at which these processes occur. Recovery of a coral reef from large scale (tens – hundreds of km) disturbance can take more than a decade (Connell et al. 1997; Ninio et al. 2000) and this process is likely to be even longer in a situation where reefs are not part of an archipelagic system of habitats such as the Great Barrier Reef (GBR). At present, there are few studies that have monitored coral reefs at sufficient time scales to fully document patterns of recovery, particularly in the case of isolated coral reef systems such as atolls (Halford and Caley 2009).

The Scott Reef system is a remote group of shelf-edge atolls in the Indian Ocean between Timor and the north-west coast of Australia (Figure 6.3.1 and Figure 1.2.1). 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 (Halford et al. 2004; Bellwood et al. 2006). At Scott Reef, genetic analyses of fishes and corals indicates that exchange with its neighbouring systems occurs only sporadically and there may be intervals of years, decades, or even longer periods between inputs of exogenous larvae into reef populations (Underwood et al. 2009). This genetic evidence implies that many communities at Scott Reef rely on their own reproductive output to respond to disturbances such as cyclones and coral bleaching events and that as a consequence, they may be less resilient than reefs within an inter-connected, archipelagic system such as the GBR.

The Australian Institute of Marine Science (AIMS) initiated long-term monitoring of fish and benthic communities at Scott Reef in 1994. This database provides a unique opportunity to examine the resilience, recovery and restructuring of reef fish communities at decadal scales after widespread and pervasive disturbance events involving both coral bleaching (Smith et al. 2008) and cyclonic storms (Gilmour and Smith 2006). The monitoring program recorded densities of fishes and the percentage contributions of benthic life-form groups in shallow waters (6 to 9 m) on fixed transects at sites nested within seven locations at Scott Reef. The results were subjected to general additive mixed modelling (GAMM) and multivariate analyses to address the following questions: (1) How do patterns of benthic cover and the abundance and species richness of reef fishes change in response to two major disturbances over a 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) What are the key species and functional groups most responsible for any community changes in response to disturbance and are therefore essential for maintaining ecosystem resilience?

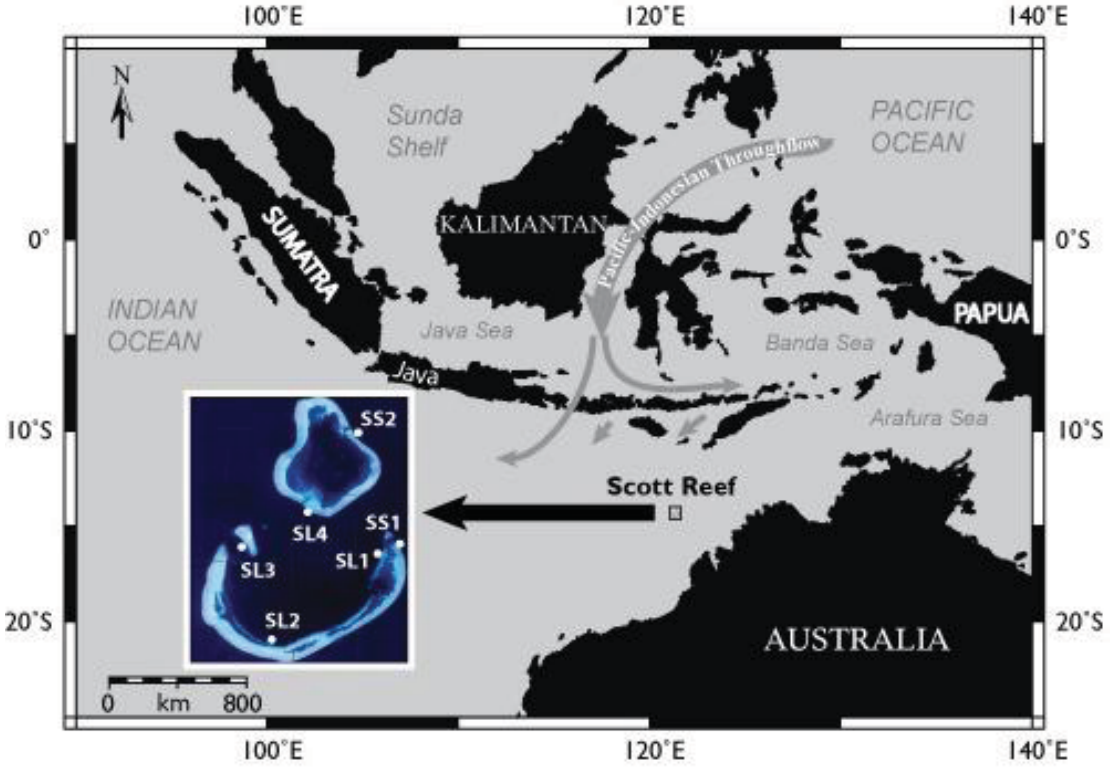


Figure 6.3.1. Location of Scott Reef in the north-eastern Indian Ocean.

Materials and Methods

Study area and sampling regime

The study was conducted at Scott Reef, an isolated offshore reef system consisting of north Scott, south Scott and Seringapatam Reefs, which rise sharply from a water depth of *ca* 450 m in the tropical north-eastern Indian Ocean (Figure 6.3.1). The reef system occupies an area of *ca* 800 km^{-2} and is biogeographically important as it intersects the Indonesian and north-west Australian faunal provinces (Jones 1973; Wilson and Allen 1987). The system is largely unaffected by many of the typical anthropogenic stressors of coral reefs close to the coast due to its isolation, distance from shore and the absence of human habitation. However, Scott Reef is an important site for fishing by Indonesia whose fishers target a range of reef organisms (mostly shark, trepang and trochus). Stocks of these animals are chronically over-fished (Cappo et al. 2004; Meekan et al. 2006).

To quantify temporal changes in reef fish communities at Scott Reef, seven locations were surveyed in the same period (October to January) during 11 surveys between 1994 and 2008 as part of the long-term monitoring programme at the Australian Institute of Marine Science (Heyward et al. 1998). The 1998 survey was undertaken in November *ca* 8 months after a reef-wide coral bleaching event that began in March 1998 (Smith et al. 2008).

Three locations (SS1, SS2 and SS3) were sampled on the outer reef slope and four locations (SL1, SL2, SL3 and SL4) were sampled on the inner reef slope (Figure 6.3.2). Within each location, fish were sampled at three sites, separated by a distance of *ca* 250 m. At each site, five permanently marked 50 m long transects were positioned parallel to the reef crest in water depth ranging between 6 - 9 m, each separated by a distance of 10 to 20 m. Each transect was censused by a diver on SCUBA who identified and recorded the number of fishes belonging to 10 non-cryptic families (Acanthuridae, Chaetodontidae, Labridae, Lethrinidae, Lutjanidae, Scaridae, Serranidae, Siganidae, Zanclidae and Pomacentridae). The smaller, more site-attached or territorial species from the family Pomacentridae were surveyed along a 50 x 1 m corridor within the transect, while the larger, more mobile species from all other families were surveyed along a 50 x 5 m corridor. Fishes were classified into seven trophic groups based on their diet and feeding behaviour (see Appendix S1 for full species list and trophic classification). Species classified as corallivores included both obligate and facultative coral feeders (Pratchett 2005; Wilson et al. 2006). Herbivorous species were identified as by Green and Bellwood (2009) while detritivores (including epilithic algal matrix feeders), invertivores, planktivores, omnivores and piscivores followed Froese and Pauly (2009) and Wilson et al. (2003).

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

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

Long-term trends of fish fauna

Temporal trends in the densities of fish families were examined at the reef level and within each reef using generalized additive mixed models (GAMMs) (Pinheiro and Bates 2000; Zuur et al. 2009). These models were used to examine the relationship between fish abundance and any long term trend. Two models were developed; firstly trends of abundance at the reef level and secondly within each reef location. The relationship between the long term trend and abundance of Pomacentridae, non-Pomacentridae, functional categories of fishes and individual fish species and species richness were explored. As the predictor (independent) variables were either linear or non-linear, GAMMs were applied because these models can accommodate both types of variables.

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

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

Multivariate analysis

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

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

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

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 of fish species data 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 × category data matrix that best mirror that division are also provided. The complementary sample × 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 was performed at each node of the tree to ascertain whether the particular group of samples being subdivided contained significant internal differences, except in those cases when a test carried out at a broader division returned a non-significant result (Clarke et al. 2008). The LINKTREE and SIMPROF routines thus produced a linkage tree with terminal nodes comprising groups of samples that precisely represented 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.

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

Results

Temporal trends in reef faunas

Between 1994 and 1997 coral cover at Scott Reef was relatively stable and averaged around 40% of the benthic community. In 1998 there was a reef-wide and pervasive bleaching event that resulted in a steep decline of live corals to approximately 10% cover of benthic habitats. This was followed by a rise in abundance of algae, which grew over the skeletons of the recently dead corals (Figure 3.2.3.1a; Smith et al. 2008). Mean coral cover then remained low (< 20%) through to 2005, but recovered to approximately pre-disturbance levels (35%) by 2008.

Temporal trends in densities of both pomacentrid (damselfishes) and non-pomacentrid fishes and the number of fish species were fitted by GAMM models with interactions between location and year. The trend in the mean densities of the damselfishes was non-linear ($p < 0.0001$) with values declining from 1995 through 1999 before returning to higher levels in subsequent years (Figure 6.3.2b). In contrast, the densities of larger and more mobile fishes (non-Pomacentridae) and numbers of fish species increased linearly throughout the entire 15 year study period (Figure 6.3.2c,d), with the trend being greater for non-pomacentrids ($p < 0.0001$) than number of species ($p < 0.001$).

The composition of the fish community at Scott Reef changed throughout the entire 15 year study and a pronounced shift occurred following the 1998 bleaching (Figure 6.3.3a). The SIMPROF test of significanct structure classified the samples into distinct pre-bleach, immediate post-bleach and late post-bleach communities (phases). A nMDS ordination of the same data showed the trajectory of faunal change through time and indicated that the late post-bleach community in 2008 was tracking away from earlier pre-bleach communities (Figure 6.3.3b). Species composition differed mostly among the six locations (ANOSIM $R = 0.872$, $P < 0.001$) but also differed among time periods (ANOSIM $R = 0.550$, $P < 0.01$). Pair-wise ANOSIM comparisons showed that the species composition of the fish faunas in each time period differed significantly from that in each other period (all $P < 0.001$), with R-statistic values ranging from 0.198 for the 1994-96 *vs* 1997-98 comparison to 0.781 between the earliest (1994-96) *vs* the most recent period, *i.e.* 2008 (Table 6.3.1). ANOSIM R values for comparisons between faunas of temporally contiguous periods were far less than those that were widely-separated.

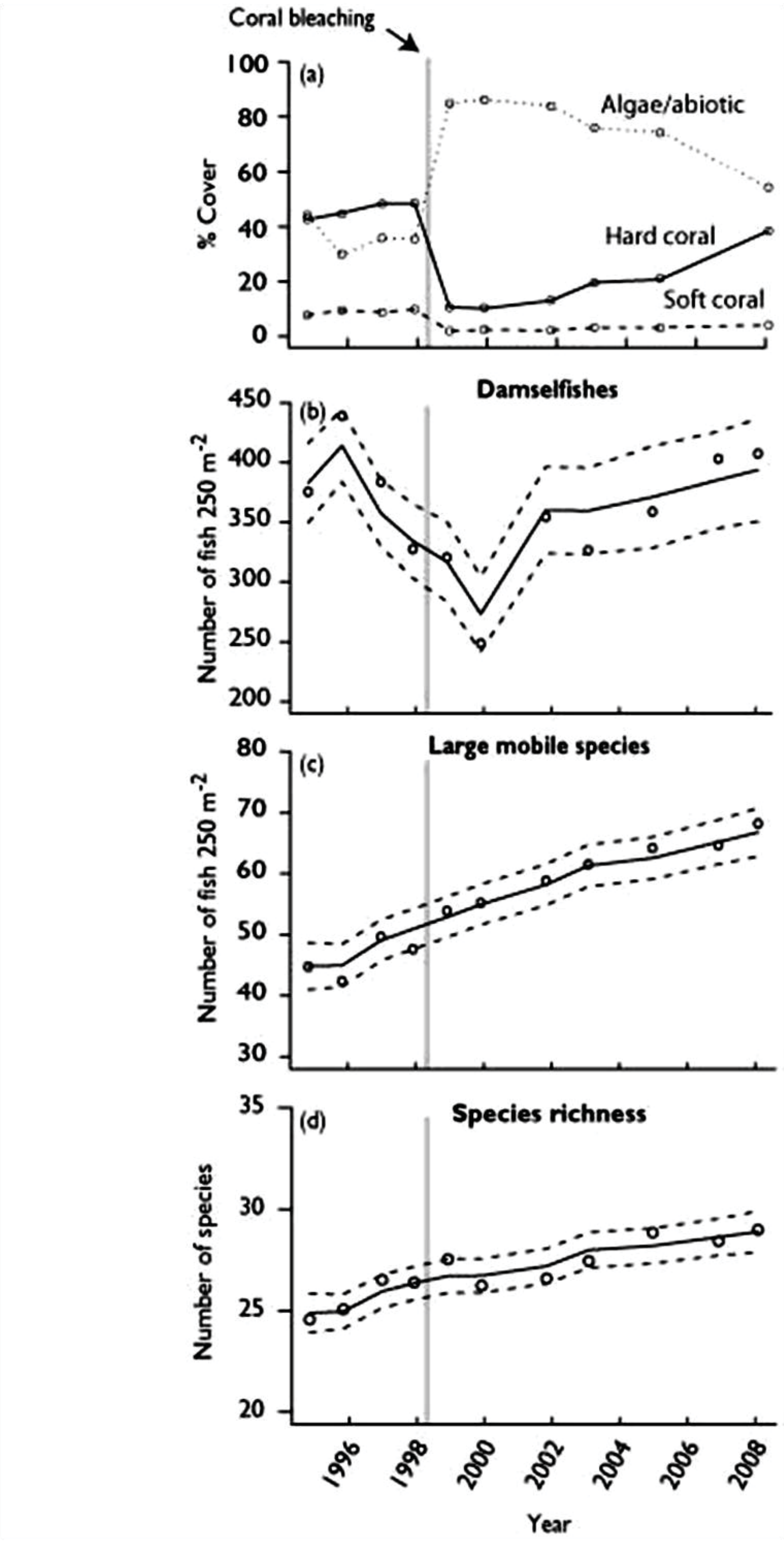


Figure 6.3.2 Algal/abiotic cover and mean densities of pomacentrid and non-pomacentrid fishes and species richness of fishes at Scott Reef between 1994 and 2008. Solid lines are general additive mixed model (GAMM) fits, dashed lines indicate 95% confidence intervals, circles are the observed men densities and grey line indicates period of coral bleaching. All analyses were conducted at the transect level.

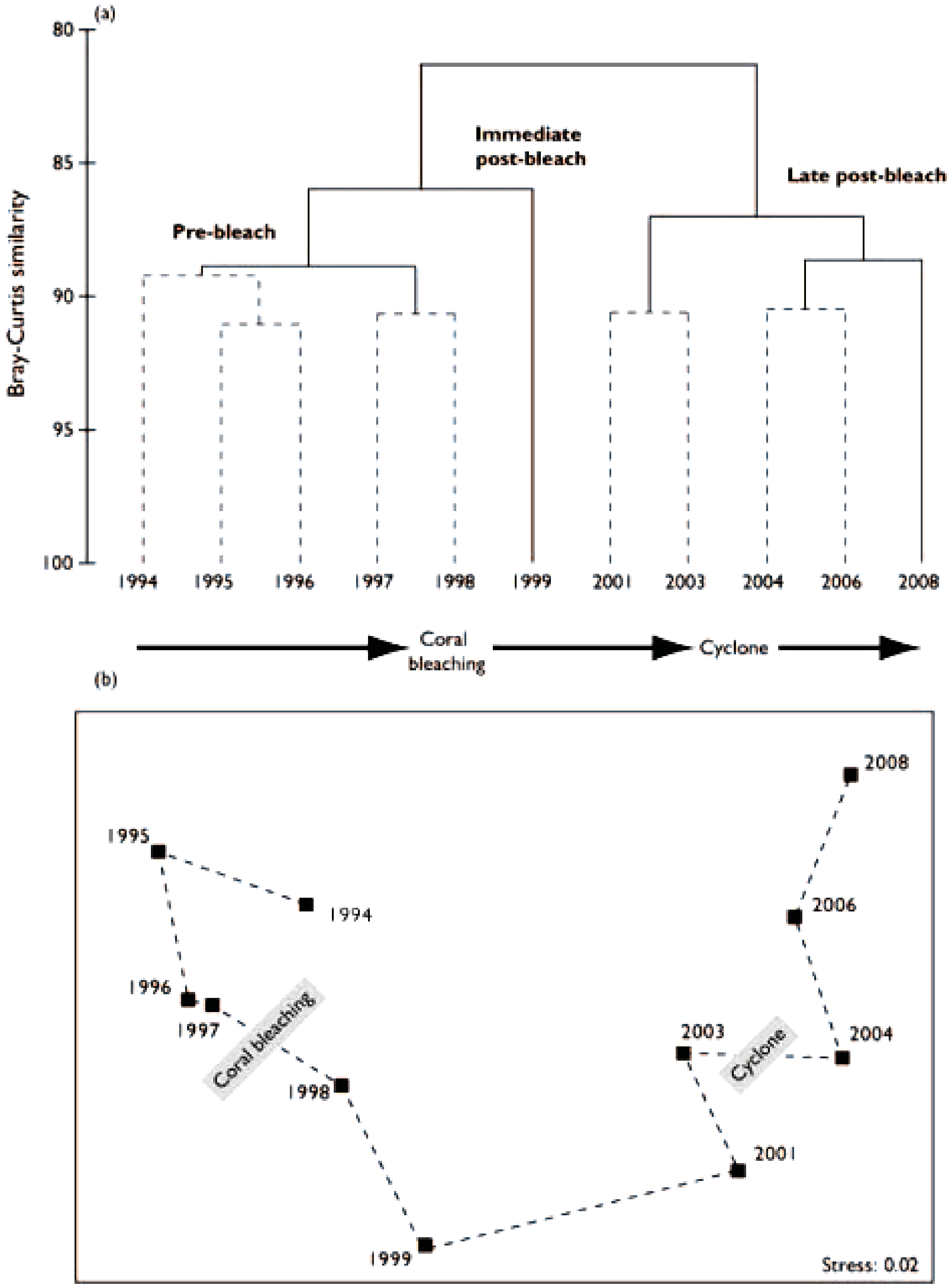


Figure 6.3.3 CLUSTER analysis (a), with SIMPROF of the species compositions of reef fish communities at Scott Reef between 1994 and 2008. Solid lines indicate groups that SIMPROF determined were significantly different from each other and (b) Non-metric multidimensional scaling (nMDS) ordination showing the trajectory of change in the structure of fish communities at Scott Reef between 1994 and 2008.

Table 6.3.1 Pairwise R-statistic values for disturbance period derived from 2-way crossed ANOSIM (Location x Period) of the fish communities at Scott Reef between 1994 and 2008.

Period	1994 - 96	1997 - 98	1999	2001 - 03	2004 - 06
1997 - 98	0.198**				
1999	0.621***	0.204*			
2001 - 03	**0.755*****	0.592***	0.459***		
2004 - 06	**0.775*****	**0.667*****	**0.665*****	0.287***	
2008	**0.781*****	**0.668*****	0.611***	0.596***	0.273**

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. R values > 0.65 in bold.

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).

Trends in fish communities at Scott Reef were dominated by the response of fishes to the catastrophic bleaching event that removed *ca* 75% of all live coral cover in early 1998 (Smith et al. 2008). This response was most striking in species that are reliant on coral for food. Densities of this group declined from a high in 1997 to lows from 2001 through 2004 before a modest increase in the last two years of the study (Figure 6.3.4). A similar decline in planktivores occurred following the bleaching event, although in contrast to coral feeding species, numbers of these fishes returned to pre-bleaching levels within 2-3 years of the event. Numbers of herbivores increased after the bleaching event as dead coral surfaces were overgrown by algae, and then returned to pre-bleaching levels by 2006. The abundance of detrital-feeding species also increased after the bleaching event, but have not declined and have remained higher than at pre-bleaching levels throughout the study period. In contrast to these trophic groups, numbers of omnivores, invertivores and piscivores displayed no obvious response to the bleaching event in 1998. Indeed, the latter two groups have increased in abundance throughout the study.

Species that characterised each of the time periods included the surgeonfish *Ctenochaetus* spp. which consumes detrititus within the epilithic algal matrix (EAM) and the damselfish species *Pomacentrus lepidogenys*, *P. philippinus* and *P. vaiuli* (Table 6.3.2). The fauna of the early pre-bleaching period was distinguished from that in all other post-bleaching periods by greater numbers of the damselfishes *Chromis ternatensis*, *Pomacentrus moluccesnsis* and *Pomacentrus lepidogenys* and the butterflyfish *Chaetodon punctatofasciatus*, and in most cases, lower densities of herbivorous species such as the territorial damselfish *Plectroglyphidodon lacrymatus*, the parrotfishes *Chlororus sordidus*, *Scarus dimidiatus* and/or *Scarus Schlegeli* and the detritus feeding surgeonfish *Ctenochaetus* spp. The fauna in 2008 was distinguished by relatively greater contributions of the planktivores *P. philippinus* and *Chromis margaritifer* and the omnivorous humpback snapper *Lutjanus gibbus* and by lower densities of *Zebrasoma scopas* and *P. lacrymatus* (Table 6.3.2).

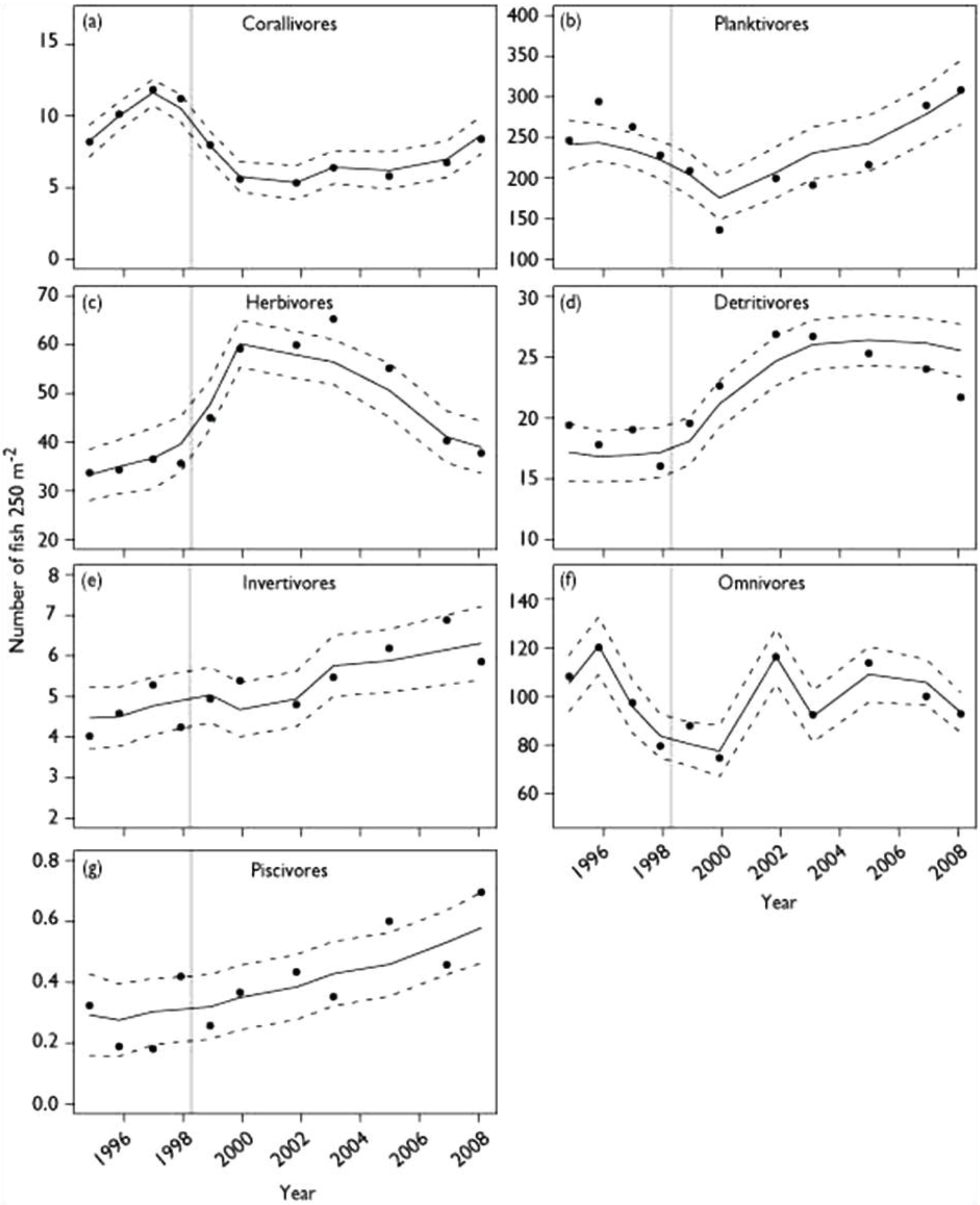


Figure 6.3.4 Mean (± 95% C.I.) densities of functional groups of fishes at Scott Reef between 1994 and 2008. Solid lines are general additive mixed model (GAMM) fits, dashed lines indicate 95% confidence intervals, circles are the observed men densities and grey line indicates period of coral bleaching. All analyses were conducted at the transect level.

The temporal trends for densities of the key fish species identified by the above SIMPER analysis were modeled with GAAMs and highlight contrasting trends among species belonging to the same trophic group (Figure 6.3.5). Mean densities of *Chaetodon punctofasciatus* and *C. trifasciatus*, which are both coral feeders, decreased following the 1998 bleaching event, with the latter species showing a recent increase in abundance (Figure 6.3.5a). In contrast, *C. vagabundus*, which also consumes coral polyps, exhibited constant increases through the bleaching to 2008. The mean densities of the herbivorous *Chlororus sordidus* and *P. lacrymatus* increased following the 1998 bleaching through to 2004 before decreasing to 2008, whereas *Acanthurus nigricans* maintained an increasing trend in abundance through the bleaching event to 2008 (Figure 6.3.5b). Densities of the plankton feeding damselfish *Chromis ternatensis* decreased following the bleaching and remained low through 2004 before increasing to 2008, whereas numbers of *Pomacentrus philippinus* and *Chromis margaritifer*, also planktivores, increased immediately following the bleaching and maintained that trend so that these species are now in greater abundance than they were prior to the bleaching (Figure 6.3.5d).

Table 6.3.2 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.
pk, planktivore; om, omnivore; he, herbivore; iv, invertivore; dv, detritivore; pi, piscivore; cv, corallivore.

Period	**Early pre-bleach 1994 to 1996**	**Late pre-bleach 1997 to 1998**	**Immediate post bleach 1999**	**Post-bleach 2001 to 2003**	**Post-bleach 2004 to 2006**	**Late post-bleach 2008**
1994 to 1996	*Pomacentrus lepidogenys* *Chromis ternatensis* *Pomacentrus vaiuli* *Pomacentrus philippinus* *Ctenochaetus spp.* *Chromis margaritifer* *Plectroglyphidodon lacrymatus* *Zebrasoma scopas*					
1997 to 1998	*pk Chr ternatensis* $^{94/96}$ *pk Pom lepidogenys* $^{94/96}$ *pk Chr xanthura* $^{94/96}$ *om Chrys rex* $^{94/96}$ *om Pom vauili* $^{94/96}$ *om Ambly. curacao* $^{97/98}$ *he Chlor sordidus* $^{97/98}$ *iv Mono grandoculis* $^{94/96}$	*Pomacentrus lepidogenys* *Chromis ternatensis* *Pomacentrus philippinus* *Pomacentrus vaiuli* *Ctenochaetus spp.* *Plectroglyphidodon lacrymatus* *Zebrasoma scopas* *Scarus niger*				
1999	*pk Chr ternatensis* $^{94/96}$ *pk Pom lepidogenys* $^{94/96}$ *om Pom vauili* $^{94/96}$ *he Plectro. lacrymatus* ^{99} *he Chlororus sordidus* ^{99} *he Scarus dimidiatus* ^{99} *he Acanth ncans* ^{99} *cv Chaet puncto* $^{94/96}$ *om Pom. moluccensis* $^{94/96}$	*pk Chr ternatensis* $^{97/98}$ *pk Pom lepidogenys* $^{97/98}$ *om Ambly. curacao* $^{97/98}$ *he Plectro. lacrymatus* ^{99} *he Chlororus sordidus* ^{99} *he Naso elegans* ^{99} *he Scarus schlegeli* ^{99} *dv Ctenochaetus spp* ^{99} *cv Chaet uliet* $^{97/98}$	*Pomacentrus lepidogenys* *Plectroglyphidodon lacrymatus* *Pomacentrus philippinus* *Ctenochaetus spp.* *Pomacentrus vaiuli* *Chlororus sordidus* *Zebrasoma scopas* *Chlororus sordidus* *Scarus niger*			
2001 to 2003	*pk Chr ternatensis* $^{94/96}$ *pk Pom lepidogenys* $^{94/96}$ *om Chrys rex* $^{01/03}$ *om Pom. moluccensis* $^{94/96}$ *he Acanth nfusc* $^{01/03}$ *he Acanth ncans* $^{01/03}$ *dv Ctenochaetus spp* $^{01/03}$ *cv Chaet puncto* $^{94/96}$	*pk Chr ternatensis* $^{97/98}$ *pk Pom phillipinus* $^{01/03}$ *pk Pom lepidogenys* $^{01/03}$ *om Chrys rex* $^{01/03}$ *om Ambly. curacao* $^{97/98}$ *he Acanth nfusc* $^{01/03}$ *dv Ctenochaetus spp* $^{01/03}$ *cv Chaet puncto* $^{97/98}$	*pk Chr ternatensis* ^{99} *pk Pom phillipinus* $^{01/03}$ *pk Pom lepidogenys* $^{01/03}$ *om Chrys rex* $^{01/03}$ *he Plectro. lacrymatus* ^{99} *he Acanth nfusc* $^{01/03}$ *he Scarus dimidiatus* ^{99} *dv Ctenochaetus spp* $^{01/03}$	*Pomacentrus philippinus* *Pomacentrus lepidogenys* *Chrysiptera rex* *Ctenochaetus spp.* *Pomacentrus vaiuli* *Plectroglyphidodon lacrymatus* *Chlororus sordidus* *Zebrasoma scopas*		
2004 to 2006	*pk Chr ternatensis* $^{94/96}$ *pk Pom phillipinus* $^{04/06}$ *pk Pom lepidogenys* $^{94/96}$ *om Chrys rex* $^{04/06}$ *he Plectro. lacrymatus* $^{04/06}$ *he Acanth nfusc* $^{04/06}$ *dv Ctenochaetus spp* $^{04/06}$ *cv Chaet puncto* $^{94/96}$ *om Pom. moluccensis* $^{94/96}$	*pk Chr ternatensis* $^{97/98}$ *pk Pom phillipinus* $^{04/06}$ *pk Pom lepidogenys* $^{04/06}$ *pk Chr xanthura* $^{04/06}$ *om Chrys rex* $^{04/06}$ *he Acanth nfusc* $^{04/06}$ *he Scarus schlegeli* $^{04/06}$ *dv Ctenochaetus spp* $^{04/06}$ *iv Mono grandoculis* $^{04/06}$	*pk Pom phillipinus* $^{04/06}$ *pk Pom lepidogenys* $^{04/06}$ *om Chrys rex* $^{04/06}$ *he Plectro. lacrymatus* ^{99} *he Zeb scopas* ^{99} *he Acanth nfusc* $^{04/06}$ *he Scarus dimidiatus* ^{99} *dv Ctenochaetus spp* $^{04/06}$ *iv Mono grandoculis* $^{04/06}$	*pk Pom lepidogenys* $^{04/06}$ *pk Pom phillipinus* $^{04/06}$ *pk Chr xanthura* $^{04/06}$ *he Plectro. lacrymatus* $^{01/03}$ *he Scarus schlegeli* $^{01/03}$ *he Chlor sordidus* $^{01/03}$ *dv Ctenochaetus spp* $^{01/03}$ *iv Mono grandoculis* $^{04/06}$ *pi Lutjanus gibbus* $^{04/06}$	*Pomacentrus philippinus* *Pomacentrus lepidogenys* *Chrysiptera rex* *Ctenochaetus spp.* *Pomacentrus vaiuli* *Plectroglyphidodon lacrymatus* *Chromis xanthura* *Chromis margaritifer* *Chlororus sordidus*	
2008	*pk Chr ternatensis* $^{94/96}$ *pk Pom phillipinus* ^{08} *pk Pom lepidogenys* $^{94/96}$ *om Pom vauili* $^{94/96}$ *he Acanth ncans* ^{08} *he Scarus schlegeli* ^{08} *he Zebrasoma scopas* $^{94/96}$ *dv Ctenochaetus spp* ^{08} *cv Chaet puncto* $^{94/96}$ *pi Lutjanus gibbus* ^{08} *om Pom. moluccensis* $^{94/96}$	*pk Chr ternatensis* $^{97/98}$ *pk Pom phillipinus* ^{08} *om Chrys rex* ^{08} *he Plectro. lacrymatus* $^{97/98}$ *he Zebrasoma scopas* $^{97/98}$ *he Scarus schlegeli* ^{08} *he Acanth ncans* ^{08} *dv Ctenochaetus spp* ^{08} *cv Chaet puncto* $^{97/98}$ *pi Lutjanus gibbus* ^{08} *cv Chaet vagabundus* ^{08}	*pk Pom phillipinus* ^{08} *pk Pom lepidogenys* ^{08} *pk Chr ternatensis* ^{08} *om Chrys rex* ^{08} *om Pom. moluccensis* ^{99} *he Plectro. lacrymatus* ^{99} *he Zebrasoma scopas* ^{99} *he Chlor sordidus* ^{99} *dv Ctenochaetus spp* ^{08} *pi Lutjanus gibbus* ^{08}	*pk Chr ternatensis* ^{08} *pk Chr xanthura* ^{08} *pk Pom lepidogenys* ^{08} *pk Pom phillipinus* ^{08} *pk Pom vauili* $^{01/03}$ *pk Chr margaritifer* ^{08} *he Plectro. lacrymatus* $^{01/03}$ *he Acanth nfusc* $^{01/03}$ *he Zebrasoma scopas* $^{01/03}$ *pi Lutjanus gibbus* ^{08}	*pk Pom phillipinus* ^{08} *pk Chr margaritifer* ^{08} *pk Pom lepidogenys* $^{04/06}$ *om Chrys rex* $^{04/06}$ *he Plectro. lacrymatus* $^{04/06}$ *he Acanth nfusc* $^{04/06}$ *he Zebrasoma scopas* $^{04/06}$ *dv Ctenochaetus spp* $^{04/06}$ *iv Mono grandoculis* $^{04/06}$ *pi Lutjanus gibbus* ^{08}	*Pomacentrus philippinus* *Pomacentrus lepidogenys* *Chromis margaritifer* *Chrysiptera rex* *Pomacentrus vaiuli* *Ctenochaetus spp.* *Chromis xanthura* *Chlororus sordidus* *Chaetodon trifasciatus* *Acanthurus nigricans*

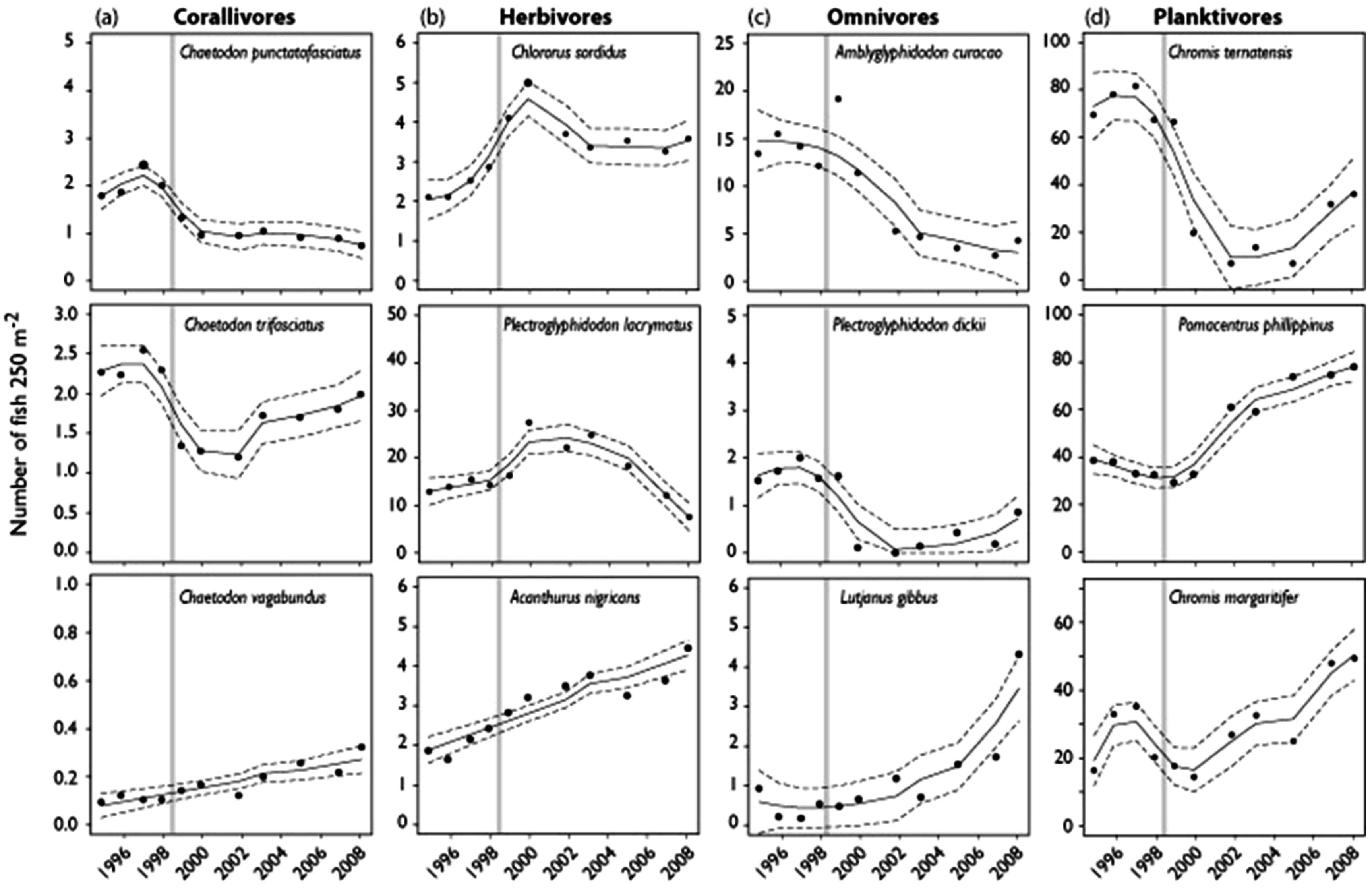


Figure 6.3.5. Mean (± 95 C.I.) densities of fish species identified by SIMPER as distinguishing particular time periods at Scott Reef between 1994 and 2008.
Solid lines are general additive mixed model (GAMM) fits, dashed lines indicate 95% confidence intervals, circles are the observed men densities and grey line indicates period of coral bleaching. All analyses were conducted at the transect level

Relationship between fish community and benthic composition

The linkage tree, representing the separation of the temporal groups identified by a divisive cluster analysis, together with 'explanations' of those bifurcations in terms of thresholds on individual benthic categories, are provided in Figure 6.3.6. 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. Thus, the separation of the fish fauna prior to the 1998 coral bleaching from that after the bleaching was related to a greater contribution of soft, brooding *Isopora*, corymbose and digitate *Acropora* corals and a lower cover of algae (includes turfing and coralline). The fauna immediately after the bleaching (1998 to 1999) was distinguished from the late-bleached community by greater contributions of macroalge and reduced contributions of massive and encrusting corals. Marked increases in tabulate *Acropora*, *Pocilloporidae*, soft and massive corals defined the 2008 community from the previous 2004 and 2006 community which was characterised by greater algal cover (Figure 6.3.6).

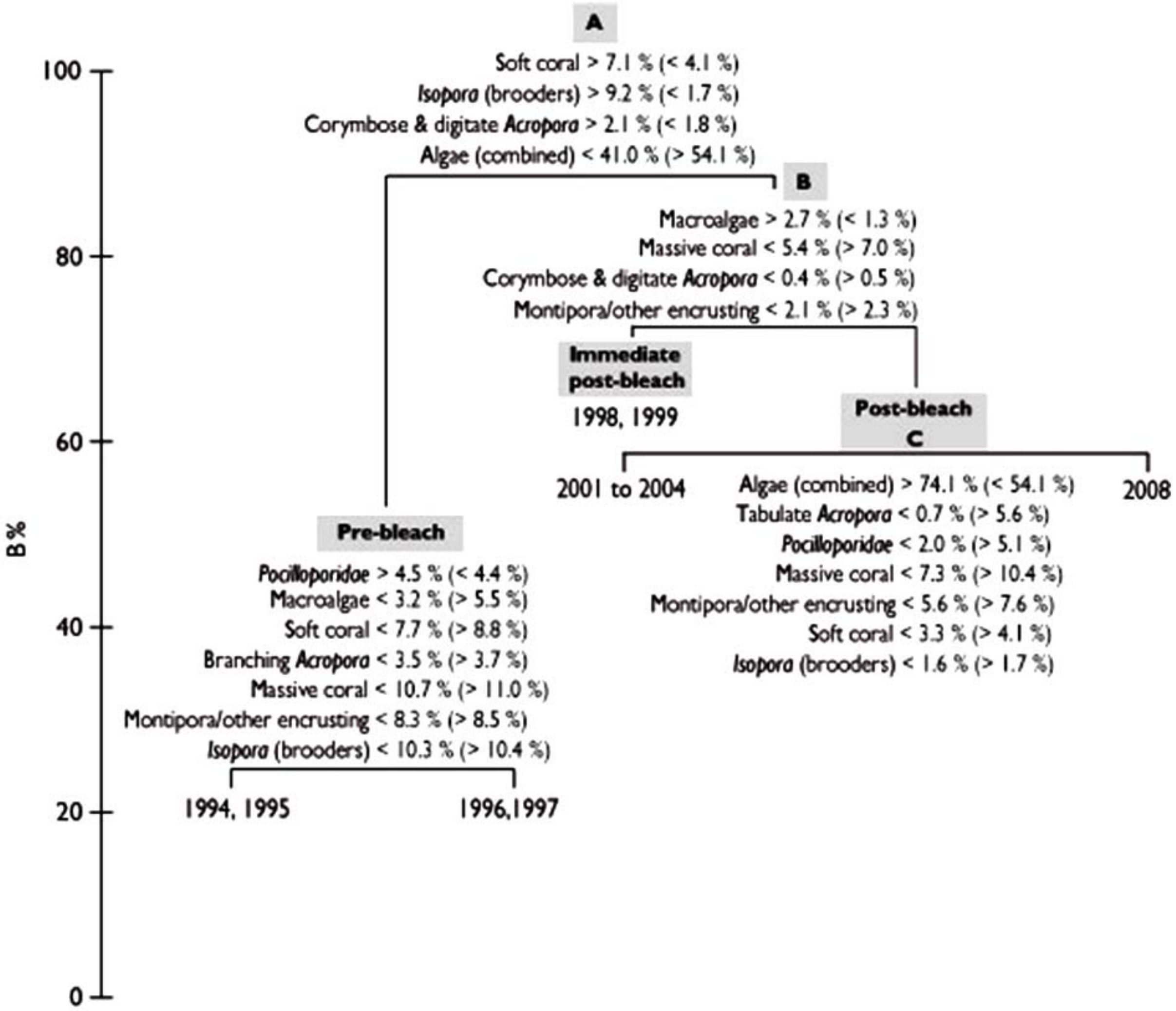


Figure 6.3.6.Multivariate linkage tree showing the benthic groups mainly responsible for the separation of the fish assemblages in the cluster analysis (Figure 6.3.3). The first value given for each benthic category shows that a left path should be taken through the tree and the bracketed values indicate a right path.

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

The fact that the ANOSIM *R*-statistic values were greatest for the comparison between faunas of 2008 and those in the first year of sampling (0.785) and least for comparisons between faunas of temporally contiguous periods (< 0.300), is strong evidence that the reef fish faunas at this isolated system are undergoing continuous succesional change, but are now comprised of a suite of species that differs to those at the reef prior to the 1998 coral bleaching. This result implies that an earlier suggestion that fish communities at Scott Reef in 2003 were returning to pre-bleaching structures by Halford and Caley (2009) has not been realised. The reasons for this may include destructive waves generated by the passage of Cyclone Fay directly over Scott Reef in early 2004 (Gilmour and Smith 2006), which may have caused additional changes to the composition of the benthic community and stalled the recovery of the fish community towards a pre-bleach structure. In any event, our long-term (15 year) dataset revealed a sequence of ongoing increases and decreases in the abundance of functionally significant groups of fishes that may not be readily apparent in short and medium-term studies (e.g. Sano et al. 1984).

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

Characteristics of pre-bleached and post-bleached communities

A review of the effects of coral bleaching on reef fishes (Pratchett et al. 2008) has highlighted that coral cover and topographic complexity are the critical components of coral reef habitats that shape their fish communities. Our use of multivariate linkage trees (LINKTREE) has clearly demonstrated that the pre-bleach fish community at Scott Reef was correlated with greater cover of soft corals, branching *Isopora* and corymbose and digitate *Acropora* corals, each of which suffered massive mortality in the subsequent coral bleaching. 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 lepidogenys* and *Chaetodon punctatofasciatus*. The intermediate post-bleach fish community between 2001 and 2004 was distinguished from that in 2008 by greater contribution of algae and reduced contributions of tabulate *Acropora*, pocilloporids, massive and encrusting corals and sponges. It is not surprising that the fish species that distinguished this community (e.g. *Plectroglyphidodon lacrymatus*, *Ctenochaetus* spp. and various labrids) are not as reliant on live coral and feed predominantly on algae that they farm and defend aggressively (Ceccarelli et al. 2001) or graze within it to consume the detrital material that comprise their diet (Wilson et al. 2003). The decrease in numbers of *P. lacrymatus* in the late post-bleach period (after 2005) presumably reflects the gradual erosion of the dead branching corals utilised as algal farm sites by this territorial herbivore and the increase in tabulate *Acropora* that is not used by this species for algal farming.

The increase of *Pomacentrus amboinensis* during the intermediate post-bleaching period is likely to be related to their association with 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). The greater and more consistent densities of *Pomacentrus philippinus* and *Chromis margaritifer* in 2008, played an important role in distinguishing the reef fish fauna of this period. These two planktivorous damselfishes are not associated with coral and utilise a wide variety of reef microhabitats. Such generalist species are predicted to be more resilient to changing resource availability than specialists with a narrower niche breadth such as *C. ternatensis* (Wilson et al. 2008).

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

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. (2006) on the GBR, our results contrast, to some degree, with the traditional abundance and diversity metrics presented by their study. On the GBR, there was a gradual increase in abundance of cryptobenthic fishes following the 1998 bleaching, however, there was no discernible trend for species richness. The use of a range of traditional community metrics and species composition data in the present study highlights that while the increases in the abundance and species richness of fishes could be interpreted as a sign of the resilience of the coral reef ecosystem (sensu Kokita and Nakazono 2001; Booth and Beretta 2002; Halford et al. 2004b), 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 and Syms (1998) and Bellwood et al. (2006) 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, particularly in the case of piscivorous and invertivore feeding species belonging to the families Lethrinidae, Lutjanidae and Serranidae. This increase in abundance was accompanied by an increase in the number of fish species recorded on our transects. These trends were apparently unaffected by the major bleaching event or the passage of cyclones across the reef.

One possibility is that these patterns were the result of increasing fishing pressure on Scott Reef by Indonesian fishermen that have targeted large predatory reef fish and sharks over the last decade. Stocks of some of these species are now chronically over-fished (Cappo et al. 2004). Studies on other reef systems (DeMartini et al. 2008; Sandin et al. 2008) have shown that apex predator release can result in fundamental changes to the biomass and abundance of lower trophic levels in coral reef ecosystems, which might account for some of the changes recorded by our study. In particular, this might explain the increasing number of piscivore and invertivore 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.

7. DEMOGRAPHY OF CORAL POPULATIONS

Summary

The size frequency distribution, survival and growth rates were measured yearly for populations of *Acropora spicifera* and *Goniastrea spp* (*G. edwardsii* and G. retiformis) at four reef slope locations, from 2006-2010 for *A. spicifera* and 2008-2010 for *Goniastrea spp*. These two coral groups have contrasting life history strategies, which influence their susceptibility and recovery following different disturbances. The mean growth rate of *Goniastrea spp* (<1cm yr^{-1}) was lower and less variable than that of *A. spicifera* (2-9cm yr^{-1}), and survival rates were higher in *Goniastrea spp* (>83%) than *A. spicifera* (>70%) during years without major disturbance (2008-2010). Survival rates for *A. spicifera* were significantly reduced at locations SL3 and SL4 during the first and second survey periods 2006-2007 and 2007-2008, due to disturbance by Cyclone George which affected the region two months before the end of the first survey period, with the greatest proportion mortality seen in the largest size classes. Cyclone George is also the likely cause of negative mean growth rates for large size classes of *A. spicifera* at SL3 and SL4 between 2006 – 2008, due to partial mortality and injury. No major disturbances occurred over the following two survey periods (2008-2010) and consequently survival rates were relatively high at all locations for both *Goniastrea spp* and *A. spicifera*. In the fourth survey period 2009-2010, the incidence of injury or partial mortality due to bleaching or disease was more prevalent than in the preceding period. The incidence of disease in the largest size class of *A. spicifera* at locations SL1 and SL2 increased from 2 – 4 % in 2009, to 10 – 18% in 2010. The effect of disease on *Goniastrea spp* was negligible. In contrast, the number of bleached colonies in 2010 was considerably higher for Goniastrea than *A. spicifera*. Between 10-60% of *Goniastrea spp* colonies were bleached in 2010 at the worst affected locations SL1 and SL3. The differing life history strategies, survival and growth rates of these contrasting species have important consequences for their population stability and recovery following disturbance.

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. 2007a; 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.

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.

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. 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 southern part of north Scott 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 Scott, respectively, and exposed to moderate currents; SL2 was at the southern part of the south Scott 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, so sites were pooled and data analysed and presented at the scale of the location.

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.

Results

Growth and survival: *Acropora spicifiera* and *Goniastrea spp*.

The rates of growth and survival of *A. spicifera* colonies during the first two years (2006-2007; 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 (Figure 5.2.15) and size classes 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 (Figure 7.1, 7.2). 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 (Figure 7.1; 7.2) By comparison, there was limited evidence of cyclone impact at location SL1 and no apparent impact at SL2 (Figure 7.1; 7.2).

Rates of survival of all size classes at locations SL1 and SL2 were > 80% yr^{-1} during the first two survey periods (2006-2008) (Figure 7.1). 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 (Figure 7.2). 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 (a low rate of injury of 8% at SL3 was an artefact of few colonies surviving long enough to be recorded with an injury, due to their high and rapid rates of mortality following the cyclone).

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; 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 (Figure 7.1).

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 (Figure. 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 (Figure 7.2). 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}).

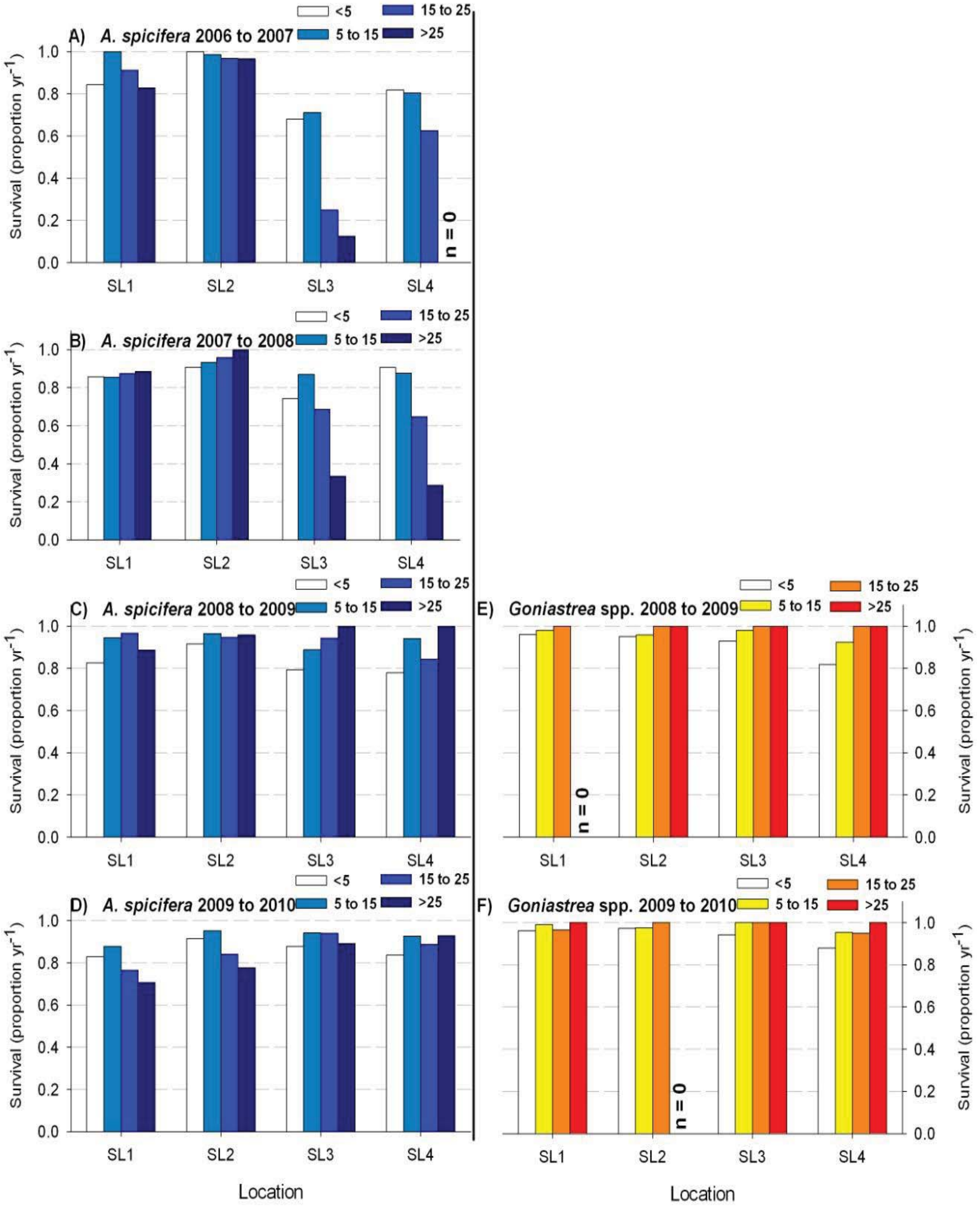
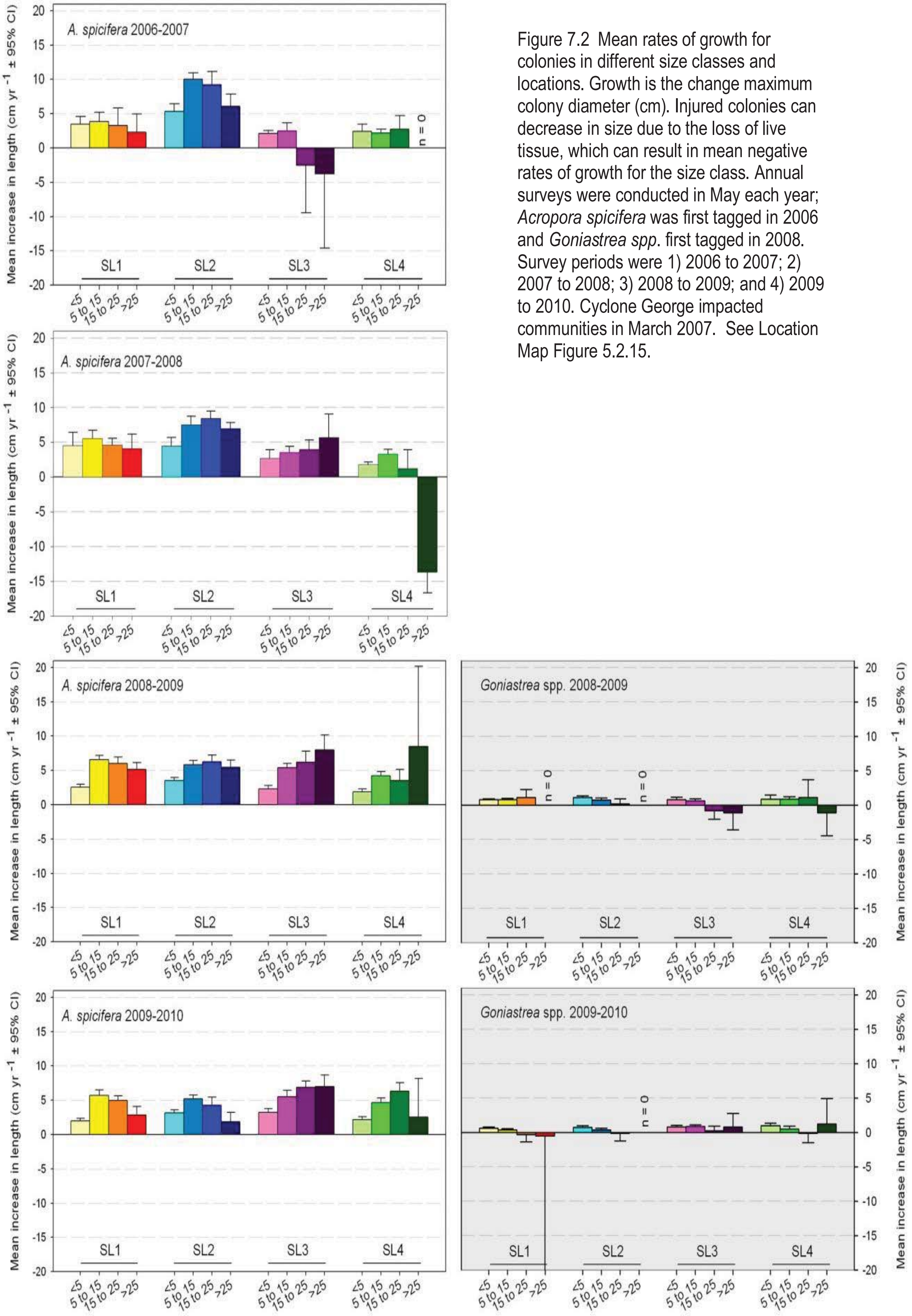


Figure 7.1 Rates of survival for colonies in different size classes and locations. Annual surveys were conducted in May each year; *Acropora spicifera* was first tagged in 2006 and *Gonisastrea* spp. first tagged in 2008. Survey periods were 1) 2006 to 2007; 2) 2007 to 2008, 3) 2008 to 2009, and 4) 2009 to 2010. Cyclone George impacted communities in March 2007. Location Map Figure 5.2.15.

Figure 7.2 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; 3) 2008 to 2009; and 4) 2009 to 2010. Cyclone George impacted communities in March 2007. See Location Map Figure 5.2.15.



During the second survey period (2007 to 2008), the impacts of the cyclone were still evident at locations SL3 and SL4, but in different ways to the previous year. The impacts were still mostly restricted to the larger (>15cm) size classes, but rates of survival for all size classes at SL3 were higher than in the previous year (Figure 7.1). 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%) (Figure 7.1). 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 (Figure 7.1) (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 or fourth survey periods (2008 to 2009 and 2009 to 2010, respectively). 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* (Figure 7.1), and the rates of growth much slower across both survey periods (Figure 7.2). The rates of survival of *Goniastrea spp*. were >93% for all size classes and locations, with the exception of the smallest size class at one (SL4) location where rates of survival ranged from 82% to 88% in the third and fourth survey periods, respectively. This compares with survival rates of > 70% for *A. spicifera* across all size classes and locations during these two periods. 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}) across these two periods.

During the calm conditions of the third and fourth survey periods, the rates of growth and survival of *A. spicifera* were generally higher than in the two previous survey periods. There was no clear pattern to the variation in growth and survival among the locations and size classes for the third survey period (2008 to 2009). The rates of survival of *A. spicifera* for the third survey period, while generally lowest for the smallest size class, displayed no consistent pattern among size classes or locations. The difference in survival between the smallest size class and the next lowest rate was at most 6% (3 to 6%) at any location. Both species displayed similar rates of survival and growth between the third and fourth survey periods. The only exception to this general pattern was the larger size classes of *A. spicifera* at Locations SL1 and SL2. The rate of survival of the largest size class decreased from 89 – 96% in the third period to 71 – 78% in the fourth survey period. Similarly, growth rates decreased from 5.1 – 5.4 to 1.8 – 2.9 cm.yr^{-1} over the same time period. (Figure 7.1) This reduction in survival and growth appeared to be related to a marked increase in the incidence of disease in the larger size classes of *A. spicifera* at locations SL1 and SL2 (Figure 7.3). The incidence of disease in the largest size class of *A. spicifera* at these two sites increased from 2 – 4 % in 2009, to 10 – 18% in 2010. The incidence of disease was negligible for *Goniastrea spp*. with only 6 colonies (0.6%) affected across all locations and size classes.

In marked contrast to disease, very few colonies of *A. spicifera* were affected by bleaching (overall mean = 1%; Figure 7.3). Bleaching of *Goniastrea spp*. was considerably higher than that of *A. spicifera*, and was generally lower at location SL3 than the other three locations. There was, however, no clear pattern among size classes, with the proportion of bleached colonies increasing with size at locations SL1 and SL2, and decreasing with size at SL4. The extremely high proportion of bleached colonies in the largest size class at Location SL1 (67%) may be an artefact of the limited number of colonies of this size (n = 3). Of all the bleached *Goniastrea spp*. colonies recorded (n = 163), 83% were partially bleached, while the remaining 17% were completely bleached.

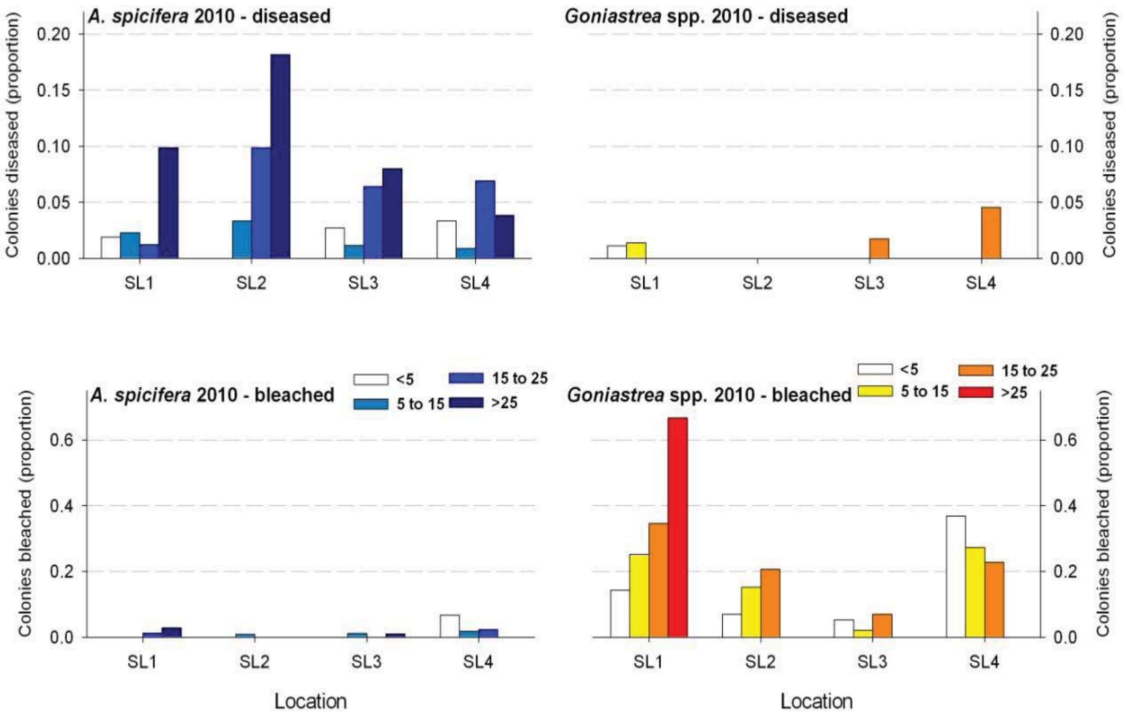


Figure 7.3 Variation in the proportion of *A. spicifera* and *Goniastrea spp*. colonies injured by disease or bleaching among size classes and locations. Of the bleached colonies only 14% (n = 2) of *A. spicifera* and 17% (n = 27) of *Goniastrea spp*. were completely bleached. See Location Map Figure 5.2.15.

Size frequency distributions:

The differences in life history parameters such as growth rate, survival and reproduction, between *A. spicifera* and *Goniastrea spp*. are reflected in the size frequency distributions of their populations. Over the two survey periods 2008-2010, total *A. spicifera* numbers increased by 70% (from 1446 to 2447 colonies), while numbers of *Goniastrea spp*. stayed more stable, increasing by only 5% (4920 to 5144 colonies), reflecting the slower population turnover *Goniastrea spp*. The size frequency distributions of *Acropora spicifera* are also more skewed to the right (a higher number of the smallest size classes) than *Goniastrea spp*. (Figure 7.4) which is a general pattern seen in coral groups with life histories characterised by high growth rates, high levels of reproduction and lower survival (Meesters et al. 2001). There were no major disturbances during the survey periods in which both *A. spicifera* and *Goniastrea spp* were measured, and between 2008 and 2009 there is an increase in adult numbers at all locations for both coral groups. Between 2009 and 2010 however, the reduction in growth and survival due to bleaching and disease was evident in *A. spicifera* populations as a loss of large adult colonies at SL2 (from 126 to 67), and small adult colonies at SL1 (from 155 to 121). For *Goniastrea spp*. there was a decrease in numbers of large and small adults at SL1 and SL2, and a decrease in large-adults at SL3 and SL4, possibly due to partial mortality and subsequent reduction in size. In fact the total number (across locations) of large *Goniastrea spp*. colonies decreased between the first survey in 2008 and the last in 2010 from 98 to 70 colonies. This overall decrease in the largest size class during years of no major disturbance may indicate that the slow growth rate of *Goniastrea spp*. is unable to keep up with the rate of injury and partial mortality seen at this size under the current environmental conditions, Or may be an artefact of extrapolating two-dimensional estimates of size for three-dimensional colonies. In contrast, in *A. spicifera* (Figure 7.1), the total number of large adult colonies increased from 271 in 2008 to 357 in 2010, reflecting their higher rates of growth and reproduction.

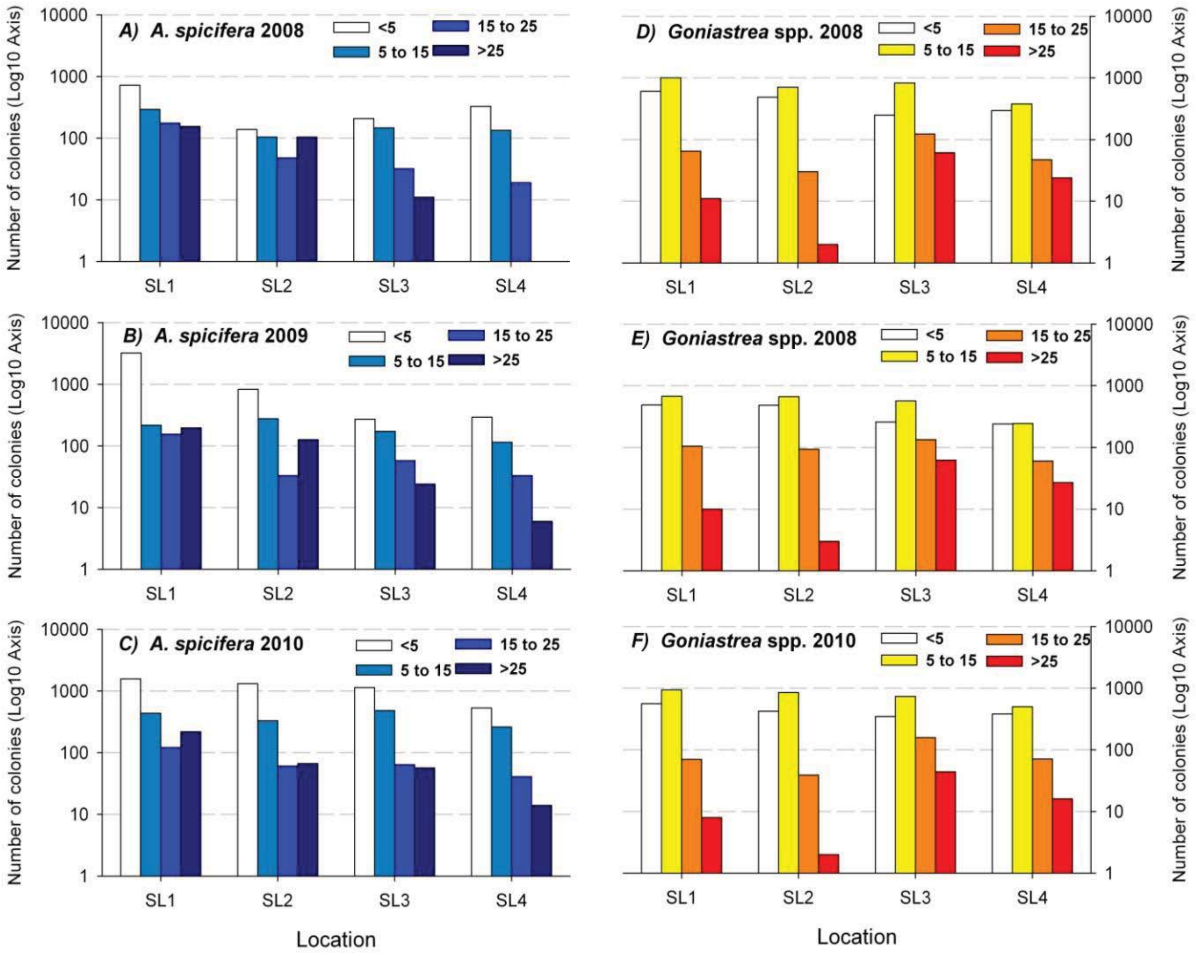


Figure 7.4 The size frequency distribution of *Acropora spicifera* and *Goniastrea spp* populations in 2008, 2009 and 2010. Size Classes <5cm = Recruits; 5-15cm = Juveniles; 15-25cm = Small Adults; >25cm = Large Adults. See Location Map Figure 5.2.15.

The numbers of *A. spicifera* recruits seen at different locations in 2009 and 2010 closely follows the patterns of settlement seen on our experimental settlement plates at those locations in the previous year. (see Chapter 10) *A. spicifera* recruit numbers are highest at location SL1 in all studied years, with a particularly high spike in 2009 of 3215 recruits. This cohort reflects the particularly high settlement of Acropora seen on our settlement plates at SL1 the previous year (2008). In fact most of the strong patterns in Acropora recruit supply seen on our settlement plates in these locations in years 2008 and 2009 appear to be reflected in the size frequency distributions of *A. spicifera* in the following years. For example on the settlement plates in 2008 there is very high settlement at SL1 but lower settlement at all other sites. This pattern can be clearly seen in the <5cm group of *A. spicifera* in 2009. In 2009 settlement on our plates is not as high in SL1 as the previous year, but more evenly distributed accross locations, with SL1 SL2 and SL3 recieving very similar numbers of recruits per tile, and SL4 recieving less. This pattern can also be seen in the <5cm group in 2010. (Figure 7.4). The correlation between settlement rates and recruit cohorts at the location scale suggest that spatial variation in larval supply, along with survival, growth rates and disturbance, may strongly shape the size frequency of coral communities at Scott Reef.

Discussion

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

During the years 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 (Babcock 1991; Hall and Hughes 1996; Connell 1997; Connell et al. 2004; Harrison and Booth 2007; 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. 2006b; Smith et al. 2008).

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 had 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 than 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.

Bleaching and disease

There is an increase in the incidence of bleaching and disease in the fourth survey period (2009-2010). Disease is more prevalent in *A. spicifera* than in *Goniastrea spp*., which is unsurprising given that the family *Acroporidae* has been found to be particularly susceptible to many of the prevalent coral diseases including black band disease, white syndrome, Atrementous necrosis, and brown band disease, and was ranked second behind *Pocilloporidae* as the families most susceptible to disease on the GBR (Aronson and Precht 2001; Page and Willis 2006; Page and Willis 2008; Page 2009).

Interestingly, *A. spicifera* was less affected by bleaching than *Goniastrea spp*. *Goniastrea*, in the family Faviidae, are generally recognised as being more resilient to thermal stress, with Acropora being amongst the most susceptible (Marshall and Baird 2000; LaJeunesse et al. 2003). This is a phenomenon seen on a number of reefs in recent times, and requires research into the underlying mechanisms, including the environmental factors which triggered the bleaching and even possible selective adaptation by coral communities heavily diminished by previous bleaching events. Location SL3 was again the location seen to be least affected by bleaching, as it was during the 1998 bleaching event.

Due to their high growth rate and recruitment, populations of *Acropora* are capable of rapid increases in abundance during good conditions following disturbances (Baird and Hughes 2000; Halford et al. 2004; Harrison and Booth 2007). 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. 2006b). 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). It remains to be seen whether the increased incidence of disease seen in the *A. spicifera* populations at Scott Reef in 2009-2010 is periodic, or if it will continue to be a serious chronic stressor for the coral community.

Combinations of disturbances can have dramatic consequences for the resilience of communities, precluding recovery and causing long-term degradation in the worst instances. For example, coral populations at Scott Reef may be resilient to cyclone 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, an increase in chronic stressors such as coral disease or reduced water quality at Scott Reef, 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. 2007b; Wilkinson 2008).

8. PATTERNS OF GENE FLOW AND CONNECTIVITY AMONG REEF FISH POPULATIONS

8.1 Summary: Population connectivity of corals and fishes among the remote atolls of north-west Australia

For most species that live on coral reefs, dispersal is achieved by pelagic larvae that have the potential to "hitchhike" long distances on the ocean's currents. However, it is not clear how many larvae use these oceanic highways and survive the long journey to eventually settle at distant reefs. Because the persistence of populations through time requires a balance between the input of new individuals (recruitment) with the loss of established individuals (mortality), knowledge of the degree of dispersal among reefs (or "population connectivity") is crucial for the evaluation of the potential benefits of different conservation management approaches. For example, populations that receive little input from immigrant larvae will be slow to recover after disturbance compared with populations that receive a regular and large supply of immigrants. Each of these scenarios will require different strategies for management and protection.

Because genetic differences accumulate when populations are reproductively isolated and do not exchange genes, a spatial analysis of genetic variation provides an invaluable method for measuring patterns of population connectivity. This project used genetic and ecological analyses to assess patterns of connectivity among populations of two hard corals (Figure 8.1.1) and four coral reef fishes (Figure 8.1.2) between Scott Reef and its neighbouring offshore reefs, the Rowley Shoals, and is the first of its kind in this region. Genetic results from all species showed significant differences in the composition of populations between these two systems (illustrated clearly for four species in Figure 8.1.3). Furthermore, data from satellite-tracked drifters and oceanographic modelling indicates a low (<1%) probability of physical transport by oceanic currents of larvae with life spans of less than two months between Scott Reef and the Rowley Shoals. Together, these results suggest that few larvae regularly disperse between Scott Reef and the Rowley Shoals and that local production of larvae is responsible for most recruitment to each system over ecological time scales (i.e. years to a few decades). Furthermore, evidence for occasional dispersal of small numbers of larvae was detected along with the greater levels of overall genetic diversity in three of the six species at Scott Reef compared with the Rowley Shoals (Figure 8.1.4), and this suggests that Scott Reef acts as a reservoir for genetic diversity via occasional long-distance dispersal to the Rowley Shoals over evolutionary time (decades to centuries) in these species.

Although all species exhibited genetic differences between Scott Reef and Rowley Shoals, genetic differences in populations of two corals and the damselfish were detected among sites within the Scott Reef system. Additionally, there was a strong positive relationship between coral cover and number of new corals arriving from the plankton to replenish populations. Considered together with *in situ* measurements of larval development and local water currents, these results suggest that the majority of coral larvae are retained within 10 km of their natal (parent) reef patch. Thus, larval dispersal of these species is restricted and largely occurs at small scales (metres to a few tens of km) within reefs at Scott Reef.

The principal implication of this research is that, for species from corals to reef fishes, Scott Reef does not act as an ecologically important source of large numbers of larvae to the Rowley Shoals, and likewise does not regularly receive large numbers of larvae from the Rowley Shoals. Thus, recovery of coral reef communities after disturbances will not be driven by input of new recruits from outside each system over ecological time scales that are relevant to management. For this

reason, conservation strategies should aim to enhance replenishment of corals and fishes at the scale of individual reefs. This requires the preservation of patterns of connectivity between reef areas within each system through the maintenance of replicate healthy populations, and therefore, a buffer against disturbance at all but the largest (entire system) scales. Finally, occasional dispersal of small numbers of larvae means that Scott Reef may act as a reservoir for genetic diversity for the Rowley Shoals for some species, and this connectivity may be important for their ability to adapt to environmental change over evolutionary relevant time scales.

Figure 8.1.1 Hard corals used in the genetic study of connectivity, a brooder *Seriatopora hystrix* (left), and a broadcast-spawner, *Acropora tenuis* (right).

Figure 8.1.2 The benthic-spawning damselfish, the half and half puller (*Chromis margaritifer*; top left), and the mouth-brooding cardinalfishes, the Five-lined Cardinalfish (*Cheilodipterus quinquelineatus*; bottom left), and the Wolf cardinalfish (*Cheilodipterus artus*; bottom right;) used in the genetic study of connectivity.

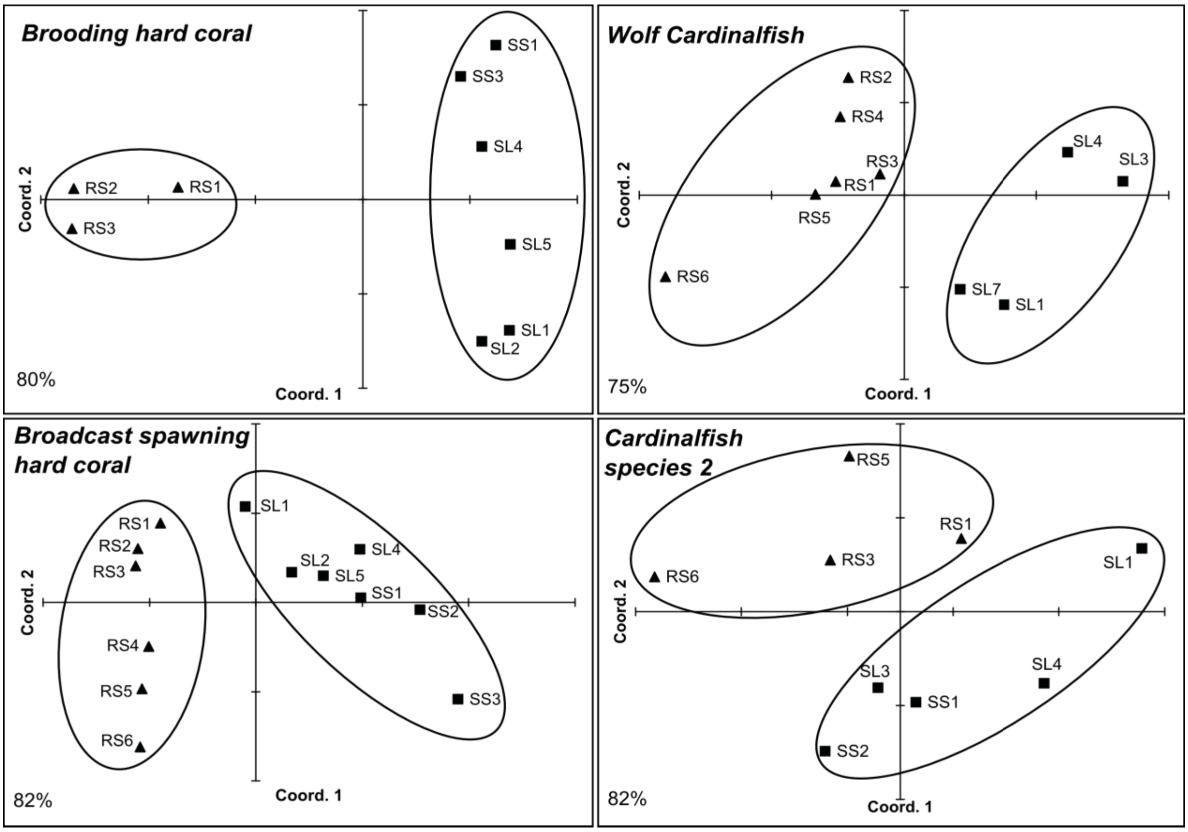


Figure 8.1.3 Principal Coordinate Analysis (PCoA) of genetic similarity among sites from Scott Reef and Rowley Shoals depicting greater similarities between sites from within each system compared with comparisons between systems in four coral reef species (refer to Figure 8.2.1 for site locations). Species are; a brooding hard coral (*Seriatopora hystrix*), a broadcast spawning hard coral (*Acropora tenuis)*, and two coral reef fish, the Wolf cardinalfish *(Cheilodipterus artus*) and an undescribed cardinalfish (*Cheilodipterus* cf. *artus)*. The amount of variation explained by the first two axes is given in left hand corner of each plot.

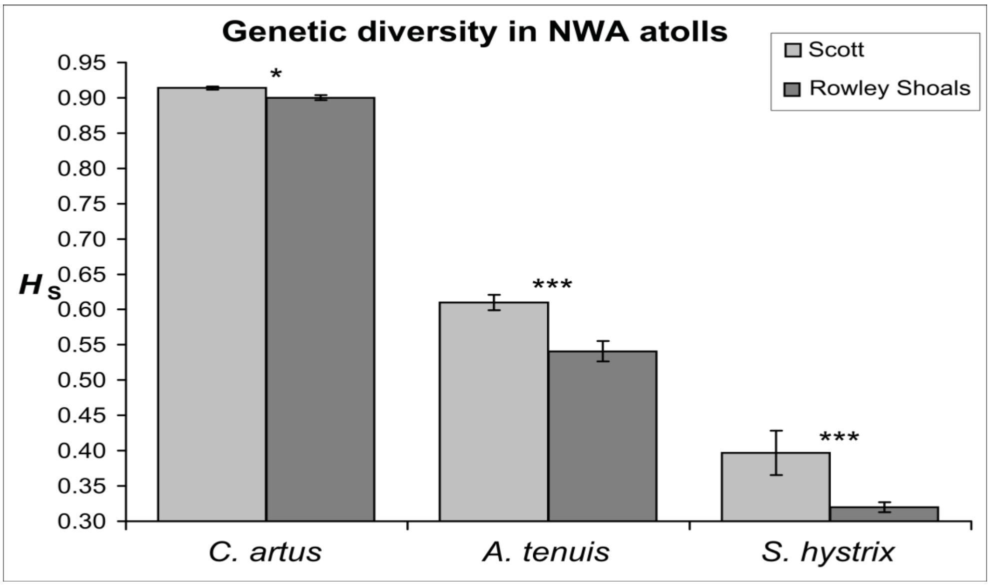


Figure 8.1.4 Comparisons of genetic diversity between Scott Reef and Rowley Shoals for the Wolf cardinalfish (*C. artus*), a broadcast spawning coral (*A. tenuis*) and a brooding coral (*S. hystrix*). Gene diversity (H_S; a metric based on number of genes at each locus) was averaged across loci and sites at each system and accounted for unequal sample siz es. Error bars ± standard error. Tests for difference in diversity between systems for each species were based on 1000 permutations (* $P \leq 0.05$, *** $P \leq 0.001$).

8.2 Population connectivity of a damselfish among remote coral atolls of north-west Australia

Summary

Ecological, oceanographic and genetic data were used to infer the scale and strength of population connectivity in the coral reef damselfish, the half and half puller *(Chromis margaritifer)* at two remote atoll systems in the north-west Australia and thus assess the extent larval exchange between reefs and systems of ecological and evolutionary time scales. This study is the first of its kind in this region. Significant genetic differentiation was detected between Scott Reef and Rowley Shoals, and a model estimated a low (<1%) probability of physical transport of these damselfish larvae by oceanic currents between the Scott Reef and Rowley Shoals systems. These independent lines of evidence indicate regular exchange of large numbers of larvae does not occur between the Scott Reef and Rowley Shoals systems. This means that the population replenishment is driven by local production within each system, and the input of fish from outside each system is unlikely to facilitate recovery after disturbance.

Introduction

A pelagic larval stage provides the opportunity for many otherwise sedentary marine organisms to disperse long distances on oceanic currents and thus contribute demographically and genetically to distant populations. However, the actual numbers of individuals that disperse away from their natal area and then locate and reproduce at a destination population, depends on the interplay between a wide range of biological and physical parameters. Consequently, patterns of realised (or reproductive) population connectivity may be restricted to smaller scales than those suggested by maximum dispersal potential (Pineda *et al.* 2008). Since these patterns of reproductive connectivity underpin the maintenance, distribution and diversity of marine populations, realistic estimates of the extent of larval exchange and survival among populations are essential for predicting and reducing the impacts of climate change and other human activities through the implementation of conservation strategies such as marine reserve networks (Gerber et al. 2003; Palumbi 2004; Cowen et al. 2007). Although considerable progress in this field has been made recently (Cowen and Sponaugle 2009), fundamental questions remain such as: over what spatial scales will healthy populations supplement recruitment to disturbed populations, and how do these connectivity patterns influence the temporal scales of recovery after severe disturbance?

Coral atolls in the eastern Indian Ocean off north-west Australia (NWA) have several characteristics that make them high priorities for conservation. First, these atolls have a diverse array of flora and fauna (Bryce *et al.* in press) and currently a relatively low intensity of most local human impacts. Second, the three emergent atolls that lie along the edge of the continental shelf are separated from each other and the mainland by several hundreds of kilometres of open water (Figure 8.2.1), and this geographic isolation means that the probability of pelagic larvae locating a favourable habitat is low and locally derived recruits are likely to be crucial to population maintenance (Strathmann *et al.* 2002). Therefore, these atoll systems are probably vulnerable to impacts; a prevalence of locally produced recruits not only suggests that exogenous larvae are unlikely to drive recovery after severe disturbances (Ayre and Hughes 2004), but also leads to increases in genetic subdivision, endemism and inbreeding, and reductions in genetic diversity that are often observed at offshore systems compared with coastal or mainland systems (e.g. Johnson et al. 1994; Frankham 1998; Bell 2008). Third, a catastrophic bleaching event in 1998 caused by elevated sea-water temperatures at one of the NWA atoll systems, Scott Reef, resulted in a relative decrease in coral cover of >75% in shallow-water (< 20m) and recovery has taken more than a decade (Smith et al. 2008). Therefore, it is crucial that conservation planning in NWA incorporates knowledge of the extent to which geographic isolation confers demographic independence of these coral atolls.

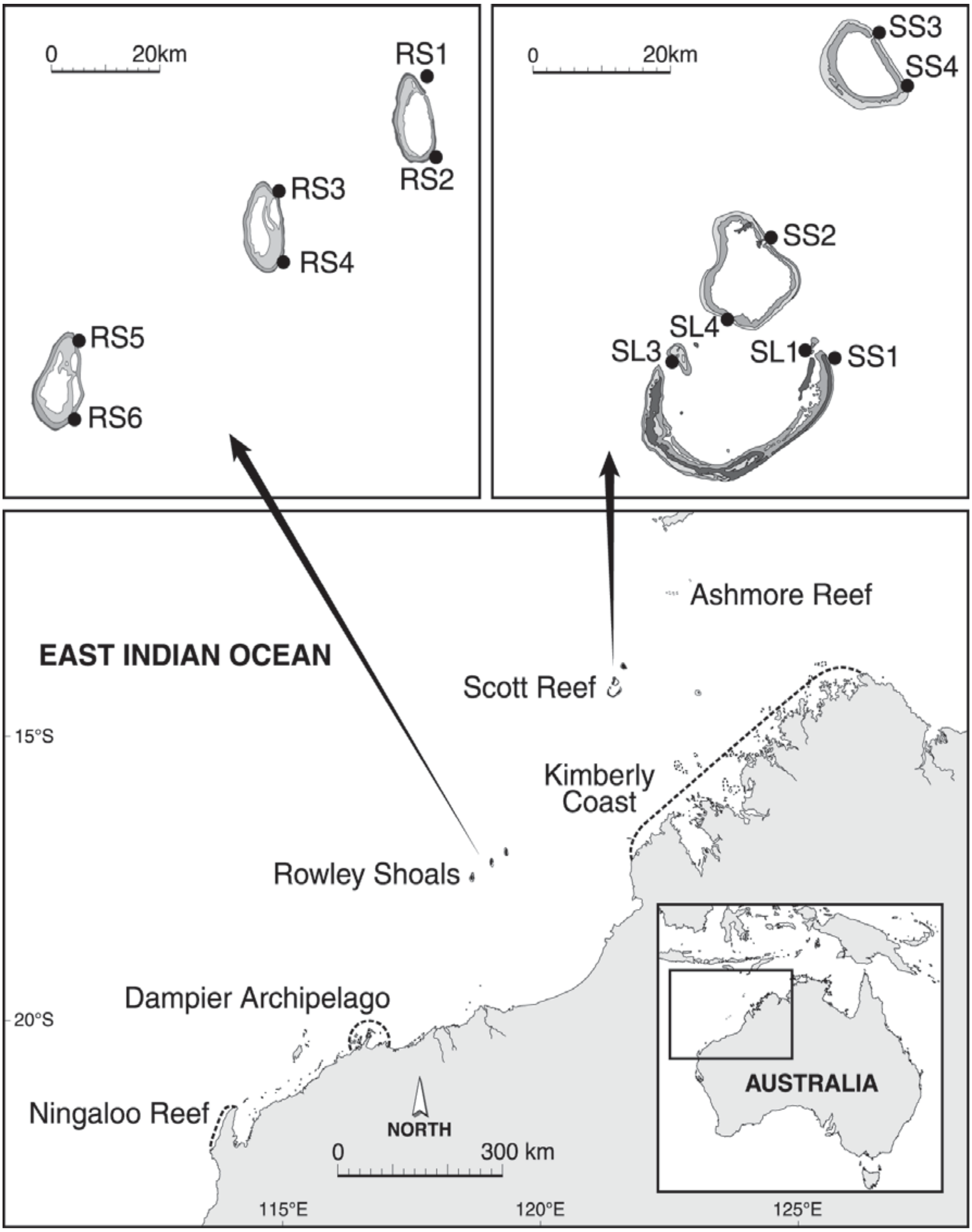


Figure 8.2.1 Map of the major coral reef systems in north-west Australia showing sampling sites of the half and half puller *(Chromis margaritifer)* collected from Rowley Shoals and Scott Reef.

In NWA, there are two major surface currents that have the potential to transport larvae long distances; in the austral autumn and winter, a slow moving (~ 0.2 ms^{-1}) current originates near Indonesia and flows polewards along the continental shelf margin, while in the austral spring and summer, seasonal south-west winds induce a weak reversal of the current to the north-east (Cresswell *et al.* 1993; Holloway 1995). *In situ* satellite-tracked drifters suggest that transport of propagules between the atoll systems of NWA would take between one and two months (Cresswell et al. 1993; Gilmour et al. 2009b). These estimates are supported by studies of realised connectivity in hard corals. *In situ* observations following spawning, and spatial analyses of genetic structure of brooding and broadcast spawning species, suggest that the majority of recruits were retained close to their natal reef and settled when competent within a week (Underwood et al. 2007; Gilmour et al. 2009b; Underwood et al. 2009). However, in contrast to coral larvae, most fish larvae must spend at least several weeks in the plankton before they are able to settle, and planktotrophic larvae may also be able to delay metamorphosis without energetic costs. Although these larval characteristics may promote long-distance dispersal, fish larvae are clearly not passive particles; they are not only able to vertically orientate themselves in the water column, but can also sustain swimming speeds that are faster than average current speeds and can sense and swim towards reefs (Leis 2006). Considerable evidence is accumulating that these behaviours facilitate localised recruitment in many coral reef fish (e.g. Doherty et al. 1995; Almany et al. 2007; Gerlach et al. 2007).

Here, we investigate for the first time the extent of connectivity among populations of a coral reef fish on offshore atolls of NWA. Our primary aim was to determine the frequency and spatial scale of dispersal of a common reef damselfish, the half and half puller *(Chromis margaritifer)*, within and between the atoll systems of the Rowley Shoals and Scott Reef. We used a combination of ecological, oceanographic, and genetic data to discriminate patterns of contemporary (ecological) and historical (evolutionary) connectivity of this species, while also identifying some of the biological and physical drivers of these connections. *C. margaritifer* has a long mean pelagic larval duration (PLD) relative to most damselfish of 33 days (Wellington and Victor 1989), and is highly abundant and widely distributed, occupying a variety of reef habitats (including inshore and offshore slopes and lagoons) from the central Pacific Ocean to the east Indian Ocean (Allen 1991). Therefore, the expectation is that connections among populations at the scales of reefs and systems for this damselfish will be strong relative to corals and probably representative of the upper limits of dispersal of many reef organisms with similar life-history traits in these systems.

Methods

Otolith analysis

To estimate mean PLD and it variation among individuals, otoliths were analysed from 223 juveniles (<40mm) of the half and half puller *(Chromis margaritifer)* collected from Rowley Shoals and Scott Reef in 2008. The sagittal otoliths of these fish were extracted and cleaned, and one from each fish was weighed, 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. We assumed that increments were deposited on a daily basis in the otoliths of this species. Settlement marks corresponded to the type 1a abrupt settlement marks of Wilson & McCormick (1999). PLD was determined by counting the number of increments (days) between hatching (first increment) and settlement.

Visual census surveys

Given that population size has a crucial influence of genetic structure (Hellberg 2009), and that reproductive output influences the number of long-distance dispersers (Steneck *et al.* 2009), we obtained course estimates of population size and hence potential reproductive output of *C. margaritifer*. Underwater visual census was used to estimate densities of *C. margaritifer*. Permanent transects were deployed and were censused five times at Rowley Shoals (three locations), and 12 times at Scott Reef (six locations), between 1994 and 2008. Each location consisted of three sites, and five 50 × 1m belt transects per site at nine metre depths (for details, see Heyward et al. 1995a). Mean densities (± 95% CI) across all sites and years were calculated for each reef system. Population size was calculated estimating the total area of suitable reef habitat available for *C. margaritifer* from aerial photographs and multiplying this by the mean estimates of density from transect counts. These estimates are coarse since they are based on counts made at nine metres only (densities are likely to vary with depth), and accurate habitat maps are not available for these systems.

Oceanographic model

To explore the potential for advection of passive propagules by oceanic currents in this region, we utilised the model system Connle, developed by CSIRO (Condie and Andrewartha 2008). This is a three-dimensional non-linear hydrodynamic model that calculates circulation patterns forced by realistic wind, temperature and salinity fields. A particle-tracking module was embedded within the model that allowed estimation of connectivity by tracking neutrally-buoyant particles seeded randomly through the water column across the model domain. The circulation and particle movement calculations were conducted simultaneously, with particle positions 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 over 7 (1st quarter), 28 and 56 days when the north-easterly flow was dominant; and then particles released from Scott Reef in autumn over 7 (2nd quarter), 28 and 56 days when the south-westerly flow was the strongest. Particle distributions for all scenarios were estimated across the entire dispersion period (within lifetime option) and averaged across all years for which data were available (six years; 1994-1999).

Genetic sampling

In April 2008, 580 adult *C. margaritifer* individuals were collected by divers using a combination of hand nets, barrier nets and clove oil from six sites at Rowley Shoals and seven sites at Scott Reef (Figure 8.2.1). On average, 45 individuals were collected per site (sample sizes ranged from 32 to 53), and replicate sites were sampled on each reef (details in Table 8.2.1). Seven months later (October 2008), 98 recruits (15-30 mm) were collected from three sites at Scott Reef (SL1, SL3, SS2) and one site at Rowley Shoals (RS3), with average samples sizes of 25 individuals per site (details in Table 8.2.2). A dorsal fin clip was placed in 100% ethanol (analytical grade) pending DNA extraction, and whole samples were frozen for otolith extraction.

Table 8.2.1 Details of the ten microsatellite markers of the half and half puller (*Chromis margaritifer*) adults from Rowley Shoals and Scott Reef. Number of individuals genotyped at each site are given in brackets, along with the number of alleles (NA), the unbiased proportion of expected (HE) heterozygotes per locus and site, and FIS calculated for each locus and each site (numbers in bold indicate significant heterozygote deficits). Also given are average number of alleles per locus (mean NA), average unbiased expected heterozygosity (mean HE), the average (mean FIS) for each loci across all sites, and the number of private alleles (PVA) 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	

Table 8.2.2 Details of the ten microsatellite markers of the half and half puller (*Chromis margaritifer*) recruits collected from Rowley Shoals and Scott Reef. Number of individuals genotyped at each site are given in brackets, along with the number of alleles (NA), the unbiased proportion of expected (HE) heterozygotes per locus and site, and FIS calculated for each locus and each site (numbers in bold indicate significant heterozygote deficits). Also given are average number of alleles per locus (mean NA), average unbiased expected heterozygosity (mean HE), the average (mean FIS) for each loci across all sites (refer to Figure 8.2.1 for site locations).

Site		Cm_A119	Cm_B007	Cm_B117	Cm_D006	Cm_A110	Cm_A115	Cm_A011	Cm_B102	Cm_D103	Cm_D114
Rowley Shoals											
RS3_R (30)	N_A	24	11	20	21	2	14	9	5	18	27
	H_E	0.96	0.87	0.95	0.95	0.18	0.85	0.84	0.71	0.94	0.95
	F_{IS}	-0.019	0.060	0.106	0.109	-0.111	**0.324**	-0.096	0.039	0.167	**0.178**
SL1_R (30)	N_A	25	13	17	17	3	9	7	6	24	31
	H_E	0.96	0.86	0.92	0.93	0.16	0.68	0.75	0.68	0.97	0.97
	F_{IS}	0.050	0.097	**0.229**	0.133	-0.075	**0.381**	-0.038	0.151	0.035	0.092
SL3_R (22)	N_A	24	10	18	13	3	7	8	6	11	19
	H_E	0.96	0.86	0.94	0.93	0.25	0.70	0.80	0.67	0.92	0.94
	F_{IS}	0.080	-0.030	**0.209**	0.171	0.245	0.170	0.302	0.188	**0.380**	**0.209**
SS2_R (16)	N_A	17	9	12	14	3	7	6	7	18	15
	H_E	0.96	0.86	0.93	0.91	0.18	0.52	0.73	0.67	0.96	0.92
	F_{IS}	-0.078	0.026	**0.235**	-0.067	-0.079	**0.380**	0.028	-0.153	0.122	**0.300**
	mean N_A	23	11	17	16	3	9	8	6	18	23
	mean H_E	0.96	0.86	0.93	0.93	0.19	0.69	0.78	0.68	0.95	0.95
	mean F_{IS}	0.008	0.038	0.195	0.087	-0.005	0.314	0.049	0.056	0.176	0.195

Microsatellite genotyping

DNA for genotyping 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) that was diluted by one third with millepore purified water to a final concentration of about 10-20 ng. The development of the microsatellite library, characterisation of final 10 loci, and genotyping procedure were described by Underwood (Underwood in press). To mitigate and report scoring error of microsatellites, quality control procedures suggested by Bonin *et al.* (2004) and DeWoody *et al.* (2006) were implemented. Specifically, genotyping each individual involved the implementation of negative controls and the visual inspection of all automated allele calls, and individuals with suspect electropherograms were repeated. Furthermore, a genotype error rate (0.83%) was measured by repeating the genotyping procedure, from DNA extraction through to final allele scoring, using a subset of blind samples (n = 24) selected from three sites randomly spread across the sampling area.

Allelic patterns of the 580 adult fish collected from 13 sites, and 98 recruits collected from 4 sites, were calculated with GenAlEx v6 (Peakall and Smouse 2006). The number of alleles, the unbiased expected heterozygosity, the fixation index, and the number of private alleles at each of ten microsatellite loci at each population and averaged across populations for adults and recruits respectively are presented in Table 8.2.1 and Table 8.2.2 (refer to figure 1.3.1.1 for site locations). 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 were detected at 12 out of the 13 sites in the adult samples for each of the loci Cm_A115, Cm_B007 and Cm_D114, and 3 out of the 4 sites in the recruit samples. Analysis with Micro-Checker v2.2 (van Oosterhout *et al.* 2004) indicated that these homozygote excesses were most likely due to null alleles at a frequency of between 0.09 and 0.17 per locus. 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. 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, the 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.

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 for adults at Scott Reef and Rowley Shoals and for recruits at Scott Reef calculated across all sites within each system, and significance was tested by 1000 permutations of a randomized data set.

To measure the amount of genetic variation that was geographically structured, we implemented analysis of Molecular Variance (AMOVA) framework in GenAlEx v6 (Peakall and Smouse 2006) to partition the genetic variation between systems (F_{RT}), among sites relative to variation within systems (F_{SR}), and among sites relative to overall variation (F_{ST}). 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. 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 (F'_{RT}, F'_{SR} and F'_{ST}) according to the method of Meirmans (2006). To assess the significance of spatial and temporal differentiation among adult and recruit samples with a more powerful test that is better suited to unbalanced sample sizes (Goudet *et al.* 1996), we also applied a Fisher exact test with Genepop v4.0 (Raymond and Rousset 1995), using the default Markov chain parameters.

To visualise the genetic relationships among sites, we performed a Principle Coordinates Analysis, PCoA (*sensu* Jombart *et al.* 2009). Two independent and complimentary estimates of genetic distance were employed; 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). D_S, Nei's standard genetic distance and the final PCoA analysis was calculated in GenAlEx v6 (Peakall and Smouse 2006).

To estimate the number of migrants per generation (Ne_m) between Scott Reef and Rowley Shoals, we employed the method of Barton and Slatkin (1986) that uses a quasi-equilibrium theory to calculate Ne_m from the number of private alleles implemented in Genepop v 4.0 (Raymond and Rousset 1995). We treated each system as a single population (or deme) for this analysis. We present results of Ne_m based on the estimate corrected for sample size

Individual-level statistics

In addition to the above summary statistics based on allele frequencies across populations, we utilised the genetic identity and geographic location of individual fish to further interrogate spatial patterns of genetic structure. These analyses, akin to "landscape genetics" approaches, 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 (Manel *et al.* 2003; Selkoe *et al.* 2008).

First, 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 (conducted in GenAlEx v6 Peakall and Smouse 2006). 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. When dispersal is restricted and neutral loci are utilized, the autocorrelation coefficient will be a positive value at short distance classes and will then decline through zero and become a negative value at larger distance classes (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. To test 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.

Results

Pelagic larval duration and population size

The mean (± 95% CI) PLD of recently recruited *C. margaritifer* was 35 d (± 8), and ranged from 16 to 42 d. There was little difference in PLD between the reef systems, with a mean of 34 d (± 8) calculated for fish from Scott Reef and 36 d (± 12) for fish collected at the Rowley Shoals.

Both the density and population size of *C. margaritifer* were more than three times greater at the Rowley Shoals than at Scott Reef. Mean density (± 95% CI) was 116 (± 7) fish (250m^2) at the Rowley Shoals and 35 (± 9) fish at Scott Reef. Similarly, when the overall densities were scaled to the total area of available habitat, there were an estimated 31 320 000 *C. margaritifer* at Rowley Shoals (270 km^2) and 10 765 000 fish at Scott Reef (305 km^2).

Oceanographic model

There was a clear reversal of oceanic currents from predominantly north-east in austral summer (1st quarter) to south-west in the austral autumn (2nd quarter) in all years (Figure 8.2.2). Irrespective of the season, there was a high probability (20% - 65%) that particles were retained within 10 kilometres of the source reef within a dispersion period of one week, while areas of low dispersal probability (0.1 - 1%) extended no more than 100 kilometres from the source reef (Figure 8.2.2 A and D). This general pattern of retention of most particles within a few tens of kilometres of each system remained after a month of dispersal, although the blue area of low probability (0.1 - 1%) expanded considerably (Figure 8.2.2 B and E). For particles with a dispersion period of 56 days, the outer edge of the dispersal kernel of particles released from Rowley Shoals in summer reached the south section of Scott Reef, and similarly, particles released from Scott Reef in autumn reached the northern reef of Rowley Shoals (Figure 8.2.2 C and F). Although the mean probability of particles dispersing between the systems was very low (< 1%), simulations over different years showed a degree of interannual variability. For example, in the second quarter of 1998, particles released from Scott Reef extended to within 30 kilometres of Rowley Shoals after 56 days with a probability of 5% (insert in Figure 8.2.2 F). This filament was not only larger and stronger compared with probability averages across the six years in the same time period (main panel in Figure 8.2.2 F), but also contrasted markedly to probability distributions in 1994, 1996, 1997 and 1999 in which outer edge of the dispersal kernel did not come within 100 kilometres of Rowley Shoals (data not shown).

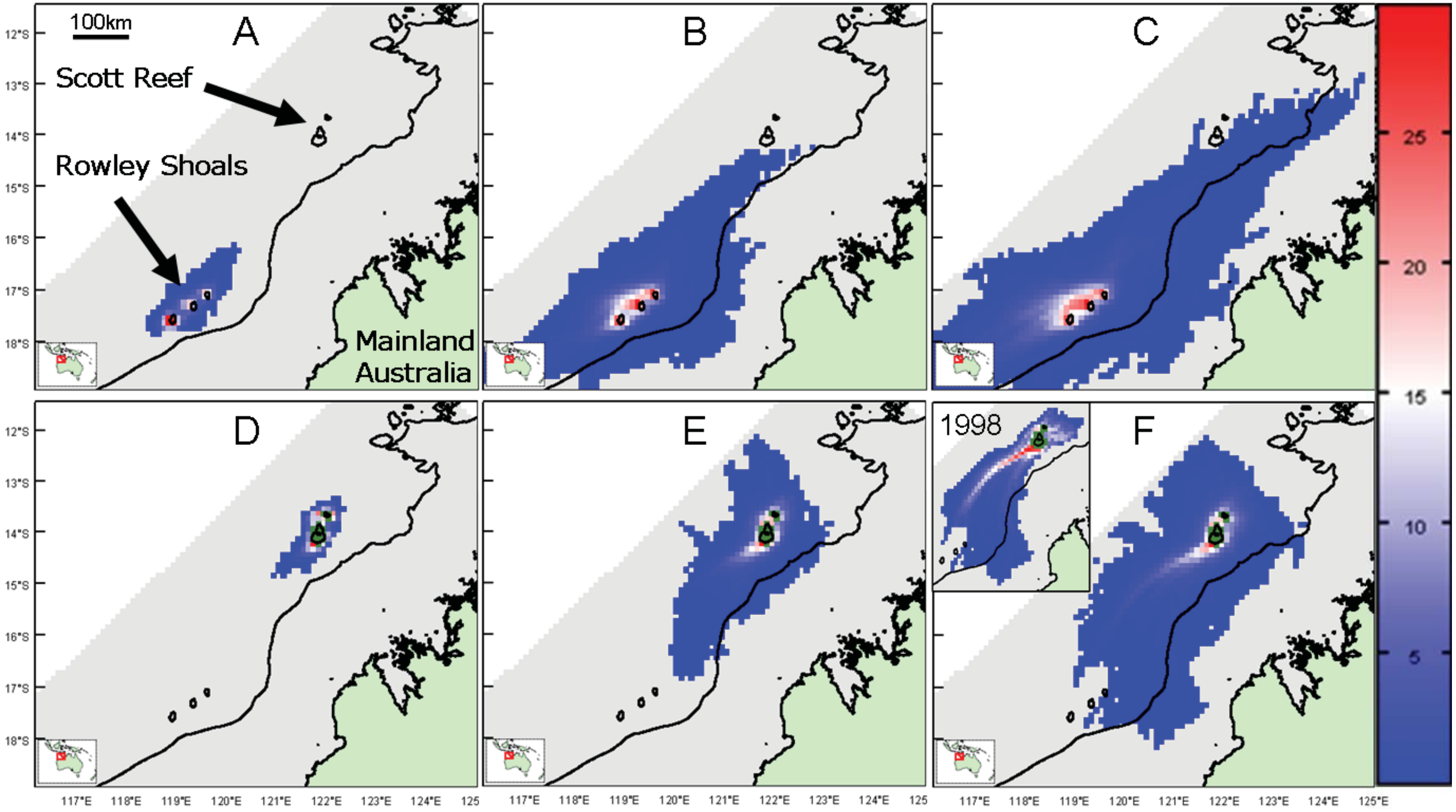


Figure 8.2.2 Probability distributions of passive particle transport between Scott Reef and Rowley Shoals estimated from a three-dimensional hydrodynamic model. Panes A, B and C show results of particles released from Rowley Shoals in the first quarter and run for 7, 28 and for 56 days respectively. Panes D, E and F show results 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.

Spatial genetic structure of adults

Genetic diversity of *C. margaritifer* was high at both atoll system and did not differ significantly (p = 0.254) between Rowley Shoals (mean H_{SK} = 0.811) and Scott Reef (mean H_{SK} = 0.809). Across the entire sample area, genetic subdivision among sites was low (F_{ST} = 0.002) and non-significant (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} = 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 ($F_{SR\ scott}$) and Rowley Shoals ($F_{SR\ rowleys}$) was zero and non-significant in both systems. When these estimates were standardised to within population diversity (according to Meirmans 2006), the subdivision levels increased considerably but the relative distribution of variation remained the same; F'_{RT} and F'_{ST} = 0.011, while variation among sites within systems (F'_{SR}) 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. Although Meirmans method is not amenable to permutational testing, the Fisher Exact test for differentiation among sites within each system revealed that differences among sites within Scott Reef were significant ($p < 0.001$), but not at Rowley Shoals (p = 0.236). The private allele method estimated 25 migrants per generation between Scott Reef and Rowley Shoals.

The genetic divergence between Scott Reef and Rowley Shoals detected by the AMOVA was well illustrated in Principal Coordinates Analysis (PCoA) plots of genotype ratio distance (D_{LR}) and Nei's standard genetic distance (D_S) (Figure 8.2.3). Although there was no clear separation of sites from each system, sites from the Rowley Shoals clustered tightly together within the much broader spread among the Scott Reef sites and there was no obvious overlap of sites from either system.

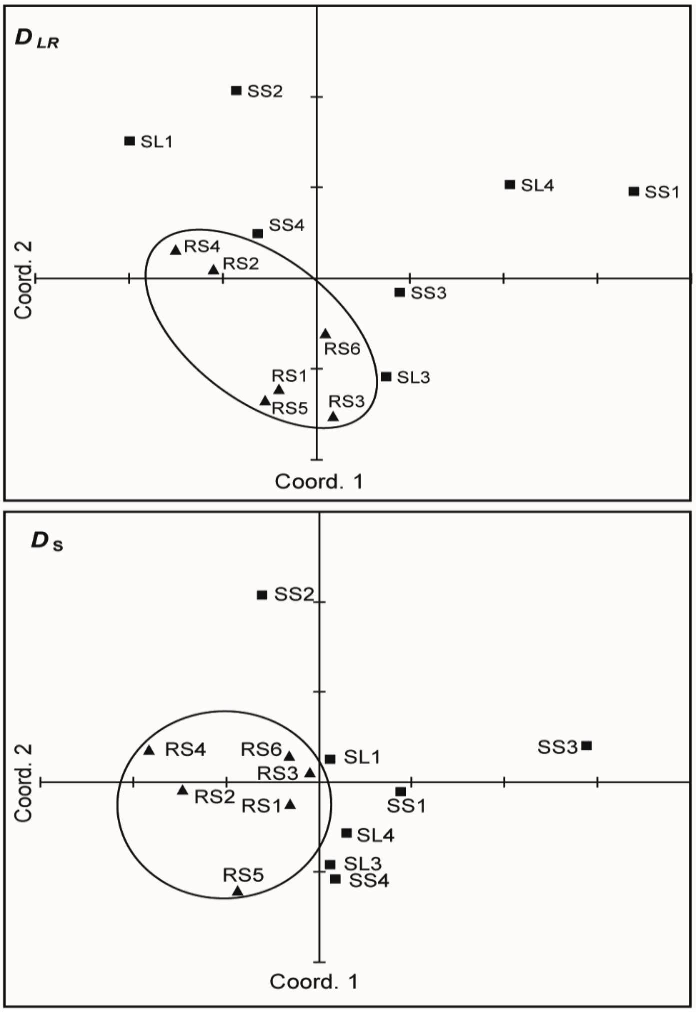


Figure 8.2.3 Principal Coordinate Analysis (PCoA) of genetic relationships of the half and half puller (*Chromis margaritifer*) among sites from Scott Reef and Rowley Shoals. Estimates of pairwise genetic distances were derived from the genotype likelihood ratio distance, DLR, and Nei's standard genetic distance, DS. The first two axes explained 56% and 60% of the variation for DLR and DS respectively. Refer to Figure 8.2.1 for site locations.

The spatial autocorrelation analysis tested whether the differences in genetic differentiation within Scott Reef and Rowley Shoals were due to high levels of gene flow among geographically proximate fish. Despite the large number of pairwise comparisons at each distance class (min n = 1227, max n = 14748), and the high power of the permutational test (Double *et al.* 2005), 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 due to the geographic distance within these systems (Figure 8.2.4).

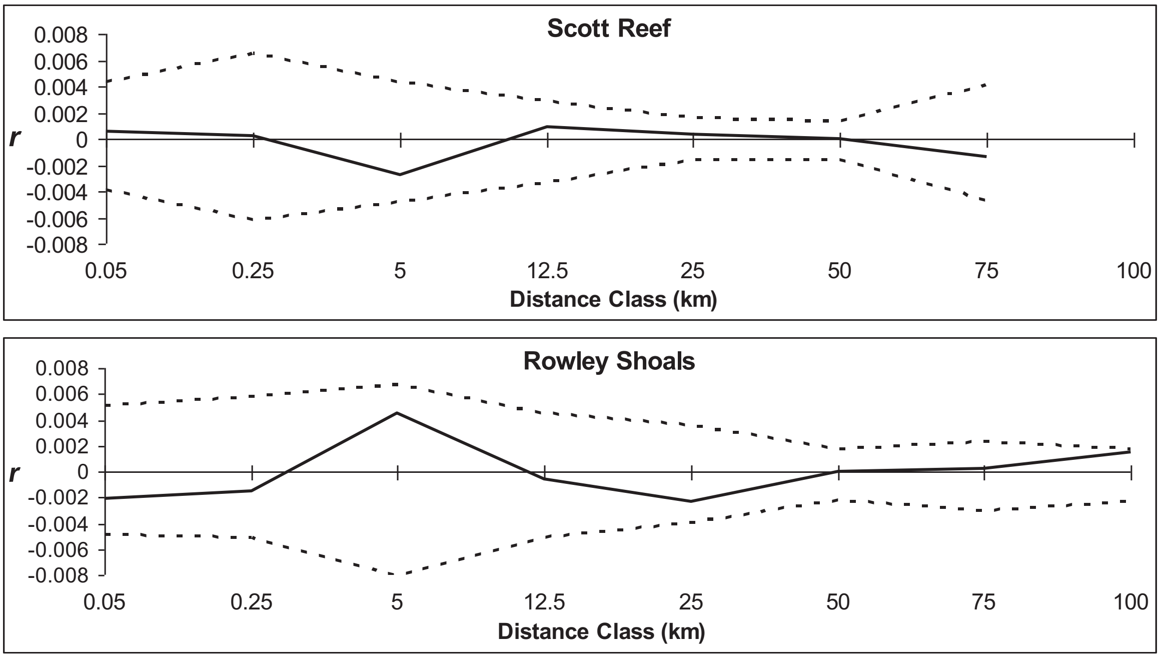


Figure 8.2.4 Spatial autocorrelation analyses of the genetic correlation coefficient (r) as a function of distance for the half and half puller (*Chromis margaritifer*) at Scott Reef and Rowley Shoals in NWA calculated with GenAlEx v6. Dotted lines indicate the upper and lower bounds of the 95% confidence interval defined by 1000 random permutations.

Spatial and temporal genetic structure of recruits

Although the genetic diversity of *C. margaritifer* recruits at Scott Reef did not differ from the adults (mean H_{SK} = 0.788 *vs* 0.799, respectively), the average genetic diversity of recruits from the Rowley Shoals was greater (mean H_{SK} = 0.820) than those from Scott Reef. However, because recruits were only collected at one site (RS3) at the Rowley Shoals, a test of significance for this difference was not possible.

Genetic subdivision of recruits collected from RS3, SL1, SL3 and SS2 (F_{ST} = 0.007; refer to Figure 8.2.1 for site locations) was very similar to the levels of subdivision of adult samples collected from these four sites (F_{ST} = 0.008). Furthermore, no significant temporal differences were detected between adult populations and recruits sampled seven months later within any site; the exception was a marginally significant difference (p = 0.041) at SL1 (Table 8.2.3). Additionally, significant differences between the Rowley Shoals site (RS3) and all three of the Scott Reef sites (SL1, SL3 and SS2) (Table 8.2..3; refer to Figure 8.2.1 for site locations) were detected by the Fisher exact tests, as were differences among all the three recruit sites within the Scott Reef system ($P \leq 0.001$).

Table 8.2.3. Results of the Fisher exact test of pairwise differentiation between recruit samples (spatial comparison) and between recruit and adult samples (temporal comparison). Refer to Figure 8.2.1 for site locations.

Pop pair	ChI^2	df	p-value
Spatial comparison			
RS3_R & SS2_R	32.34	20	0.040
RS3_R & SL3_R	42.21	20	0.003
SL1_R 7 SL3_R	45.29	20	0.001
SL1_R & SS2_R	30.50	20	0.062
SL3_R & SS2_R	40.38	20	0.004
RS3_R & SL1_R	40.75	20	0.004
Temporal comparison			
RS3 & RS3_R	23.29	20	0.275
SL1 & SL1_R	32.27	20	0.041
SS2 & SS2_R	15.80	20	0.729
SL3 & SL3_R	28.59	20	0.096

Discussion

The primary conclusion of this study is that ecological replenishment of the half and half puller populations at Scott Reef and Rowley Shoals is predominantly driven by production of larvae from within each of these coral atoll systems. However, our analyses also showed that long-distance larval dispersal of this widespread and abundant damselfish between these atoll systems of north-west Australia probably occurs sporadically during atypical biophysical conditions, and supports the emerging consensus that localised recruitment and long-distance dispersal are not mutually exclusive processes (Cowen et al. 2007; Planes et al. 2009; Puebla et al. 2009; Christie et al. 2010). In summary, there is enough exchange to prevent the evolution of separate species on each reef but not enough to assist in the recovery of populations following major impacts.

Long-term genetic connections between systems

Patterns of genetic variation of *half and half Puller* populations between Scott Reef and Rowley Shoals indicate that dispersal of larvae between systems is frequent enough to exchange most genes that arise through mutation and replace other genes that are lost through genetic drift. High levels of genetic diversity were detected, but this diversity did not differ between systems, and a low level of spatial subdivision was detected across the scale of the study (F'_{ST} = 0.011). These results show that genetic connectivity throughout these systems is much stronger than in a brooding (F'_{ST} = 0.312) and a broadcast spawning (F'_{ST} = 0.080) hard coral (Underwood et al. 2009). Therefore, a pelagic larval duration of more than a month, putative behavioural abilities of the later stage larvae, and atypical physical conditions during some years has apparently enabled sufficient ongoing larval exchange between the reef systems to prevent fixed genetic differences and thus the divergence into distinct genetic lineages. The oceanographic model indicated that potential for dispersal between Rowley Shoals and Scott Reef over a similar time period was very low (<1%) during most years, but that during one of the six years there was a 5% probability that propagules from Scott Reef were transported to within 30 kilometres of Rowley Shoals (Figure 8.2.2F). Thus, over several years there is a chance that favourable oceanographic conditions could combine with a productive spawning season to produce a significant pulse of recruits from Scott Reef to the Rowley Shoals. Furthermore, the half and half puller reproduces throughout the year (unpublished data) and is highly abundant at these offshore atolls, increasing the range of biophysical conditions encountered during the larval pelagic stage (for example, particularly strong flow regimes during a cyclone or high survival under floating rafts of *Sargassum* macroalgae), and thus their potential for occasional dispersal between the atoll systems. Therefore, it is likely that sporadic dispersal maintains connections between the Scott Reef and Rowley Shoals populations of the half and half puller that are important for evolutionary processes over multi-generational time scales.

Alternately, strong genetic connectivity over evolutionary time could be a product of past connections, and equilibrium between migration, mutation and drift has not yet been reached (see Benzie 1999). The Rowley Shoals and Scott Reef systems may have been connected by fringing reefs that existed along the continental shelf margin during low sea level stands, but if present, such reefs would have drowned 18,000 years ago when sea levels rose at the end of the last glaciation (Lindsay Collins pers. comm.). Thus, considering the likely short generation times of the half and half puller and the high mutation rate of microsatellite markers, the genetic signal of such historical connections is likely to have eroded over the thousands of generations since these quaternary sea level changes (Waples and Gaggiotti 2006). Therefore, we conclude that contemporary (Holocene) influences are the dominant drivers of the overall genetic structure of *C. margaritifer* in NWA.

Short-term 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 indicated an absence of regular dispersal of large numbers of larvae over ecological time scales. Differentiation between the two systems accounted for all of the geographic structure in the genetic variation of adult fish, and this spatial differentiation was maintained among new recruits into the next generation. Further, there was also no overlap of Scott Reef and Rowley Shoals sites on PCoA plots (Figure 8.2.3), Finally, our private allele estimate of effective number of migrants per generation (Nem) showed that 25 successful migrants per generation are required to maintain these genetic patterns. In an ecological context, and given that the census population size of the half and half puller at each system was in the tens of millions, 25 migrants per generation equates to a very low migration rate (m). Even accounting for the possibility that the effective population size (Ne) may be up to three orders of magnitude less than the census size in marine fish (e.g. Turner et al. 2002), this migration rate is still far lower than the 10% required for demographically important exchange (Hastings 1993). Therefore, taken together with otolith and oceanographic analyses that also estimated a low rate of exchange between systems (< 1%) over most years for this damselfish, we conclude that long-distance dispersal between the Scott Reef and Rowley Shoals systems is unlikely to contribute to the ecological maintenance of half and half puller populations on a generation-by-generation basis.

Connectivity within systems

In addition to inferences about dispersal of the half and half puller over hundreds of kilometres between systems, we also gained insights into dispersal over scales of tens of kilometres within each system. A weak signal of geographic structure detected by the *F*- statistics within Scott Reef but not at the Rowley Shoals was confirmed by exact tests. Further, larger genetic distances between sites within Scott Reef relative to sites within the Rowley Shoals was illustrated by greater spread of sites at the Scott Reef on the PCoA plots. Lastly, because significant differentiation within Scott Reef was also detected among collections of recruits, this genetic patchiness seems to be temporally stable at least into the next generation. Differences in the degree of structure at these two systems were also observed in two species of hard coral, suggesting the complex geography of the reefs complicates and restricts current flow within the Scott Reef system, retaining larvae close to their natal reef patch and contributing to self-recruitment of coral larvae over smaller spatial scales compared with Rowley Shoals (Underwood et al. 2009). Although the damselfish data indicate a spatially chaotic pattern of genetic patchiness not associated with a signal of self-recruitment back to the natal reef area (i.e. no spatial autocorrelation), the complicated flow patterns at Scott Reef may also explain the restricted connectivity in this damselfish among some reefs and reef areas within this system. Furthermore, the large semi-circular reef that creates the deep-water southern lagoon of Scott Reef forms highly unique and heterogeneous habitats that are not clearly lagoon or reef slope in physical character and biological assemblage. Such environmental heterogeneity may result in locally adapted subpopulations, resulting in phenotype-environment mismatch that reduces connectivity within this system because recruits produced in different environments may be less fit than local recruits (Marshall et al. 2009). However, irrespective of the precise causes of the restricted connectivity at

Scott Reef compared with Rowley Shoals, the evidence suggests that the physical idiosyncrasies of each system have a dominant influence on patterns of larval dispersal and recruitment that is consistent among organisms with vastly different life histories that include obligate periods of planktonic development that range from approximately a few days to several weeks.

In addition to local physical properties, differences in the population and larval ecology may also be driving the fundamental differences in genetic structure between Scott Reef and Rowley Shoals. Our census estimates indicate that the population at Rowley Shoals is three times larger than at Scott Reef. If we accept that a certain percentage of the larval pool will successfully disperse a particular distance between reefs, then the initial numbers produced by adult stocks have the potential to greatly influence the final numbers recruiting, particularly if the distances are in the area of the dispersal kernel where percentage of successful recruits drops off rapidly (see Figure 2 in Steneck *et al.* 2009). Thus, the larger population size and hence reproductive output at the Rowley Shoals may result in greater dispersal between reefs within this system and result in the genetic signal of panmixis that was not observed within the Scott Reef system. Fine-scale biophysical models are required to discriminate the relative importance of local hydrodynamics, environmental heterogeneity, or reproductive output in driving the different dispersal patterns within Rowley Shoals and Scott Reef.

Conservation management implications

Because rare long-distance dispersal of a few individuals is sufficient to homogenise genetic structure, but not maintain population numbers or increase short-term resilience to disturbance, the "tipping point" where populations become demographically independent usually occurs when the underlying genetic signal is weak (Waples and Gaggiotti 2006). Therefore, combining high resolution genetic tools with other multidisciplinary approaches is crucial to elucidating ecological patterns of connectivity that are relevant to management and conservation of biodiversity (Waples *et al.* 2008). This study demonstrates that *C. margaritifer* disperses regularly over tens of kilometres between many reefs, but few larvae successfully disperse over the hundreds of kilometres between systems. These results augment a growing list of recent fish (e.g. Purcell et al. 2006; Almany et al. 2007; Gerlach et al. 2007), invertebrate (e.g. Johnson and Black 2006; van Oppen et al. 2008), oceanographic (Cowen *et al.* 2006) and population modelling (e.g. Hastings and Botsford 2006) studies showing that locally produced larvae contribute disproportionately to recruitment in many marine species.

This study of *C. margaritifer* builds on previous research on hard corals that is beginning to provide a community perspective on connectivity (sensu Kinlan and Gaines 2003) among the coral atolls of NWA for species with a wide variation of life histories; populations of this benthic spawning damselfish, a brooding and a broadcast spawning coral (Underwood et al. 2009) are primarily maintained by larval production from within each of the Scott Reef and Rowley Shoals systems. The implication is that many communities inhabiting these geographically isolated atolls are demographically closed at the system level or lower, and their recovery from disturbances will not be driven by input of new recruits produced from outside each system over time scales that are relevant to management. With severe disturbances to coral reefs now acting over large spatial scales (e.g. bleaching, acidification, diseases), protecting a significant proportion of the local breeding population in replicate areas within each of these reef system from more localised impacts (e.g. degraded water quality, overfishing) is critical (see Mumby and Steneck 2008). However, because fine-scale patterns of dispersal differ among taxa with different life histories, optimal reserve design will also differ among species. For example, routine dispersal of *C. margaritifer* within and among many reefs within the Scott Reef and Rowley Shoals systems is likely to buffer these populations against severe disturbance events (notwithstanding the decimation of an entire system). This means that replicate protected areas at the reef-scale (~ 30 km) are likely to be adequate for this abundant and widespread damselfish that has a PLD range of three to six weeks. In contrast, for species whose larvae are retained at their natal reef or reef area (e.g. corals), protected areas need to be replicated at smaller, within-reef scales (~ 10 km or less).

8.3 Population connectivity of three cardinalfishes among remote coral atolls of north-west Australia

Summary

Here, we analyse mitochondrial sequence and microsatellite DNA data to assess the scale and strength of population connectivity in three species of cardinalfish at Scott Reef and Rowley Shoals and thus assess the extent of larval exchange between reefs and systems at ecological and evolutionary time scales. Significant genetic differentiation was detected between the coral reef systems of Scott Reef and Rowley Shoals for all three species. These results demonstrate that dispersal is limited between these two systems, and that populations are primarily maintained each generation by the local production of larvae. Thus, Scott Reef does not act as an ecologically important source of recruits to, and does not regularly receive large numbers of larvae from, the Rowley Shoals atolls. Therefore, recovery of these cardinalfish populations after disturbances is unlikely to be driven by input of new recruits produced outside each system over time scales that are relevant to management. However, evidence for occasional (evolutionary-scale) dispersal between systems was detected along with higher genetic diversity at Scott Reef compared with the Rowley Shoals. This suggests that Scott Reef may act as a reservoir of genetic diversity for the Rowley Shoals and could therefore be important for the ability of the Rowley Shoals population to adapt to a warmer climate.

Introduction

The persistence of populations through time requires a balance between the input of new recruits and the loss of established individuals through mortality (Hastings and Botsford 2006). The pelagic larval stage provides many marine species with the opportunity for widespread dispersal, which means that new recruits can either come from local or exogenous sources. Therefore, understanding and predicting the recovery and resilience of populations to disturbance requires knowledge of the extent of genetic and demographic exchange (population connectivity) among geographic populations. The biophysical factors that affect population connectivity are not only complex but also temporally and spatially variable, and these patterns are notoriously difficult to quantify in the marine environment. Although evidence is accumulating that a large proportion of larvae of several marine species 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), for most taxa, the relative proportions of local versus exogenous recruits remain unknown. This is one of the most critical knowledge gaps limiting effective sustainable management of marine systems (Sale et al. 2005; Fogarty and Botsford 2007; McCook et al. 2009).

Population genetic methods are an invaluable tool for estimating patterns of connectivity because they measure the genetic signal of surviving individuals and therefore integrate over generations and life history stages (Hedgecock et al. 2007). Hence, studies that investigate the distribution of intraspecific genetic lineages across geographic locations not only play a crucial role in identifying the appropriate units of biodiversity (Moritz 2002). For example, genetic affinities among populations shed light on migration and hence the contribution of exogenously derived larvae to recruitment, while the amount of genetic variation within a population provides important information on the evolutionary potential to adapt to changing environments, (van Oppen and Gates 2006; Rocha et al. 2007). Rare long-distance migration of a few individuals every generation is sufficient to prevent the accumulation of major genetic differences, but does not contribute to demographic processes (Palumbi 2003). Therefore, the underlying genetic signal is often weak in marine populations that are not exchanging ecologically meaningful numbers of migrants (i.e. demographic independence) (Waples 1998). However, provided sampling and analysis is rigorous, significant differentiation (even if of low magnitude) is a powerful indicator of true population structure (Bentzen 1998). Furthermore, genetic methods are particularly valuable when synthesised across species and combined with other interdisciplinary approaches (Hedgecock et al. 2007).

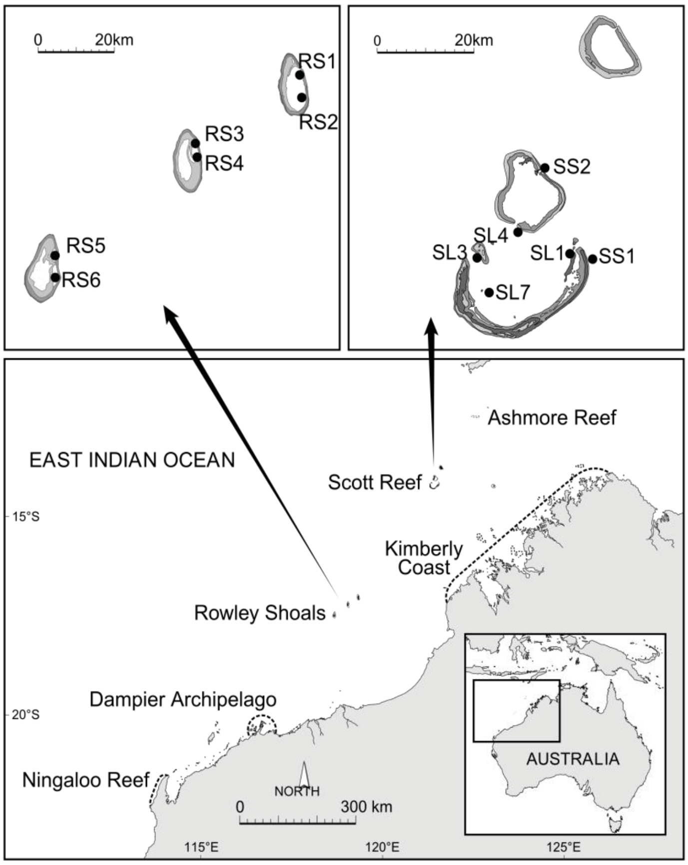


Figure 8.3.1. Map of north-west Australia showing sites where *Cheilodipterus sp.* were sampled at Rowley Shoals and Scott Reef.

Genetic evidence from several reef organisms indicates that the 400 kilometres of open ocean between Scott Reef and Rowley Shoals in north-west Australia (NWA; Figure 8.3.1) is a significant barrier to dispersal for species with different life history characteristics. For both a brooding and broadcast spawning species of hard coral, significant genetic structure was detected between systems (>100 km), and among (>10 km) or within reefs (<10 km), implying that many reefs and some reef patches were demographically independent (Underwood et al. 2007; Underwood et al. 2009). Further work on a benthic spawning coral reef damselfish, the half and half puller *(Chromis margaritifer)*, indicates that although genetic connections are probably maintained by sporadic long-distance dispersal between Scott Reef and Rowley Shoals, regular exchange of large numbers of larvae is unlikely to occur between these atoll systems (Chapter 1.3.1). These genetic data were further supported by independent otolith and oceanographic analyses demonstrating a low (<1%) probability of transport of passive propagules by oceanic currents between the Scott Reef and Rowley Shoals systems (> 400 km) over time scales encompassed by the relatively long pelagic larval duration of this damselfish (mean = 35 days).

The present study builds on the burgeoning community perspective of connectivity between and within the isolated atoll systems of NWA by exploring the patterns of genetic connectivity in three species of coral reef cardinalfish (the Wolf cardinalfish, *Cheilodipterus artus, an undescribed cardinalfish*

Cheilodipterus cf. *artus,* and the Five-Lined Cardinalfish *Cheilodipterus quinquelineatus*; see Figure 8.3.2). Cardinalfish feed off the reef at night, and therefore provide a crucial ecological role in bringing nutrients from the pelagic environment back onto the reef where they live in sheltered diurnal resting sites (Marnane and Bellwood 2002). Cardinalfish brood their eggs in their mouth before releasing larvae into the water column for duration of about three weeks (Brothers et al. 1983). Furthermore, cardinalfish larvae appear to prefer the odour of water from their home reef over water from other reefs (Gerlach et al. 2007), and the adults have strong homing behaviour to these diurnal resting sites (Marnane 2000). This suggests that not only adults, but also larvae, of cardinalfish have the ability to sense and return to their home reef, and may explain the significant genetic structure detected in one study among reefs despite a strong potential for mixing by ocean currents (Gerlach et al. 2007). If such a homing tendency is strong and sustained over time, reproductive isolation among geographic locations may result in the evolution of distinct genetic lineages in cardinalfish, as has occurred in the cleaner goby, *Elacatinus evelynae* (Taylor and Hellberg 2003). *Cheilodipterus artus* and *C.* cf. *artus* are morphological identical sibling species that often occur in the multi-specific aggregations in their diurnal resting sites but appear to be better adapted to different habitats, suggesting strong mechanisms for reproductive isolation that may have evolved sympatrically (Appendix 1.3). Here, we analyse mitochondrial sequence and microsatellite DNA data to infer patterns of intraspecific population connectivity in *Cheilodipterus artus, C.* cf. *artus* and *C. quinquelineatus* at Scott Reef and Rowley Shoals. In so doing, we explore the historical (evolutionary) and contemporary (ecological) forces that shape the genetic structure of these species. In addition, because pelagic larval durations for *C. artus* and *C.* cf. *artus* have not been published, we analysed otoliths of these species to gauge the potential for long-distance dispersal via oceanic currents.

Figure 8.3.2 Photos of the five-lined cardinalfish (*Cheilodipterus quinquelineatus*; left) and the wolf cardinalfish (*Cheilodipterus artus*) or an undescribed cardinalfish (*C.* cf. *artus*; right - species are morphologically indistinguishable).

Methods

Pelagic larval duration

To estimate mean pelagic larval duration (PLD: the number of days larvae have spent in the pelagic environment before recruiting to the reef) and its variation among individuals and systems and thus gauge the maximum potential for dispersal via oceanic currents, 74 juveniles (<50mm) of *Cheilodipterus artus* and *Cheilodipterus* cf. *artus* were collected from Rowley Shoals and Scott Reef during March of 2008 (sample sizes given in Table 8.3.1). The sagittal otoliths were extracted and cleaned, and one from each fish was weighed, 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. Settlement marks corresponded to the type 1a abrupt settlement marks of Wilson & McCormick (1999). PLD was determined by counting the number of increments (days) between hatching (first increment) and settlement. Average PLD (± 95% CI) was determined at Rowley Shoals and Scott Reef.

Genetic sampling

In April 2008, 370 *C. artus*, 213 *C.* cf *artus*, and 84 *C. quinquelineatus* fish were collected by divers using a combination of hand nets, barrier nets and clove oil (sample sizes given in Table 8.3.2, 8.3.3 and 8.3.4 respectively) from sites at Scott Reef and Rowley Shoals (Figure 8.3.1). An average of 37 *C. artus* fish per site were collected from four sites at the Scott Reef system and six sites at the Rowley Shoals, and replicate sites were sampled on most reefs. For *C. cf. artus*, an average of 24 fish per site were collected from five sites at the Scott Reef system and four sites at the Rowley Shoals. For *C. quinquelineatus,* an average of 21 fish per site, were collected from two sites at each of the Scott Reef and Rowley Shoals systems. A dorsal fin clip was placed in 100% ethanol (analytical grade) pending DNA extraction, and whole samples were frozen for otolith extraction.

Mitochondrial DNA sequencing and analysis

To explore the evolutionary histories of *Cheilodipterus* cf. *artus,* we targeted the Hypervariable Mitochondrial (mtDNA) Control Region I (D-loop) in a subset of the *Cheilodipterus* sample (n=58) 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 µL of 10 µM dNTP's, 0.4 mM of each primer, 20 ng template DNA). The PCR cycling profile involved an initial 2 minute 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 38 *C. artus,* 20 *C.* cf. *artus* fish. A 435 bp sequence was amplified in 19 *C. quinquelineatus fish*. Forward and reverse sequences were aligned with the program Sequencher 4.8 (Gene Codes).

A phylogenetic analysis was conducted using the Maximum Parsimony method with MEGA v4 (Tamura et al. 2007). This method evaluates candidate phylogenetic trees according to an explicit optimality criterion; the tree with the most favorable score is taken as the best estimate of the phylogenetic relationships of the included taxa. A bootstrap consensus tree (the best tree inferred from 1000 replicates) for each species was clauclated using the Close-Neighbour-Interchange algorithm (Nei and Kumar 2000) with search level 3 in which the initial trees were obtained with the random addition of sequences (10 replicates). All alignment gaps were treated as missing data (complete deletion option). Nucleotide diversity with standard errors calculated by a bootstrap procedure (1000 replicates) within each species, and within and between each system (π) was calculated in MEGA v4. Nucleotide diversity is a measure of the degree of polymorphism within a population, and represents the average number of nucleotide differences per site between any two DNA sequences chosen randomly from the sample population, Population subdivision (G_{ST}) and significance tests for population differentiation (Chi-squared) were calculated with DnaSP v 4.5 (Rozas et al. 2003).

Microsatellite genotyping and analysis

DNA for genotyping 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) that was diluted by one third with millepore purified water to a final concentration of about 10-20 ng. The development of the *C. artus* microsatellite library, characterisation of final 10 loci, and genotyping procedure are described in Underwood (2010). To mitigate and report scoring error of microsatellites, quality control procedures suggested by Bonin *et al.* (2004) and DeWoody *et al.* (2006) were implemented. Specifically, genotyping each individual involved the implementation of negative controls and the visual inspection of all automated allele calls, and individuals with suspect electropherograms were repeated. Furthermore, a genotype error rate (1.25%) was measured by repeating the genotyping procedure, from DNA extraction through to final allele scoring, using a subset of *C. artus* and *C.* cf. *artus* blind samples (n = 24) selected from three sites randomly spread across the sampling area. In addition, we amplified reliable and polymorphic product for five *C. artus* loci (Ca_D001, Ca_B005, Ca_B104, Ca_B124, Ca_D006) in a sister species *C. quinquelineatus* at a low genotype error rate (0.66%).

The number of alleles, the unbiased expected heterozygosity, the fixation index, and the number of private alleles at each locus at each population and averaged across populations were calculated with GenAlEx v6 (Peakall and Smouse 2006). Tests for linkage and Hardy-Weinberg disequilibrium were conducted with Genepop 4.0 (Raymond and Rousset 1995) using a dememorisation number of 1000, 1000 batches and10,000 iterations per batch and significance levels and were adjusted manually with sequential Bonferroni correction for multiple tests when $p < 0.05$. Micro-Checker v2.2 (van Oosterhout et al. 2004) was used to test for the presence of null alleles, and where null alleles were detected consistently, to adjust the allele frequencies to account for null alleles.

To estimate levels of genetic diversity within each system, we calculated gene diversity with FSTAT v2.9.3 (Goudet 1995) as allelic richness (R_S) and an unbiased estimate of gene diversity (H_S) per locus and site for each species. Significant differences between systems at each species was tested by1000 permutations of a randomized data set. Further, significant differences between species were also tested by 1000 permutations of a randomized data set with the five loci that were genotyped for all species.

To assess the amount of the genetic variation that was geographically structured and infer patterns of connectivity, we implemented an analysis of Molecular Variance (AMOVA) framework in GenAlEx v6 (Peakall and Smouse 2006) to partition the genetic variation between systems (F_{RT}), among sites relative to variation within systems (F_{SR}), and among sites relative to overall variation (F_{ST}). To assess the significance of spatial and temporal differentiation among sites and between systems with a powerful test that is better suited to unbalanced sample sizes (Goudet et al. 1996), we applied a Fisher exact test with Genepop v4.0 (Raymond and Rousset 1995), using the Markov chain parameters of a dememorization number of 1000, 1000 batches and 10000 iterations per batch. 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 (F'_{RT}, F'_{SR} and F'_{ST}) according to the method of Meirmans (2006).

To visualise the genetic relationships among sites, we performed a Principle Coordinates Analysis, PCoA (sensu Jombart et al. 2009) with GenAlEx v6 (Peakall and Smouse 2006). The PCoA used a standardised covariance matrix of pairwise distances of the mean genotype log likelihood ratio across individuals from each pair of populations, D_{LR} (Paetkau et al. 1995), which was calculated with Doh (Brzustowski 2002).

Results

Pelagic larval duration

Estimates of pelagic larval duration were similar between *Cheilodipterus artus*, *C.* cf. *artus* and did not differ between systems (Table 8.3.1). PLD estimates averaged 32.8 days (± 1.53) for *C. artus* for 32.1days (±1.35) for *C.* cf. *artus,* and ranged from 26 to 43 days for both species.

Table 8.3.1 Estimates of pelagic larval durations of the wolf cardinalfish (*Cheilodipterus artus*) and an undescribed cardinalfish (*C.* cf. *artus*).

species	system	n	mean (±95% CI)	species mean (±95% CI)	max	min
C. artus	rowleys	20	32.0 (2.27)		42	26
	scott	22	33.5 (1.52)	32.8 (1.53)	43	28
C. cf. *artus*	rowleys	19	32.4 (1.60)		42	28
	scott	13	31.5 (2.46)	32.1 (1.35)	43	26

mitochondrial DNA sequence variation and structure

Nucleotide diversity (π) for each species at each system is given in Figure 8.3.3, and the mtDNA D-loop phylogenetic tree for each species is given in Figure 8.3.4. Nucleotide diversity provides an estimate amount of genetic variation within populations; if it is high, the indication is that population sizes are large, there is little inbreeding, and that there is good statistical power to detect phylogenetic structure if it exists. For *C. artus,* the overall variation in D-loop sequences was high; 127 of 385 sites were variable, and average nucleotide diversity was 0.068. Further, nucleotide diversity was higher at Scott Reef (π = 0.077) compared with the Rowley Shoals (π = 0.061). The phylogenetic tree showed a moderate genetic split (8.4 % sequence divergence) that had good bootstrap support, but this split did not correspond to any geographic structure between Scott Reef and Rowley Shoals (G_{ST} = 0.004, P = 0.378). For *C.* cf. *artus*, overall variation was lower; 49 of the 389 sites were variable and nucleotide diversity was 0.028, and this was the same for both Scott Reef and Rowleys Shoals. Further, the phylogenetic tree exhibited moderate structure, but this did not correspond to any geographic structure, and differentiation between Scott Reef and Rowley Shoals was not significant (P = 0.263) despite a G_{ST} estimate of 0.028. D-loop sequences from *C. quinquelineatus* yielded much less variation; only 22 of the 435 sites were variable and nucleotide diversity was 0.008. The resulting phylogenetic tree exhibited extremely shallow phylogenetic structure. There was no spatial structure to the tree, and measure of population differentiation between systems was low and not significant (G_{ST} = 0.005, π = 0.328).

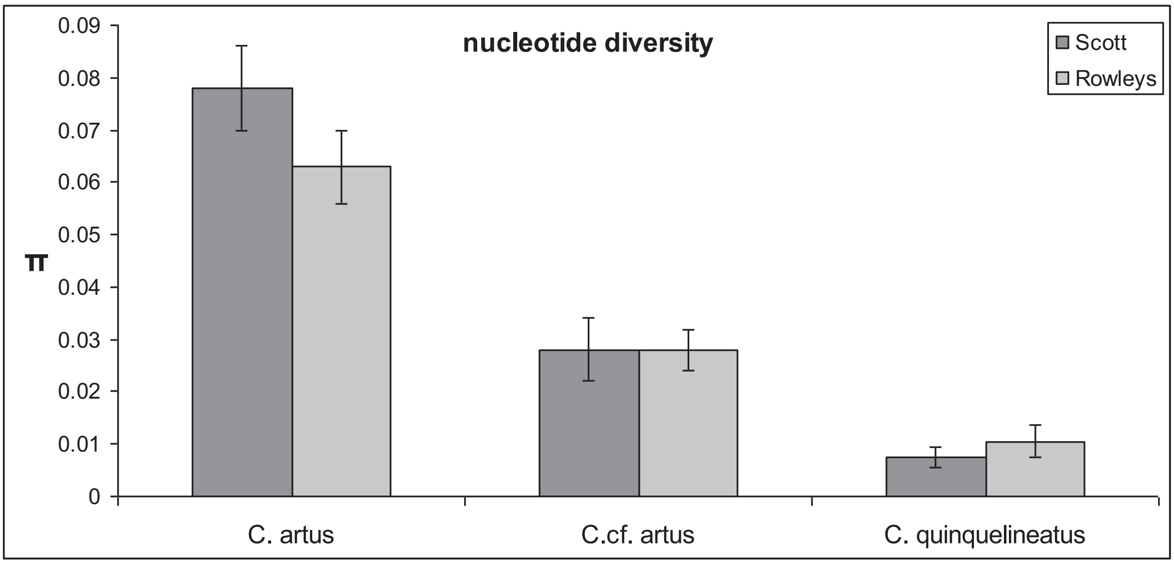


Figure 8.3.3. Nucleotide diversity from D- loop mtDNA sequences of three cardinalfish species, the wolf cardinalfish (*C. artus*), an undescribed cardinalfish (*C.* cf. *artus*), and the five-lined cardinalfish (*C. quinquelineatus*) at Rowley Shoals and Scott Reef. Error bars are standard error calculated by a bootstrap procedure with 1000 replicates.

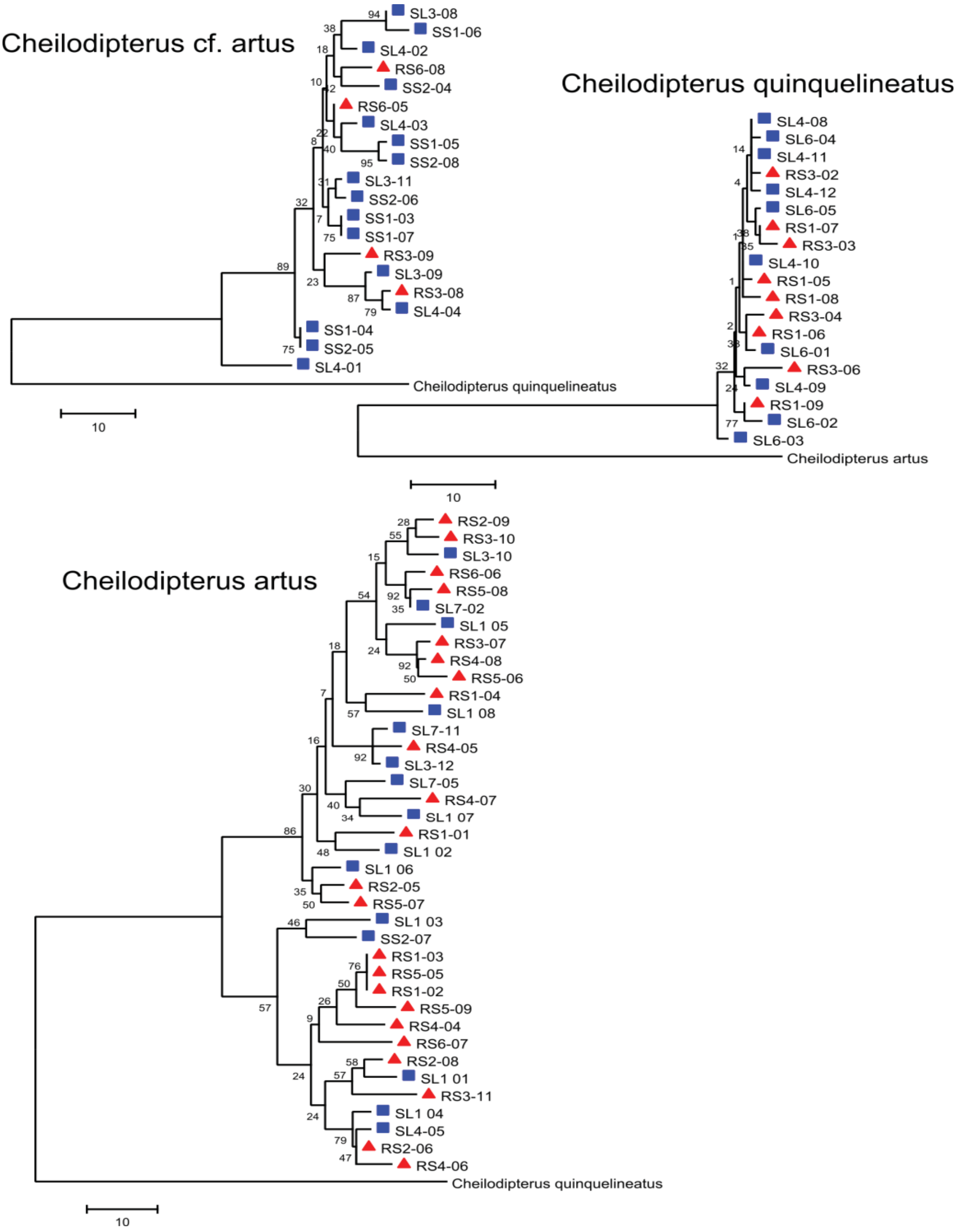


Figure 8.3.4. Bootstrap consensus tree showing phylogenetic structure among individuals of the undescribed cardinalfish species (*C.* cf. *artus*; top left), the five-lined cardinalfish (*C. quinquelineatus*; top right) and the wolf cardinalfish (C. *artus*; bottom). This tree is the best tree inferred from 1000 replicates calculated with the Maximum Parsimony method. 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 indicating genetic distance calculated using the average pathway method (Nei and Kumar 2000). Blue squares - Scott Reef sites, red triangles - Rowley Shoals sites. Almost no phylogenetic structure is observed in the five-lined cardinalfish and the undescribed cardinalfish, with short branch lengths and low bootstrap values. In contrast, for the wolf cardinalfish, two clades are identified that are distinguished by relatively long branch lengths and associated with moderate confidence according the bootstrap values. However, this clades do not have any underlying geographical structure, as indicated by an even spread of individuals collected from Scott Reef and Rowley Shoals among each clade.

Microsatellite quality control and characteristics

Ten, ten and five loci were genotyped for *C. artus*, *C.* cf. *artus*, and *C. quinquelineatus* respectively and the number of alleles, the unbiased expected heterozygosity, the fixation index, and the number of private alleles at each locus and population, and averaged across populations and loci are presented for each species in Tables 8.3.2, 8.3..3 and 8.3.4 respectively. No tests for linkage disequilibrium between pairs of loci were significant after adjusting for multiple comparisons for either species. Consistent Hardy-Weinberg disequilibrium for *C. artus* was detected at only one locus, with large F_{IS} estimates and significant heterozygote deficits detected for Ca_B107 at all 12 sites (Table 8.3.2). Analysis with Micro-Checker v2.2 (van Oosterhout et al. 2004) indicated that heterozygote deficits at this locus were most likely due to null alleles at eight of the ten sites (frequency between 0.07 and 0.15 at each site estimated with Brookfield equation 1) and not scoring error from stuttering or large allele drop out. Only one other locus, Ca-B125 exhibited significant heterozygote deficits at more than one population (with three significant tests; Table 8.3.2), but Micro-Checker detected null alleles at only one of these three sites, suggesting null alleles at this locus were not common and unlikely to bias results. Therefore, for analysis that utilised population frequency data (specifically, the Analysis of Molecular Variance, Fisher exact tests of population differentiation, genetic distance and genetic diversity calculations) we used an adjusted data set that accounted for null alleles for Ca_B107 only. Because no null homozygotes were present (i.e. all samples amplified PCR product), the adjusted allele frequencies were calculated with Brookfield equation 1 in Micro-checker *v*2.2. For the analyses that utilised individual genotypes of *C. artus*, we excluded locus Ca_B107. For *C.* cf. *artus*, no Hardy-Weinberg disequilibrium was detected. For C. *quinquelineatus*, four of the five loci were in Hardy-Weinberg equilibrium at all four sites, while significant heterozygote deficits were detected at all sites for locus Ca_D001. Micro-Checker v2.2 indicated that these deficits were most likely due to null alleles at an estimated frequency of between 0.21 and 0.28 (estimated with Brookfield equation 1). Therefore, since we only performed analysis that utilised population frequency data, we adjusted for null alleles with Brookfield equation 1 (no null homozygotes were present) in Micro-checker *v*2.2 for all analysis of *C. quinquelineatus*.

Table 8.3.2. Details of the ten microsatellite markers of the wolf cardinalfish Cheilodipterus artus 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}; a measure of genetic diversity) heterozygotes per locus and site, and the fixation index (F_{IS}; a measure of the amount of inbreeding or presence of null alleles) calculated for each locus and each site (numbers in bold indicate significant heterozygote deficits). Also shown are average number of alleles per locus (mean N_{A}), average unbiased expected heterozygosity (mean H_{E}), the average fixation index (mean F_{IS}) for each loci across all sites, the number of private alleles (P_{VA}; number of alleles unique to each site), the average expected heterozygosity and average fixation index at each site across all loci. Refer to Figure 8.2.1 for locations of sites.

Site		Ca_B003	Ca_D110	Ca_D001	Ca_B005	Ca_B104	Ca_D137	Ca_B107	Ca_B125	Ca_D109	Ca_D006	N_{A}	H_{E}	F_{IS}	P_{VA}
RS1 (30)	N_{A}	11	22	17	11	22	34	14	8	19	23	18	0.90	0.012	0
	H_{E}	0.892	0.945	0.923	0.866	0.946	0.973	0.874	0.719	0.942	0.943				
	F_{IS}	0.012	-0.041	0.008	-0.096	-0.004	-0.045	**0.147**	0.293	-0.080	-0.078				
RS2 (56)	N_{A}	12	28	19	12	20	39	13	8	21	18	19	0.89	0.046	1
	H_{E}	0.847	0.955	0.923	0.879	0.932	0.972	0.845	0.663	0.946	0.929				
	F_{IS}	0.022	-0.037	0.005	-0.046	**0.091**	0.000	**0.327**	**0.157**	-0.010	-0.047				
RS3 (22)	N_{A}	12	20	16	11	16	27	11	7	23	20	16	0.91	0.020	5
	H_{E}	0.893	0.953	0.931	0.889	0.927	0.975	0.895	0.755	0.961	0.947				
	F_{IS}	0.063	-0.024	-0.049	-0.099	0.097	0.046	**0.117**	-0.048	0.129	-0.031				
RS4 (36)	N_{A}	14	23	18	15	22	35	13	9	19	21	19	0.91	-0.002	1
	H_{E}	0.889	0.953	0.919	0.901	0.950	0.975	0.882	0.739	0.939	0.937				
	F_{IS}	-0.109	-0.005	0.050	-0.063	-0.038	-0.040	**0.169**	0.085	-0.020	-0.053				
RS5 (38)	N_{A}	11	28	17	12	25	32	13	8	20	21	19	0.89	0.019	1
	H_{E}	0.844	0.953	0.922	0.861	0.954	0.972	0.837	0.710	0.942	0.948				
	F_{IS}	0.020	-0.063	-0.099	0.040	-0.006	-0.016	**0.172**	**0.174**	-0.048	0.015				
RS6 (47)	N_{A}	13	27	19	12	24	35	13	9	21	20	19	0.90	0.003	4
	H_{E}	0.872	0.952	0.927	0.877	0.947	0.969	0.850	0.743	0.939	0.946				
	F_{IS}	-0.036	-0.016	-0.020	-0.030	-0.022	0.002	**0.165**	0.015	-0.030	0.000				
SL1 (64)	N_{A}	13	28	25	17	26	40	16	11	25	23	22	0.91	0.043	11
	H_{E}	0.860	0.957	0.937	0.878	0.954	0.971	0.913	0.742	0.946	0.945				
	F_{IS}	0.030	-0.004	0.025	0.014	0.026	-0.022	**0.345**	**0.044**	-0.049	0.017				
SL3 (32)	N_{A}	12	23	15	12	23	36	11	11	22	20	19	0.91	0.048	4
	H_{E}	0.855	0.944	0.923	0.863	0.959	0.981	0.905	0.762	0.951	0.944				
	F_{IS}	-0.002	0.025	0.106	0.007	0.007	0.031	**0.334**	0.084	-0.068	-0.042				
SL4 (15)	N_{A}	10	19	13	10	18	20	11	7	17	17	14	0.91	0.056	2
	H_{E}	0.839	0.968	0.924	0.880	0.963	0.972	0.899	0.759	0.963	0.956				
	F_{IS}	0.096	**0.145**	0.030	-0.018	-0.074	0.078	**0.156**	0.091	-0.002	0.063				
SL7 (30)	N_{A}	13	24	17	14	24	32	13	11	21	19	19	0.92	0.017	3
	H_{E}	0.883	0.936	0.933	0.900	0.963	0.974	0.918	0.814	0.936	0.940				
	F_{IS}	-0.075	-0.087	0.019	0.021	0.014	**0.060**	**0.150**	0.167	-0.050	-0.046				
	mean N_{A}	12	24	18	13	22	33	13	9	21	20	18			
	mean H_{E}	0.854	0.936	0.912	0.865	0.934	0.958	0.868	0.729	0.931	0.929		0.91		
	mean F_{IS}	0.002	-0.011	0.007	-0.027	0.009	0.009	0.208	0.106	-0.023	-0.020			0.03	

Table 8.3.3. Details of the ten microsatellite markers of the undescribed cardinalfish C. cf. artus 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; a measure of genetic diversity) heterozygotes per locus and site, and the fixation index (F_{IS}; a measure of the amount of inbreeding or presence of null alleles) calculated for each locus and each site (numbers in bold indicate significant heterozygote deficits). Also shown are average number of alleles per locus (mean N_A), average unbiased expected heterozygosity (mean H_E), the average fixation index (mean F_{IS}) for each loci across all sites, the number of private alleles (P_{VA}; number of alleles unique to each site), the average expected heterozygosity and average fixation index at each site across all loci. Refer to Figure 8.2.1 for locations of sites.

Site		**Ca_B003**	**Ca_D110**	**Ca_D001**	**Ca_B005**	**Ca_B104**	**Ca_D137**	**Ca_B107**	**Ca_B125**	**Ca_D109**	**Ca_D006**	N_A	H_E	F_{IS}	P_{VA}
RS1 (20)	N_A	3	21	15	10	12	19	10	8	17	17	13	0.84	0.016	1
	H_E	0.50	0.96	0.92	0.74	0.91	0.95	0.74	0.79	0.93	0.92				
	F_{IS}	0.276	-0.016	-0.054	0.036	-0.018	0.026	0.125	-0.109	-0.045	-0.061				
RS3 (28)	N_A	3	22	18	9	18	22	10	7	18	17	14	0.85	-0.005	5
	H_E	0.58	0.95	0.92	0.83	0.94	0.95	0.70	0.73	0.94	0.91				
	F_{IS}	-0.006	-0.033	-0.063	-0.006	-0.010	-0.031	0.164	0.009	-0.043	-0.035				
RS5 (10)	N_A	3	12	13	8	11	12	6	6	14	12	10	0.87	-0.086	1
	H_E	0.67	0.94	0.96	0.86	0.92	0.94	0.77	0.79	0.96	0.92				
	F_{IS}	-0.102	-0.124	0.011	-0.098	-0.034	-0.117	-0.096	-0.060	-0.093	-0.149				
RS6 (12)	N_A	4	12	13	9	12	17	7	6	12	12	10	0.87	-0.062	1
	H_E	0.67	0.91	0.94	0.90	0.94	0.97	0.76	0.79	0.92	0.92				
	F_{IS}	-0.297	0.040	-0.015	-0.161	-0.108	0.101	-0.024	0.009	-0.129	-0.039				
SL1 (9)	N_A	5	10	10	8	11	12	8	5	11	9	9	0.87	-0.022	4
	H_E	0.71	0.90	0.91	0.88	0.93	0.94	0.83	0.78	0.95	0.90				
	F_{IS}	0.167	-0.043	-0.165	0.067	-0.007	0.000	0.008	-0.200	0.007	-0.051				
SL3 (15)	N_A	5	18	13	10	13	17	7	7	19	10	12	0.85	0.003	2
	H_E	0.54	0.95	0.93	0.85	0.91	0.96	0.70	0.83	0.97	0.88				
	F_{IS}	-0.030	0.058	-0.037	0.106	0.020	-0.007	0.020	-0.083	0.000	-0.016				
SL4 (16)	N_A	4	16	12	7	17	17	9	7	17	14	12	0.85	-0.031	2
	H_E	0.47	0.93	0.91	0.81	0.96	0.95	0.73	0.85	0.94	0.93				
	F_{IS}	-0.099	0.032	0.011	-0.114	-0.013	-0.085	-0.143	0.166	-0.101	0.032				
SS1 (55)	N_A	4	24	19	12	22	25	12	8	25	17	17	0.84	-0.016	6
	H_E	0.40	0.95	0.93	0.79	0.93	0.95	0.74	0.81	0.94	0.92				
	F_{IS}	-0.136	-0.039	0.053	-0.026	0.036	0.016	-0.095	0.022	0.028	-0.019				
SS2 (48)	N_A	4	28	18	12	23	22	12	9	24	17	17	0.84	0.020	11
	H_E	0.45	0.95	0.93	0.84	0.93	0.95	0.73	0.80	0.94	0.93				
	F_{IS}	-0.028	0.091	0.025	0.097	-0.059	0.021	0.017	0.026	-0.008	0.022				
mean	N_A	4	18	15	9	15	18	9	7	17	14	13			
mean	H_E	0.55	0.94	0.93	0.83	0.93	0.95	0.74	0.80	0.94	0.91		0.85		
mean	F_{IS}	-0.028	-0.004	-0.026	-0.011	-0.021	-0.009	-0.003	-0.024	-0.043	-0.035			-0.020	

Table 8.3.4. Details of the five microsatellite markers of five-lined cardinalfish C. quinquelineatus 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; a measure of genetic diversity) heterozygotes per locus and site, and the fixation index (F_{IS}; a measure of the amount of inbreeding or presence of null alleles) calculated for each locus and each site (numbers in bold indicate significant heterozygote deficits). Also shown are average number of alleles per locus (mean N_A), average unbiased expected heterozygosity (mean H_E), the average fixation index (mean F_{IS}) for each loci across all sites, the number of private alleles (P_{VA}; number of alleles unique to each site), the average expected heterozygosity and average fixation index at each site across all loci. Refer to Figure 1.2.1 for locations of sites.

Site		**Ca_D001**	**Ca_B005**	**Ca_B104**	**Ca_B125**	**Ca_D006**	N_A	H_E	F_{IS}	P_{VA}
RS1 (19)	N_A	18	8	14	19	10	14	0.90	0.132	9
	H_E	0.952	0.809	0.905	0.952	0.898				
	F_{IS}	**0.460**	-0.048	0.179	0.091	-0.024				
RS3 (22)	N_A	17	6	11	21	15	14	0.89	0.098	3
	H_E	0.944	0.730	0.893	0.930	0.934				
	F_{IS}	**0.587**	0.045	-0.147	0.050	-0.045				
SL4 (23)	N_A	18	8	13	21	15	15	0.90	0.116	4
	H_E	0.950	0.773	0.909	0.950	0.935				
	F_{IS}	**0.579**	-0.035	-0.075	0.111	0.002				
SL7 (20)	N_A	13	6	13	18	15	13	0.89	0.074	2
	H_E	0.919	0.726	0.901	0.955	0.928				
	F_{IS}	**0.442**	0.081	-0.081	-0.020	-0.050				
mean	N_A	17	7	13	20	14	14			
mean	H_E	0.94	0.76	0.90	0.95	0.92		0.87		
mean	F_{IS}	0.517	0.011	-0.031	0.058	-0.029			0.105	

Microsatellite diversity and structure

Genetic variation differed between species; allelic richness (R_S) and gene diversity (H_S) were highest for *C. artus*, intermediate for *C. quinquelineatus* and lowest for *C.* cf. *artus* (Figure 8.3.5), and these differences were significant (P for R_S = 0.002 and P for H_S = 0.007). Furthermore, for *C. artus*, significantly higher allelic richness was detected at Scott Reef compared with Rowley Shoals (P = 0.010), while the same trend was detected for gene diversity but this significance was marginal (P = 0.055). No significant differences were detected between the two systems for the other two species, although small sample sizes may have limited the power to detect a higher amount of diversity by both measures at Rowleys Shoals compared with Scott Reef for *C. quinquelineatus*.

Patterns of geographic structure of the genetic variation were highly congruent across all three species with low but significant subdivision detected across the entire sample area (F_{ST} for *C. artus* = 0.002, F_{ST} for *C.* cf. *artus* = 0.005, F_{ST} for *C.* cf. *quinquelineatus* = 0.003) (Table 8.3.5). When the heterozygosity within each site was accounted for with Meirman's (2006) method, F'_{ST} values increased by an order of magnitude to moderate levels of subdivision (F'_{ST} for *C. artus* = 0.027, F'_{ST} for *C.* cf. *artus* = 0.034, F'_{ST} for *C.* cf. *quinquelineatus* = 0.022). Furthermore, this geographic structure was brought about almost entirely by subdivision between systems (F_{RT}) and not to subdivision within each system (F_{SR} values were zero or negative).

The cluster analysis clearly illustrated the genetic divergence between Scott Reef and Rowley Shoals. The PCoA showed a clear separation of sites from each system for *C. artus* and *C.* cf. *artus*, and the percentage variation explained by the first to axes was high (79% and 83% respectively; Figure 8.3.6). A similar pattern was suggested for *C. quinquelineatus*, but because only two replicate sites at each system were sampled, divergence between systems cannot be clearly determined.

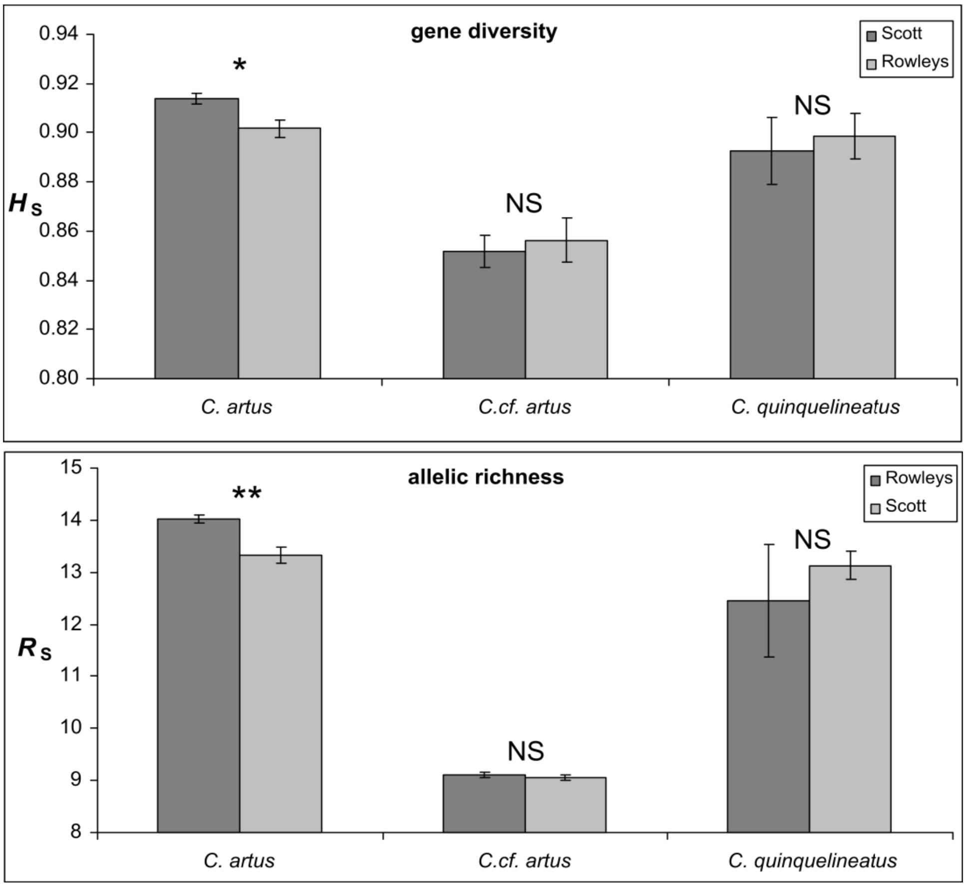


Figure 8.3.5. Comparisons of genetic diversity of three cardinalfish species, the wolf cardinalfish (C. *artus)*, an undescribed cardinalfish (*C.* cf. *artus*), and the five-lined cardinalfish (*C. quinquelineatus*), at Rowley Shoals and Scott Reef. Average gene diversity (H_S; upper panel) and allelic richness (R_S; lower panel) were calculated across loci and sites at each system. Estimates account for unequal sample sizes, and error bars show ± standard error. Tests between systems for each species were based on 1000 permutations (* $P \leq 0.05$, ** $P \leq 0.01$).

Table 8.3.5. Hierarchical Analysis of Molecular Variance calculated with respect to different alleles (F_{ST}) for the wolf cardinalfish (C. *artus)*, an undescribed cardinalfish (*C.* cf. *artus*), and the five-lined cardinalfish (*C. quinquelineatus*). Analyses estimated the proportion of variance among systems (F_{RT}), the proportion of variance among sites within systems (F_{SR}), and among all sites (F_{ST}) relative to the total variance. F'_{RT}, F'_{SR} and F'_{ST} are standardised to within population diversity according to Meirmans (2006). Tests for statistical significance were based on 1000 random permutations. Levels of statistical significance for the *F* - values are indicated by; *P<0.05; **P< 0.01, ***P<0.001.

C. artus				***C.cf. artus***				***C. quinquelineatus***			
F_{RT}	0.002***	F'_{RT}	0.027	F_{RT}	0.005***	F'_{RT}	0.034	F_{RT}	0.003**	F'_{RT}	0.022
F_{SR}	0.000	F'_{SR}	0.004	F_{SR}	-0.001	F'_{SR}	NA	F_{SR}	-0.001	F'_{SR}	NA
F_{ST}	0.003***	F'_{ST}	0.031	F_{ST}	0.004**	F'_{ST}	0.028	F_{ST}	0.001**	F'_{ST}	0.011

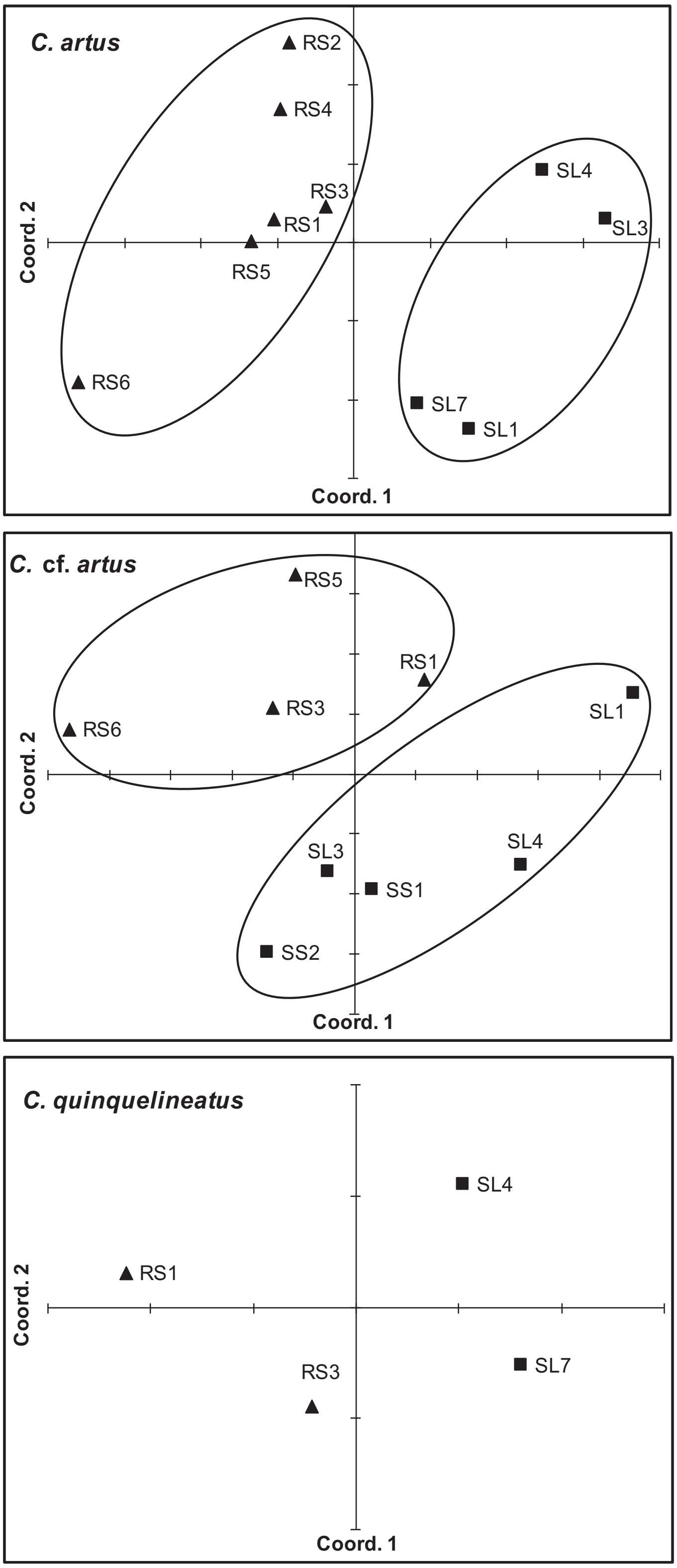


Figure 8.3.6. Principal Coordinate Analysis (PCoA) of genetic relationships of the wolf cardinalfish (C. *artus*), an undescribed cardinalfish (*C.* cf. *artus*), and the five-lined cardinalfish (*C. quinquelineatus*) among sites from Scott Reef and Rowley Shoals. Estimates of pairwise genetic distances were derived from the genotype likelihood ratio distance, DLR. The first two axes explained 79%, 83% and 100% of the variation for *C. artus*, *C.* cf. *artus* and *C. quinquelineatus* respectively. Limited replicate sites at each system for *C. quinquelineatus* precluded cluster circles. Refer to Figure 8.2.1 for locations of sites.

Discussion

This study detected significant genetic differentiation in microsatellite loci between the coral atoll systems of Scott Reef and Rowley Shoals for three sister species of cardinalfish. These results demonstrate restricted connectivity between systems, and indicate that few larvae disperse regularly and in large numbers between Scott Reef and Rowley Shoals over ecological relevant time scales. However, levels of population subdivision of microsatellite variation were low and no geographic structuring of the mtDNA sequences was detected, suggesting relatively strong genetic connections over evolutionary relevant time scales. In addition, genetic diversity was higher at Scott Reef compared with the Rowley Shoals in one species for both mtDNA and microsatellites. Therefore, Scott Reef has a larger effective population size in this species and probably receives genetic input from warmer reefs to the north. Further, Scott Reef is likely to be the primary source of migrants to the Rowley Shoals for this species, and such input may well facilitate adaptation of the Rowley Shoals population to warmer in the future.

Exchange over ecologically relevant time scales

Across the range of the study, levels of population subdivision were significant but low (F'_{ST} ranged from 0.022 to 0.037 across the three species), and all of this geographical variation was attributed to subdivision between the Scott Reef and Rowley Shoals systems. For species with short generation times and large population sizes, if variable markers are combined with careful sampling design and good quality control procedures, significant differentiation (even if of low magnitude) is a powerful and conservative indicator of true population structure and demographic independence (Bentzen 1998; Waples and Gaggiotti 2006; Hauser and Carvalho 2008). Therefore, the microsatellite data provide evidence that these two systems represent two populations that are demographically independent. Given the long larval duration of between 26 and 42 days, this genetic result is congruent with oceanographic modelling showing that dispersal via oceanic currents over these time periods is possible but of low probability (<1%) (Chapter 1.3.1).

No significant genetic differentiation was observed within the Scott Reef or Rowley Shoals systems in any of the cardinalfish species. Thus it appears that connectivity throughout these systems is strong. However, when the null hypothesis of no structure is supported, it may be due to a lack of power in the data to detect real differentiation and restricted connectivity (Waples 1998). In contrast, structure within Scott Reef was statistically significant for the damselfish and corals, and this significance was driven primarily by genetic differences between sites from the outer-slope and semi-enclosed lagoon. Therefore, it is possible that the smaller sample sizes and reduced replication of sites in this cardinalfish study reduced the power to detect real structure. Nevertheless, it is interesting that significant structure was not detected either within Scott Reef or at the Rowley Shoals here. This result contradicts our initial expectation of strong localised structure based on a study of cardinalfish on the Great Barrier Reef that revealed significant genetic structure over smaller geographic scales and strong potential for homing by larvae (Gerlach et al. 2007).

Exchange over evolutionarily relevant time scales

For all three cardinalfishes, an absence of geographical structuring of mtDNA sequences, and the presence of low level genetic subdivision at microsatellite DNA variation between the systems of Scott Reef and Rowley Shoals indicated that dispersal between atoll systems over multiple generations has prevented major genetic diversification. Thus, the evidence suggests that the populations of each species at Scott Reef and Rowley Shoals are linked as part of a over evolutionary time whereby recolonisation after extinction of local populations has occurred (i.e. metapopulation). Further, the differences in intraspecific variation detected between Scott Reef and Rowley Shoals for *C. artus* in both the mtDNA and microsatellite diversity suggest that Scott Reef has a larger effective population size and probably receives genetic input from elsewhere (most probably Ashmore Reef to the north east). Further, taken together with the implications from the interspecific study which suggest that habitat heterogeneity stimulates and maintain genetic diversification in these systems

(Appendix 1.3), these results indicate that the more heterogeneous environment of Scott Reef may be an important driving force of genetic variation. Although this assessment is based on selectively neutral loci, and therefore, it is unclear whether populations at Scott Reef and Rowley Shoals are divergent for adaptive variation in these species (see Crandall et al. 2000), input of genetic variation from warmer waters further north from, and via, Scott Reef is likely to be important for adaptation of the Rowley Shoals populations to warmer conditions in the future. Indeed, similar differences in genetic diversity between theses two systems were also observed in two hard corals (unpublished data). Given the geographic isolation of the Rowley Shoals and the oceanography of the region, these multispecies patterns indicate that Scott Reef is the major exogenous source of new genetic variation for Rowley Shoals in a many coral reef species.

Community perspective of population connectivity among NWA atolls

This study of three species of mouth-brooding cardinalfish builds on previous research on a brooding and broadcast spawning species of hard corals (Underwood et al. 2009), and a benthic spawning damselfish (Chapter 1.3.1) that is revealing a community perspective on connectivity (*sensu* Kinlan and Gaines 2003) among the coral atolls of NWA for species. We now have evidence that populations of six coral reef species (the wolf cardinalfish, *C. artus*, an undescribed cardinalfish, *C.* cf. *artus*, the five-lined cardinalfish, *C. quinquelineatus*, the half and half puller, *Chromis margaritifer*, broadcast spawning coral, *Acropora tenuis*, and a brooding hard coral, *Seriatopora hystrix*) that represent a wide range of life histories are primarily maintained by larval production from within each of the Scott Reef and Rowley Shoals systems. The implication is that many communities inhabiting these geographically isolated atolls are demographically independent at the system level or lower, and their recovery from disturbances will not be driven by input of new recruits produced from outside each system over time scales that are relevant to management. Further, evidence of high genetic diversity at Scott Reef for several of these species shows that the high interspecific diversity at Scott Reef (Bryce et al. 2009) is mirrored by intraspecific diversity. Thus, Scott Reef may be a reservoir for genetic diversity for the Rowley Shoals populations of these species, and if so, these evolutionary-scale connections are likely to enhance the ability of the Rowley Shoals populations to adapt to a warmer climate in the future.

8.4 Microsatellite and mitochondrial DNA identify cryptic species of cardinalfish

Summary

This study identified a deep genetic divergence among morphologically identical *Cheilodipterus* fish. The mtDNA tree based on control region D-loop sequences identified two clades that corresponded with 20% sequence divergence. The depth of this split is well above the level that delineates species (Avise 2000). Further, 100% concordance was detected between the nuclear markers and the mtDNA marker with little evidence of hybridisation with the clustering analysis unambiguously assigning these individuals to the correct cluster as revealed by the mtDNA tree. Thus, the genetic divergence is well supported by both mtDNA and microsatellite analyses, and shows that these two putative species are reproductively isolated. These results suggest that a taxonomic revision of the *Cheilodipterus* genus is necessary. Moreover, we identified previously unrecognised evolutionary significant units that occur in sympatry but appear to be better adapted to different habitats. Therefore, this study provides another example showing that assessments of fish biodiversity based on visual identification are probably often underestimates (see Rocha et al. 2007).

Introduction

Although phylogeographic studies are initiated to investigate the distribution of genetic lineages across geographic locations and thus identify the appropriate units of biodiversity within species, the identification of species with conservative morphologies is one of the most important, although often unexpected, contributions of phylogeographic studies to the conservation of coral reefs (Rocha et al. 2007). Cardinalfishes (Apogonidae) form a major and functionally important component of the fish biodiversity of coral reefs, commonly estimated as the second or third most abundant and species diverse of the fish families (Allen 1993; Bellwood 1996; Marnane and Bellwood 2002). However, morphological similarity among species, ontogenetic changes in morphology and multi-specific daytime aggregations make species identification of cardinalfish underwater difficult. Thus, in order to assess patterns of intraspecific population connectivity of cardinalfish in north-west Australia (Chapter 8.3.), it was necessary to clarify the taxonomy among the cardinalfish samples. Here, we assessed the genetic relatedness among cryptic cardinalfish by sequencing the control region of mtDNA of 58 individual fish collected from 12 locations at Scott Reef and Rowley Shoals. This initial analyses indicated the presence of two cryptic species, so we then sought genealogical concordance with nuclear DNA data from to assess the potential for hybridisation.

Materials and Methods

Sampling

As part of the intraspecific population connectivity study (Chapter 8.3), 593 *Cheilodipterus* fish were collected by divers from 6 sites at each of the Scott Reef and Rowley Shoals systems (Figure 8.4.1) in 2008. These fish keyed out to the Wolf cardinalfish (*Cheilodipterus artus*), and no morphological differences were detected apart from ontogenetic changes with size of fish that were consistent among and within sites. Subsequent morphological assessment with the Western Australian Museum (with Gerry Allen) confirmed a lack of distinguishable morphological features among fish. At the Scott Reef system, these cardinalfish aggregated in the daytime under reef overhangs and caves on the slopes of the semi-enclosed deep-water lagoon (DL; sites included SL1, SL3, SL4 and SL7) of the south reef and in sheltered microhabitats on the outer reef slopes (OS; sites included SS1 and SS2).

In contrast, at the Rowley Shoals, cardinalfish were found in the fully-enclosed shallow-water lagoons (SL; sites included RS2, RS4, RS5 and RS6) or at the entrance to shallow-water lagoon in the channels (SC; sites included RS1 and RS3), but not on the outer-slopes despite extensive searches.

mitochondrial sequencing and analysis

To assess the evolutionary history of the *Cheilodipterus* fish in the first step in the intraspecific population connectivity study (Chapter 1.3.2), we sequenced the Hypervariable Mitochondrial Control Region I (D-loop) in a subset of the *Cheilodipterus* sample (n=59) (details given in Chapter 1.3.2). A phylogenetic analysis was conducted using the Neighbour-Joining method with MEGA v4 (Tamura et al. 2007). A bootstrap consensus tree (was inferred from 1000 replicates using the distances calculated with Maximum Likelihood method (Tamura et al. 2004). All alignment gaps were treated as missing data (complete deletion option). A 435 bp sequence from *Cheilodipterus quinquelineatus* was used as an outgroup. General sequence diversity and population differentiation measures were estimated with DnaSP v 4.5 (Rozas et al. 2003).

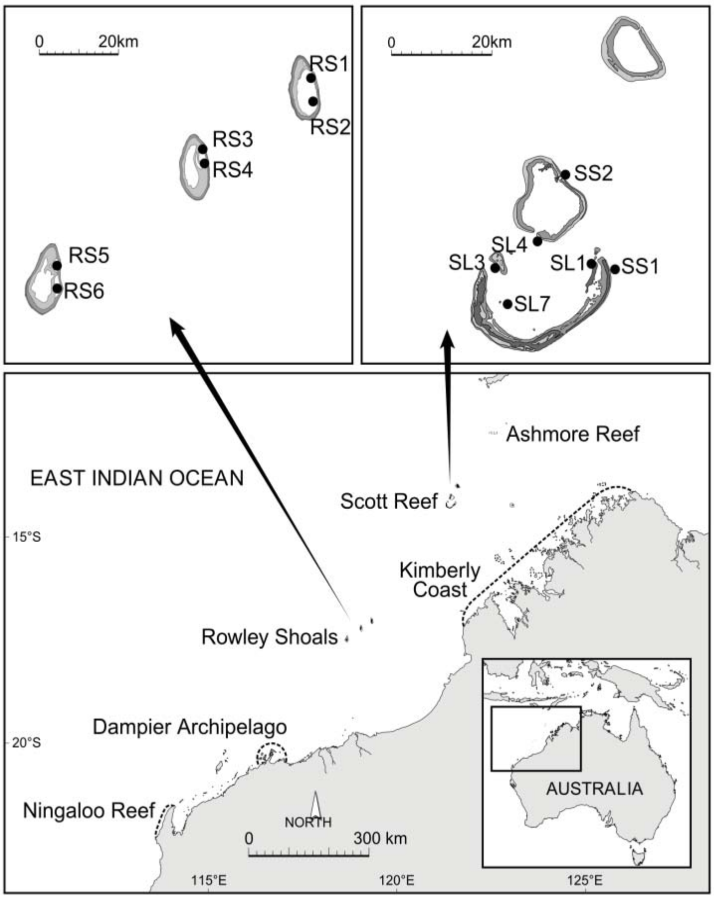


Figure 8.4.1. Map of sampling sites at the Scott Reef and Rowley Shoals systems in north-west Australia.

Microsatellite genotyping and analysis

Because mtDNA is maternally inherited and therefore does not recombine, mtDNA divergence does not exclude the presence occasional hybridisation. Therefore, test whether genetic relationships observed among the mtDNA sequences were also present in the nuclear genome, we genotyped fish at 10 microsatellite markers. Again, this genotyping was conducted as part of the intraspecific population connectivity study (for details see Chapter 1.3.2), but the resulting data was used to help assess the taxonomy of the *Cheilodipterus* fish. We conducted a Bayesian clustering analysis to explore the optimal number of clusters (K) using genotypes from all 593 fish with the program Structure v2.3(Pritchard et al. 2000). We ran an initial analysis to identify the number of differentiated clusters, K without any prior information of the individuals membership to either putative species. Mean and variance of log likelihoods and posterior probabilities of the number of clusters for $K = (1, 2, \ldots 6)$ were inferred from multilocus genotypes by running Structure five times using the admixture model with independent allele frequencies and default values (burnin period of 100,000 and MCMC repetitions after burnin of 1,000,000). We assessed the true number of clusters as suggested in the software manual (Pritchard and Wen 2003) as well as with the method of Evanno et al. (2005). Using the results from a run from the initial analysis without prior information in which K = 2, we assigned each individual to the "lagoon" or "slope" clade based on the membership coefficients (*q*), and then calculated *q* again using this prior information (i.e. the LOCPRIOR model) of membership to each putative species. All other parameters for this second round were the same as for the initial analysis, and the program was run with default values.

Results

mitochondrial DNA sequence structure

The underlying variation of D-loop sequences in *Cheilodipterus* was high; 134 out of 387 sites were variable, and average nucleotide diversity was 0.121. The Neighbour-Joining phylogenetic tree showed a deep genetic split into two clades which has 100% bootstrap support (Figure 8.4.2). These clades correspond closely to the different habitats sampled; nine of the ten individuals from outer-slope (OS) sites at Scott Reef belonged to one clade (hitherto referred to as the "slope" clade), while 16 of 18 individuals collected from shallow-water lagoon (SL) sites at the Rowley Shoals belonged to the other clade (hitherto referred to as the "lagoon" clade). Furthermore, individuals collected from the deep-water lagoon (DL) at Scott Reef , and the shallow-water channel (SC) sites at Rowley Shoals were spread evenly through both clades. Average number of nucleotide substitutions per site (Dxy) was 0.195, and F_{ST} was 0.75, between the two clades.

Microsatellite allele frequency structure

Results from Bayesian cluster analysis provided unequivocal support that the multilocus genotypes of individual fish formed two distinct clusters that corresponded with the mtDNA clades. In the first round of analysis, the Markov Chain achieved good convergence as indicated by constant α, log likelihood and log P(D) within runs, as well as highly congruent log P(D) across the five independent runs (e.g. when K of 2, SD = 0.14). Both the method of Pritchard and Wen (2003) and Evanno et al. (2005) showed that the data was clearly differentiated into two clusters, and division of the data into more than two clusters was not supported (data not shown). For K = 2, individuals had extremely high membership coefficients; only 17 individuals had a probability of less than 95% of belonging to either cluster, and only one of these (RS1-13) had a probability of less than 75% (Figure 8.4.3). Moreover, for the subset of individuals that were sequenced, there was 100% concordance among the multilocus assignments and the mtDNA tree; all individuals that made up the "lagoon" clade were clustered together by Structure, and likewise with the "slope" clade, including the potential hybrids suggested by the PCoA analysis. There was a clear pattern to cluster membership at each site with habitat type that also corresponded with the mtDNA tree; shallow-water lagoon sites (SL) were dominated by individuals belonging to the "lagoon" cluster, outer-slope sites (OS) were dominated by the "slope" cluster, while the intermediate habitats of the shallow-water channel (SC) at Rowleys Shoals and the deep-water lagoon (DL) at Scott Reef exhibited mixed membership. When prior information about membership to each putative species was used to enhance the accuracy of the Structure algorithm, all individuals had membership coefficients greater than 99%, and the membership of individuals to each cluster remained the identical.

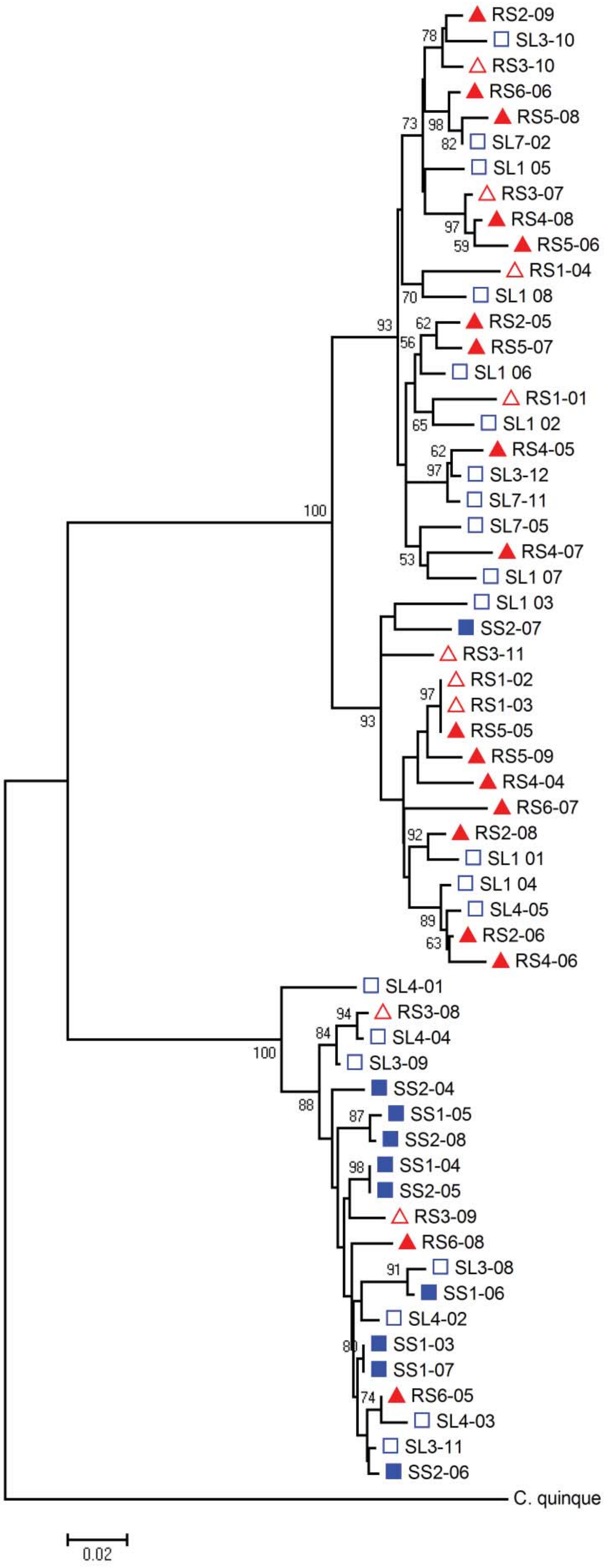


Figure 8.4.2. Neighbour-joining consensus tree of Cheilodipterus sp. inferred from 1000 replicates using the Maximum Likelihood model in MEGA v4. Bootstrap support in which the associated taxa clustered together in more than 50% replicates is shown next to the branches. The tree is drawn to scale, with branch lengths in the units of the number of base substitutions per site. Filled triangles = shallow-water lagoon sites (SL) at Rowley Shoals, empty triangles = shallow-water channel sites (SC) at Rowley Shoals, filled squares = outer-slope sites (OS) at Scott Reef, empty squares = deep-water lagoon (DL) slopes at Scott Reef. Outgroup is sister-species *C. quinquelineatus*. Refer to Figure 8.2.1 for locations of sites**.**

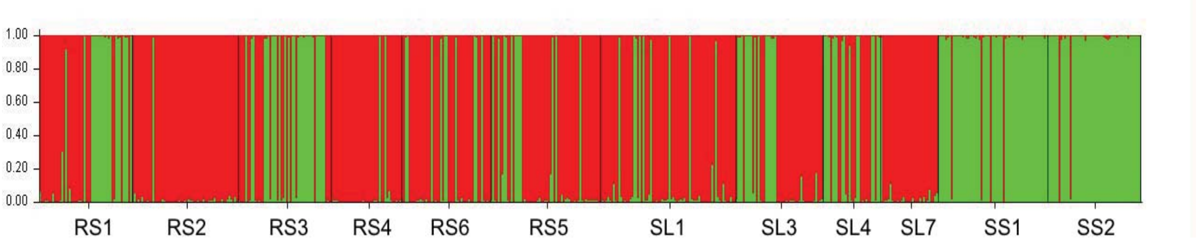


Figure 8.4.3. Results of Bayesian clustering of Cheilodipterus with Structure with no prior information for K = 2. Only 17 individuals had a membership coefficient, *q*, of less than 95% probability of belonging to either clusters. Red indicates *q* value for the "lagoon" cluster, and green indicates *q* value for "slope" cluster.

Glossary of technical terms

Benthic spawner: fish species that lay fertilised eggs on the sea floor.

Broadcast spawner: fish or corals that release sperm and eggs into water column where they are fertilised externally.

Brooder: a species (fish or coral) that has internal fertilisation and broods eggs (and larve for corals) before releasing larvae into the plankton.

Demography: the size, age structure and distribution of populations.

Demographic independence: where the reproductive output of one population has little effect on recruitment at another population – i.e. population is demographically closed.

Dispersal kernel: the theoretical distribution of dispersal distances between source and destination that captures the temporal and spatial variability in dispersal processes.

D_{LR}: the mean log-likelihood ratio across individuals from two sites calculated as the likelihood that an individual sampled in one site belongs to the other site.

Ecologically relevant: processes that occur over time scales that important for ecological replenishment of populations over times scales of one to a few tens of years.

Evolutionary relevant: dispersal that is important for exchange of genes over time scale of many tens to hundred and thousands of years, and therefore mitigates major genetic divergence.

Exogenous recruitment: recruits are produced from outside the population.

Gene flow: movement of genes through the exchange of individuals among populations that survive to reproductive age

Genetic differentiation: when genetic characteristics of one population significantly differ from another – e.g. the allele frequencies at microsatellite loci

Genetic Diversity: the total number of genetic characteristics in the genetic makeup of a species or population.

Genetic Subdivision: the amount of genetic variation that is brought about by geographic structure.

Larval dispersal: movement of larvae away from natal population or geographic area usually via oceanic currents.

Microsatellite DNA: tandem repeats of DNA sequences 1-6 base pairs in length and found in the nuclear DNA. Alleles at a specific loci differ in number of repeats, and are co-dominant.

Mitochondrial DNA: is the DNA located in organelles called mitochondria.

Population connectivity: the extent of exchange among populations of individuals that survive to reproductive age.

Recovery: the increase in population size and function back to pre-disturbance levels.

Replenishment: the input of new individual (recruits) into a population that replace loss of individuals lost through mortality.

Sagittal Otoliths: largest of two pairs of bony structures within semi-circular canals of the skull of bony fishes that functions for balance and hearing

Self-recruitment: recruits are produced within the population of interest.

Pelagic Larval Duration: the number of days larvae have spent in the pelagic environment before recruiting to the reef, usually measure bu counting the daily rings in the otoliths of coral reef fish

9. PATTERNS OF REPRODUCTION FOR CORAL COMMUNITIES AT SCOTT REEF

Summary

Multi-specific mass spawning at Scott Reef occurs biannually, with a primary spawning event in autumn (March / April) and a smaller event occurring in spring (October / November). The stage of egg development was ranked for over 2500 colonies in situ and/or in the lab, as was the size and number of more than 20 000 eggs within polyps. The participation by corals in the mass spawning in autumn (2008, 2009, 2010) and spring (2008, 2009) was inferred from samples collected from 68 species at six locations across Scott Reef. Around 200 colonies of 10 species were tagged and re-sampled through time, to investigate whether the colonies reproduce more than once a year and the time of reproduction was consistent among years. Almost 60% of species spawned only during the autumn event, about 16% spawned only in spring, and 25% spawned in both seasons. Of the species that spawned in both seasons, a higher proportion of colonies spawned during autumn. Individual colonies appeared to spawn consistently in only one season over consecutive years. There was little evidence of individual colonies spawning twice or switching between seasons, indicating that the presence of two gametogenic cycles is unlikely. Colonies that presented exceptional patterns, such as appearing to spawn outside the known spawning season for the species, are being investigated further. For species subject to histological analysis, massive Porites *spp. and three species of brooding corals reproduced over several months through spring to autumn. Additionally, every few years spawning during autumn or spring may occur over consecutive months, due to a 'split-spawning'. After adjusting for the relative abundance of the most common species at Scott Reef, roughly 40% of the community reproduces during one month in autumn (usually March), 16% during one month in spring (usually October), and 44% during other months of the year.*

Introduction

Patterns of reproduction in spawning and brooding corals

Understanding the timing of coral spawning and the degree of connectivity among communities is critical for the placement of marine protected areas and effective management of coral reefs (Underwood et al. 2009). Patterns of reproduction in coral communities are associated with either the spawning of eggs and sperm for external fertilization, or the internal brooding of larvae (Harrison and Wallace 1990). Mass-coral spawning involves the synchronous release of eggs and sperm by multiple species of corals in a single night each year, and has been documented around the world (Guest 2004; Penland et al. 2004; Guest et al. 2005; Carroll et al. 2006). Although a majority of coral species mass-spawn, some abundant and functionally important species brood and release fully developed planulae larvae following internal fertilisation and embryogenesis (Harrison et al. 1984b; Richmond and Hunter 1990b). Patterns of reproduction in coral communities vary according to their species composition, location and prevailing environmental conditions (Baird et al. 2009).

The timing of mass spawning events is strongly influenced by lunar and tidal cycles (Babcock et al. 1986b). Most commonly, multi-specific mass spawning events occur during neap tides, and within a number of days after the full moon. The primary factors are likely to be changes in temperature, insolation and hydrodynamic regimes (Oliver et al. 1988). It is expected that environmental cues work at increasingly finer scales to determine the month, the night and the time of spawning (Babcock et al. 1986b).

The timing and length of the spawning season shows considerable regional variability (van Woesik 2010). For instance, corals in the Galapagos Islands spawn in between February and October over a period of 8-9 months (Glynn et al. 1991; Glynn et al. 1994; Glynn et al. 1996), in Kenya there is a 7-month spawning period from October to April (Mangubhai and Harrison 2008), and spawning on the Great Barrier Reef occurs over two months in the austral spring (Harrison et al. 1984b; Willis 1985;

Babcock et al. 1986b). A high degree of synchronicity was found in corals of the Solomon Islands, Papua New Guinea, Singapore, Palau, the Philippines, the Red Sea and the Caribbean, but the spawning seasons were generally longer than on the GBR (Oliver et al. 1988; Szmant 1991; Schlesinger et al. 1998; Baird et al. 2001; Guest et al. 2002; Penland et al. 2004; Vicentuan et al. 2008). On northwest Australian reefs, mass spawning was originally reported a few nights after a full moon in autumn (March/April) (Harrison and Wallace 1990).

Northwestern Australian coral reefs exist in two broad zones: as an offshore system of discontinuous reefs along the edge of the continental shelf and as a coastal system adjacent to the mainland (Underwood 2007). Mass coral spawning in autumn has been documented for both offshore and coastal reefs, as far south as the Abrolhos Islands (Babcock et al. 1994), through Ningaloo (Simpson 1991b), and as far north as Scott Reef (Gilmour et al. 2009a). At Scott Reef, two distinct periods of gamete maturation and multi-specific spawning were recorded, during spring and autumn, unlike most other reefs around Australia for which a single spawning season is known (Gilmour et al. 2009a). spring spawning has now been documented on reefs at Barrow Island, the Dampier Archipelago and the Rowley Shoals (Rosser and Gilmour 2008; Gilmour et al. 2009a). It appears that the primary spawning event, in which the majority of species participate, occurs in autumn, and that a smaller proportion of colonies and species spawn in spring. This phenomenon of a primary and secondary spawning event has now been documented at multiple reefs around the world, and the magnitude of the secondary spawning event may vary among years (Wallace 1988; Baird et al. 2002; Wolstenholme 2004; Guest et al. 2005; Carroll et al. 2006; Mangubhai and Harrison 2006; Nozawa et al. 2006). The tendency for 'split-spawning', where the mass spawning event is split over two consecutive months, has also been documented on the Great Barrier Reef (Willis 1985; Simpson 1991).

Brooding species are generally common and functionally important, as competent larvae have the potential to settle quickly within the natal community and enhance recovery after disturbance (Richmond 1987; Ayre and Hughes 2000b; Fan et al. 2006). Compared to 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 (Fadlallah and Pearse 1982; Harrison and Wallace 1990). Some brooding corals may also spawn, as was observed in *Pocillopora damicornis* on reefs around Rottnest Island, and oogenesis may not be linked directly with planulation (Stoddart and Black 1985). 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.

This study aims to establish the proportion of species and colonies participating in spawning events during spring and autumn each year at Scott Reef, and whether the phenomenon is a consequence of colonies within a species spawning at different times of the year or of some colonies spawning twice a year.

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 Scott 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.

Reproductive surveys

Replicate colonies of the dominant spawning and brooding corals were sampled from replicatelocations several weeks (2 to 5 weeks) before the predicted dates of mass spawning in autumn (March/April) and spring (October/November), in 2008, 2009 and 2010 (spring only). 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.

Species selected for Tagged Reproduction study included those of the greatest habitat cover or predicted to spawn only in spring or in both seasons. Tagged corals were set up and sampled in October 2008 and then every autumn and spring until 2010, with 149 initial colonies tagged and a further 95 colonies tagged during subsequent field trips.

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. 1984b; Guest et al. 2005), according to the following criteria:

Score 1	Large pigmented (red or pink) eggs were clearly visible within polyps, indicating that colonies will spawn following the next full moon, and within one month;
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.

In autumn 2010 there was an exception to the collection of samples prior to spawning as the field trip occurred later than expected and only one location, SL1, was sampled prior to spawning. The remaining sites were sampled after the initial spawning event had occurred.

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 1988).

For the brooding corals *Isopora brueggemanni* and *Seriatopora hystrix* and *Pocillopora verrucosa*, and the spawning corals 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) and Vargas-Angel et al. (2006).

Significance of reproductive output

The percentage reproductive output for communities during different months of the year at Scott Reef depends on both the proportion of coral species reproducing that month and their relative cover within the community. Reproductive output includes the spawning of eggs, or the release of brooded larvae. Community is defined by the groups of corals that contribute to 80% of the total hard coral cover, based on surveys of communities at long-term monitoring locations during 2008. The percentage of reproductive output (spawning eggs or larvae) for different months of the year is a combination of the proportion of coral cover and proportion of corals reproducing each month. Therefore the reproductive output for each coral category (i), month (j) and reef location (k) was calculated using:

$$\text{Reproductive output}_{ijk} = \text{proportion of coral cover}_{ik} \times \text{proportion reproducing}_{ij}$$

The proportion of coral cover for each coral category is the sum cover for each coral category at each reef location divided by the sum cover over all categories for each reef location, site and transect.

From this the community reproductive output was calculated. The community of spawners, brooders and combined spawners and brooders were calculated for each month (j) and reef location (k) using:

$$\text{Community reproductive output}_{jkl} = \text{reproductive output coral category 1}_{jk} + \text{reproductive output coral category 2}_{jk} \ldots + \text{reproductive output coral category N}_{jk}$$

where l is the spawner community, brooder community or combined spawners and brooder community.

A confidence of the spawning month/s for each coral category was obtained from an expert rating their confidence in the predicted period of reproductive output from low, medium to high. These percent confidences were used as weights to calculate the confidence bounds of the reproductive output categories and communities (O'Leary et al. 2009). Specifically, for each coral category:

$$\text{Confidence Bounds} = \text{reproductive output}_{ijk} \pm (\text{reproductive output}_{ijk} \times \text{percent confidence}_{ij})$$

For example, proportion *Isopora brueggemanni* at SL2 reproducing in February is 0.075, its proportion cover of hard coral is 0.063, and thus the reproductive output is 0.004725. The experts' confidence for this spawning month is medium (percent confidence is 80%). Therefore the lower confidence bound of the reproductive output for this species in February is $0.004725 \times 0.8 = 0.00378$ and the upper confidence is $= 0.004725 \times (1+(1-0.8)) = 0.00567$. From this model, the predicted proportions of reproductive output over the months of the year were plotted, including lines for the lower and upper confidence bound. All analyses were conducted in R (R Development Core Team 2009).

Results and Discussion

Patterns of reproduction in spawning and brooding corals

Spawning corals
Of 68 species sampled at Scott Reef during one or more periods, replicate colonies of 40 (59%) spawn in autumn, 11 (16%) spawn in spring, and 17 (25%) spawn in both autumn and spring (Table 9.1). Considering only the 24 species with at least 20 replicate colonies overall and at least 10 colonies in each season, 12 (50%) spawned only in autumn, 2 (8%) only in spring and 10 (42%) in both seasons. All the species that spawn twice a year had a larger proportion of colonies spawning in autumn than in spring, providing further confirmation that the main reproductive period is during autumn (Table 9.2). However, there were some species with a high proportion of colonies spawning during spring. Of species sampled with sufficient replication (>10 colonies) that spawn during both autumn and spring, a significant percentage (30-50%) of three different *Acropora* species spawned in spring (*A. hyacinthus, A. florida* and *A. tenuis*).

Recent evidence suggests that there are 10 species that spawn exclusively in spring, but sufficient replication to confirm this was adequate for only two species, *A. cytherea* and *A. millepora*. In *A. cytherea*, 100% of the colonies that had eggs were inferred to spawn in spring (overall N=45). In *A. millepora*, 100% of the 38 colonies with eggs were inferred to spawn in spring, with none displaying eggs in autumn (overall N=136). In addition to species 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 *Porites 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 9.5).

Fifteen species were tagged to ascertain whether their times of spawning were consistent among years and whether individual colonies were able to reproduce twice a year, but almost all spawned consistently either in autumn or spring (Table 9.3). There were however some exceptions to this pattern.

- One *A. millepora* colony apparently spawned twice in one year. While *in situ* examination revealed pigmented eggs in October 2008 and 2009 and lab analysis found large eggs (600-700um) in March 2009 (600-700).
- A few colonies apparently switched their season of reproduction between years, having small unpigmented eggs at the expected times of spawning. This may reflect a number of potential scenarios: 1) the cycles of oogenesis at times other than when the majority of colonies reproduce are slow, either resulting in smaller than expected and unpigmented eggs being spawned; 2) eggs may mature and be spawned at a later month; 3) they may be reabsorbed by the colony; or 4) the eggs may remain in the colony and not mature until the next season.
- Three *A. spicifera* colonies had large eggs in October 2008, as well as March 2009 and 2010, suggesting two spawning events within a year. However, the eggs in October 2009 were small and they appeared absent *in situ*. In random sampling of *A. spicifera* prior to mass bleaching at Scott Reef in 1998, more than half of the colonies during any one year had eggs in both autumn and spring (Gilmour et al. 2009a), suggesting the potential for colonies to have two overlapping oogenic cycles within a single year (Stobart et al. 1992; Mangubhai and Harrison 2007). Since 1998, there have been no *A. spicifera* colonies, apart from the three exceptions, that were reproducing in spring. This leads to questions about the possible relationship between gametogenesis, reproductive timing, and different clades of zooxanthellae. Whether there is a link between zooxanthellae and reproduction, and how

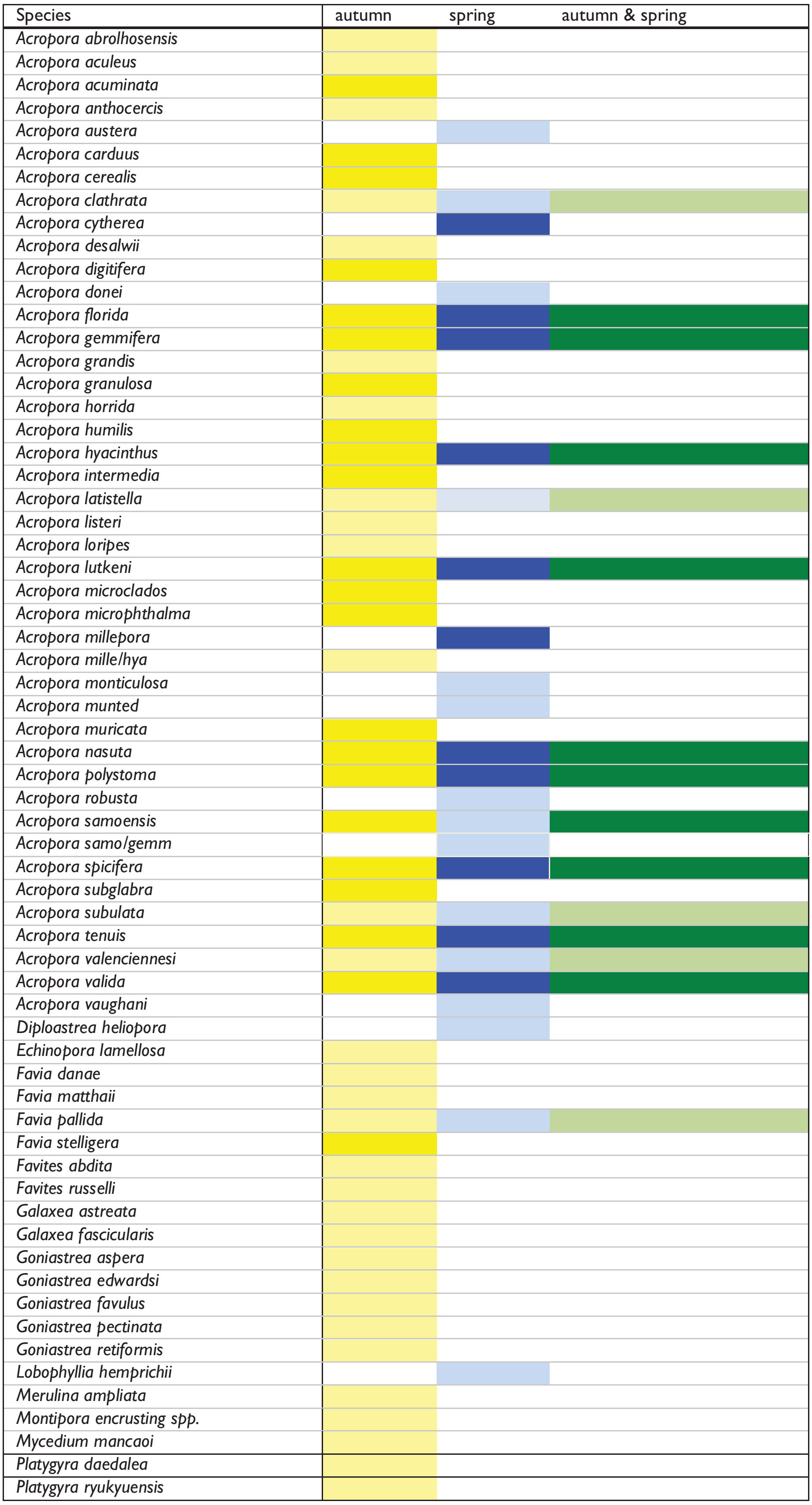
this expresses itself in colonies with clades of zooxanthellae that are more or less resistant to temperature stress, remains to be investigated.

- One *A. florida* colony appeared to spawn in spring, with pigmented eggs in October 2008 and 2009, and no eggs in March 2010. However, unpigmented eggs were visible *in situ* in March 2009, suggesting that this colony may also have spawned in April 2009. Additionally, the pigmented eggs in October 2008 were relatively small, compared to other colonies of the same species. Overall, this species had smaller eggs when spawning in spring than in autumn, and a number of colonies that appeared not to be reproducing during the study period (Table 9.4).
- Most *A. tenuis* colonies also spawned consistently either in autumn or in spring, but three colonies had egg scores and sizes that suggested spawning twice in a year, or switching between seasons, with patterns similar to those seen in *A. spicifera* (Table 9.4).

For many species, the spawning at different times by individual colonies may be a mechanism to enhance genetic diversity. 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).

Within-species growth form differences may affect individual colonies' reproductive timing. For instance, *A. florida* has a predominantly branching morphology with robust branchlets, and though this species spawns in both autumn and spring, individual colony timing appears consistent. Plate-forming species such as *A. millepora*, *A. mille/hya*, *A. samoensis* and *A. samo/gemm* had colonies with less consistent patterns in terms of spawning season. While it has previously been found that growth form in *Montipora* spp. affected fecundity and egg size, it did not appear to affect the seasonality of spawning (Stobart et al. 1992).

Colonies of the massive *Porites* spp. apparently spawned through spring to winter months. Massive *Porites* spp. had planulae and Stage IV eggs in both autumn and spring. This species has 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 1985; Babcock et al. 1986b). 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).



Species	autumn	spring	autumn & spring
Acropora abrolhosensis	🟨		
Acropora aculeus	🟨		
Acropora acuminata	🟨		
Acropora anthocercis	🟨		
Acropora austera		🟦	
Acropora carduus	🟨		
Acropora cerealis	🟨		
Acropora clathrata	🟨	🟦	🟩
Acropora cytherea		🟦	
Acropora desalwii	🟨		
Acropora digitifera	🟨		
Acropora donei		🟦	
Acropora florida	🟨	🟦	🟩
Acropora gemmifera	🟨	🟦	🟩
Acropora grandis	🟨		
Acropora granulosa	🟨		
Acropora horrida	🟨		
Acropora humilis	🟨		
Acropora hyacinthus	🟨	🟦	🟩
Acropora intermedia	🟨		
Acropora latistella	🟨	🟦	🟩
Acropora listeri	🟨		
Acropora loripes	🟨		
Acropora lutkeni	🟨	🟦	🟩
Acropora microclados	🟨		
Acropora microphthalma	🟨		
Acropora millepora		🟦	
Acropora mille/hya	🟨		
Acropora monticulosa		🟦	
Acropora munted		🟦	
Acropora muricata	🟨		
Acropora nasuta	🟨	🟦	🟩
Acropora polystoma	🟨	🟦	🟩
Acropora robusta		🟦	
Acropora samoensis	🟨	🟦	🟩
Acropora samo/gemm		🟦	
Acropora spicifera	🟨	🟦	🟩
Acropora subglabra	🟨		
Acropora subulata	🟨	🟦	🟩
Acropora tenuis	🟨	🟦	🟩
Acropora valenciennesi	🟨	🟦	🟩
Acropora valida	🟨	🟦	🟩
Acropora vaughani		🟦	
Diploastrea heliopora		🟦	
Echinopora lamellosa	🟨		
Favia danae	🟨		
Favia matthaii	🟨		
Favia pallida	🟨	🟦	🟩
Favia stelligera	🟨		
Favites abdita	🟨		
Favites russelli	🟨		
Galaxea astreata	🟨		
Galaxea fascicularis	🟨		
Goniastrea aspera	🟨		
Goniastrea edwardsi	🟨		
Goniastrea favulus	🟨		
Goniastrea pectinata	🟨		
Goniastrea retiformis	🟨		
Lobophyllia hemprichii		🟦	
Merulina ampliata	🟨		
Montipora encrusting spp.	🟨		
Mycedium mancaoi	🟨		
Platygyra daedalea	🟨		
Platygyra ryukyuensis	🟨		

Table 9.1 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 from 2007-2010. Lighter colours are used to demarcate species where less than 20 colonies were sampled for the duration of the study. Where the colour is lighter for only one of the two seasons shown, less than 10 colonies were sampled during that season.

Table 9.2 Species spawning during both autumn and spring, from autumn 2008 to autumn 2010. Where there were more than 20 colonies sampled overall and more than 10 sampled in each season. N is the total number of colonies for which spawning was inferred.

Species	N	Autumn N	Spring N	Autumn %	Spring %
Acropora florida	28	17	11	61	39
Acropora gemmifera	83	65	18	78	22
Acropora hyacinthus	52	40	12	77	23
Acropora lutkeni	26	13	13	50	50
Acropora nasuta	68	66	2	97	3
Acropora polystoma	54	50	4	93	7
Acropora spicifera	220	213	7	97	3
Acropora tenuis	126	77	49	61	39
Acropora valida	36	34	2	94	5

Table 9.3 Summary of colonies sampled prior to the mass-spawning events in spring 2008 and 2009 and autumn 2009 and 2010 at Scott Reef, WA. The participation by species in one (Autumn, Spring) or both (Autumn and Spring) of the mass-spawning events at Scott Reef each year is indicated by the column Spawning season. The total number of tagged colonies is presented for each species, as well as the number and % of colonies with inferred spawning in spring, autumn and both. A number of colonies of most species showed inconclusive evidence; some of these may not have been reproducing during the study period. For each spawning season, colonies are identified as spawning consistently in either autumn or spring, or potentially switching between seasons, based on *in situ* egg scores and laboratory measurements of the eggs. For those species reproducing in both seasons, the average egg size of colonies spawning in that season are presented where possible. Species where egg size was not measured are marked as 'unknown'.

Spawning season	Species	Total	Spring		Autumn		Both		Inconclusive		Colonies	Egg size
			N	%	N	%	N	%	N	%		
Autumn	***Acropora digitifera***	13	0	0	12	92.3	0	0	2	15.4	Consistent	Consistent
	Acropora humilis	21	0	0	18	85.7	0	0	3	14.3	Consistent	Consistent
	Acropora milli/hya	4	0	0	3	75	0	0	1	25	Consistent	Consistent
	Acropora muricata	10	0	0	3	30	0	0	7	70	Consistent	Consistent
	Acropora polystoma	8	0	0	7	87.5	0	0	0	0	Consistent	Consistent
	Acropora spicifera	27	0	0	27	100	1	3.7	0	0	Switch (?)	Consistent
Spring	***Acropora cytherea***	7	6	85.7	0	0	0	0	0	0	Consistent	Consistent
	Acropora millepora	16	15	93.7	0	0	0	0	1	6.25	Consistent	Consistent
	Acropora samo/gemm	12	9	75	0	0	0	0	3	25	Consistent	Consistent
Autumn and Spring	***Acropora florida***	25	4	16	4	16	0	0	16	64	Consistent	Larger in autumn
	Acropora gemmifera	9	2	22.2	3	33.3	0	0	1	11.1	Consistent	Larger in spring
	Acropora hyacinthus	13	8	61.5	5	38.4	0	0	0	0	Consistent	Consistent
	Acropora microclados	13	6	46.1	3	23.1	0	0	4	30.8	Consistent	Unknown
	Acropora samoensis	5	2	40	3	60	0	0	0	0	Consistent	Unknown
	Acropora tenuis	33	10	30.3	19	57.6	3	9.1	6	18.2	Switch (?)	Larger in autumn

Table 9.4 Average, modal and range of egg sizes for species spawning in autumn and/or spring, between autumn 2008 to autumn 2010. The range of egg sizes is given for the largest 60% of the eggs spawned in each season.

Species	Autumn egg size		Spring egg size	
	Mean (+/- 1SE)	Range	Mean (+/- 1SE)	Range
Acropora milli/hya	692 +/- 107	600-800		
Acropora muricata	527 +/- 67	400-600		
Acropora spicifera	575 +/- 43	400-700		
Acropora millepora			578 +/- 66	500-800
Acropora florida	679 +/- 89	500-800	561 +/- 138	500-800
Acropora gemmifera	572 +/- 79	500-700	779 +/- 116	600-900
Acropora hyacinthus	666 +/- 78	500-800	662 +/- 66	500-800
Acropora samoensis	606 +/- 143	400-700		
Acropora tenuis	617 +/- 84	400-700	518 +/- 116	300-900

Of the brooding corals that have been sampled, histological analysis has been conducted on *Isopora brueggemanni, Seriatopora hystrix* and *Pocillopora verrucosa*. For all three species, samples contained eggs and sperm in most developmental stages during each month of sampling (Table 9.5). Planulae were present in *Isopora brueggemanni* and *Seriatopora hystrix* during both the autumn and spring sampling, but not in either season in *Pocillopora verrucosa*. 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. 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 and Pearse 1982; Harrison and Wallace 1990; Richmond and Hunter 1990; Tanner 1996).

Table 9.5 Total number of colonies containing different stages of egg and testes development of in massive *Porites* spp. and the brooding corals *Isopora brueggemanni, Seriatopora hystrix* and *Pocillopora verrucosa.* Development stages were derived from histological analysis and samples collected between autumn 2008 and autumn 2010.

Season	Species	*N*	Planulae	Egg Stage				Testes Stage			
				I	II	III	IV	I	II	III	IV
Autumn	*Porites* massive spp.	53	1	7	2	2	0	8	4	1	0
	Isopora brueggemanni	62	7	18	18	20	5	21	20	12	2
	Seriatopora hystrix	71	9	19	27	29	11	14	14	9	0
	Pocillopora verrucosa	35	0	2	1	1	1	0	0	1	2
Spring	*Porites* massive spp.	25	2	5	13	4	3	3	4	2	1
	Isopora brueggemanni	34	7	7	11	14	6	2	7	6	2
	Seriatopora hystrix	39	4	7	15	12	9	2	0	2	1
	Pocillopora verrucosa	34	0	11	14	7	1	2	4	7	4

Significance of reproductive periods

The percentage reproductive output during different months of the year at Scott Reef depends on both the proportion of coral species reproducing that month and their relative cover within the community. However, quantifying the reproductive state of a random sample of colonies within the community will not accurately reflect their contribution to percentage cover. Thus, estimates of reproductive output by the community will be biased by non-random sampling, or insufficient sample size. For example, in a community consisting of two species, if half the colonies in a random sample are of species A and reproduce exclusively in October, and the other half of the colonies are of species B and reproduce exclusively in March, then it may be concluded that reproductive output is split evenly (50:50) between October and March. However, if species A contributes only 20% to community cover, then the reproductive output for the community is in fact 20% during October and 80% in March. In this hypothetical example, both species reproduce exclusively during a single month, whereas communities characteristically have corals that spawn during two or more months a year, and brooding corals that release larvae over several months within a year. Additionally, coral communities tend to have tens of species that make significant contributions to total cover. These more complex patterns of reproduction, the number of species that characterise a community, and the patchy distribution of species, means random quantification of reproductive state may not reflect community reproductive output. Consequently, it is useful to define the groups of species that characterise a community, to sample these species with appropriate replication, and to then combine their contribution to community cover with their reproductive state to formally quantify community reproductive output during different times of the year.

Formally quantifying the proportion reproductive output during different times of the year enables some measure of which periods are most likely to contribute to recruitment and maintenance of the community, and which require protection (Figure 9.1). For spawning corals at Scott Reef, the percentage of reproductive output was roughly 80% in autumn (March/April) and 20% in spring (October/November), with very few corals spawning during other months. For the brooding corals, the percentage reproductive output is roughly 55% from November to May, and 45% at other times of the year. Considering the entire community at Scott Reef (spawners and brooders) and the months of spawning, roughly 40% of reproductive output occurs in March, 16% in October and 44% during other months (mostly April or November).

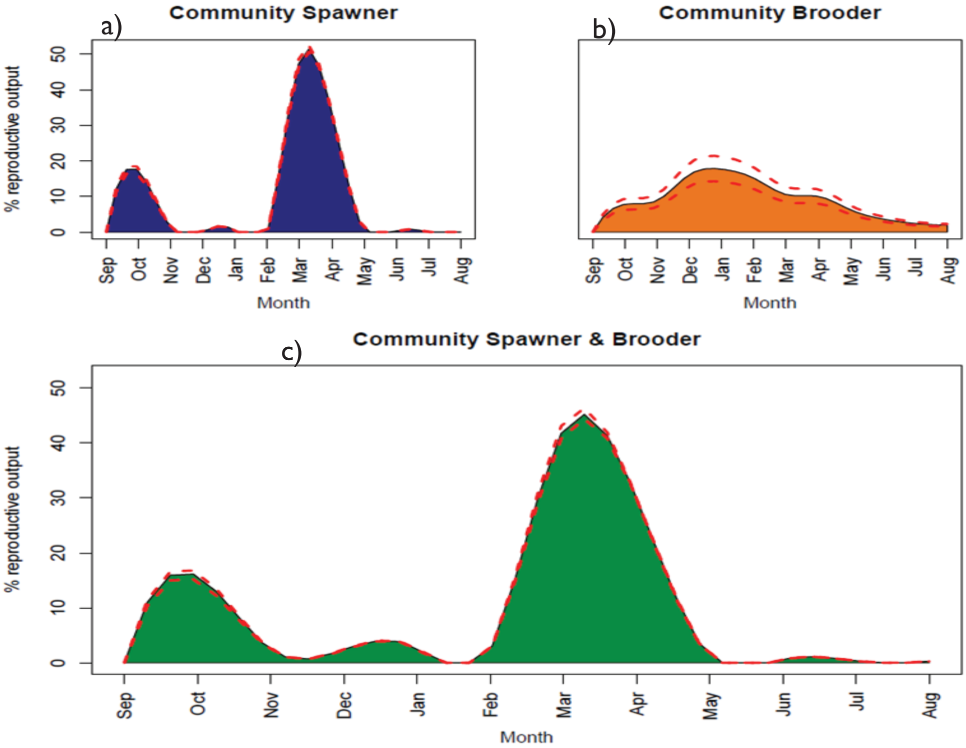


Figure 9.1 Percentage of reproductive output (± 95% C.I.) by coral communities at Scott Reef. Reproductive output is adjusted for proportion of corals reproducing and their relative cover within communities for the community of a) spawning corals spawning corals, b) brooding corals, and c) spawning and brooding corals combined. Reproductive data are summarised for colonies sampled from autumn 2008 and autumn 2010.

The proportion reproductive output during different months of the year also varies among communities with different species abundances. For example, communities with an abundance of species that spawn during autumn will have a much higher reproductive output during March than communities with an abundance of brooding corals that release planulae over several months a year from spring to winter. Variation in reproductive output among locations at Scott Reef with different community structures was investigated for locations SL1 and SL2 (Figure 9.2). However, despite the differences in relative abundance of some common corals between the communities, there was little difference in reproductive output during any one month. For communities at both SL1 and SL2, the majority of the reproductive output occurred during the autumn spawning in March (around 40%) or April (around 30%), followed by the spring spawning in October (15-20%)(Figure 9.3). Indeed, there was less than 5% difference in reproductive output at location SL1 and SL2 during any one month (Figure 9.4).

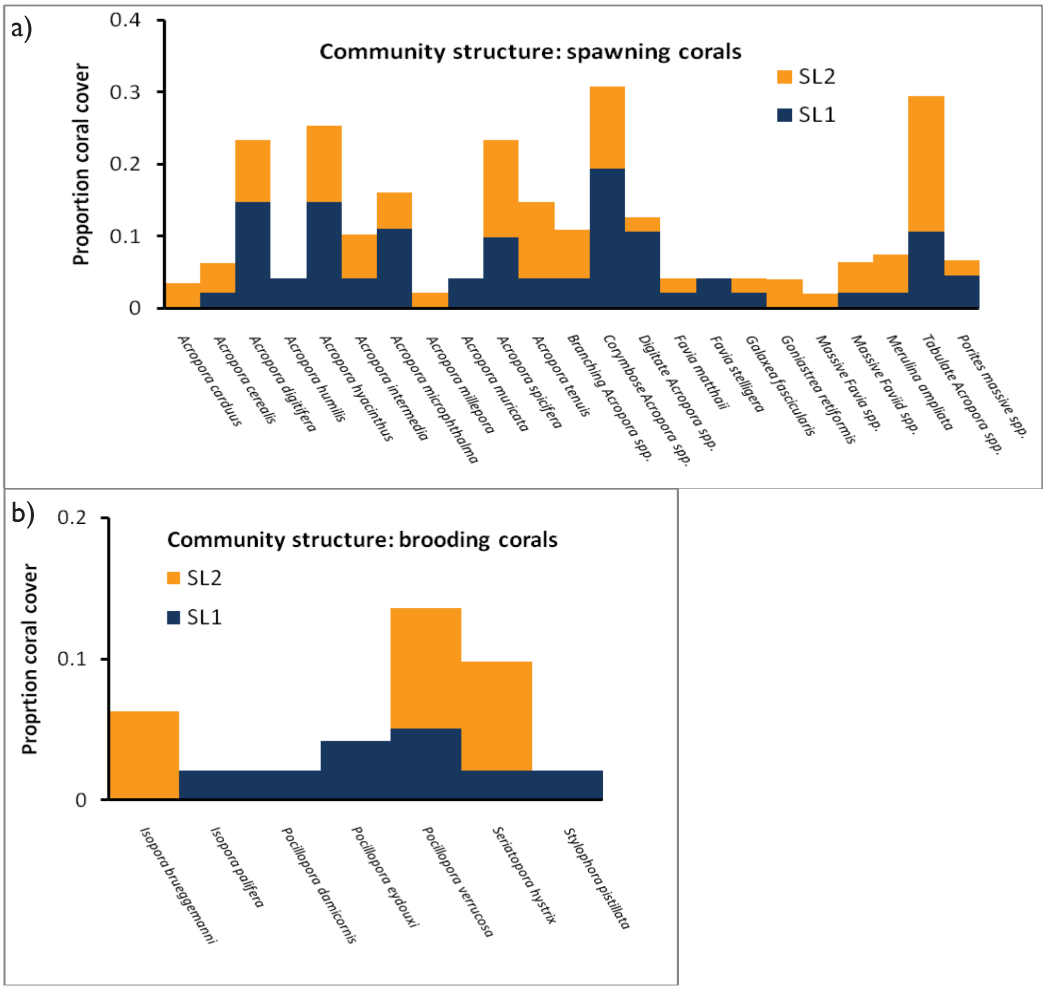


Figure 9.2. Differences in structure of communities Scott Reef. Proportion of different groups of a) spawning corals and b) brooding corals at locations SL1 and SL2. Percentage cover data are for 2008. See Location Map Figure 1.2.1.

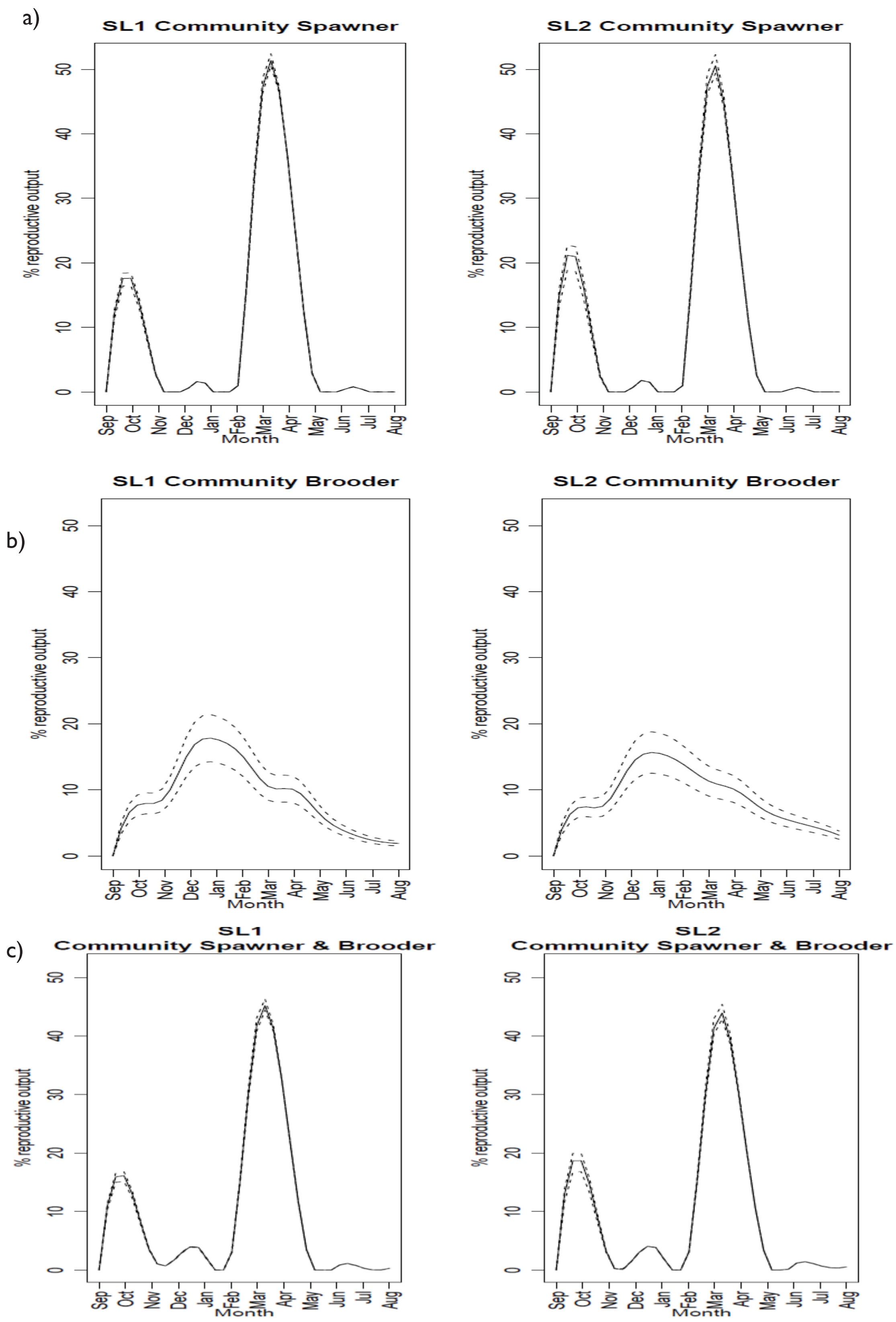


Figure 9.3. Percentage reproductive output (± 95% C.I.) of coral communities at Scott Reef. Percentage reproductive output for each month for the community of a) spawning corals, b) brooding corals, and c) spawning and brooding corals, at locations SL1 and SL2. Reproductive data are summarised for colonies sampled from autumn 2008 and autumn 2010.

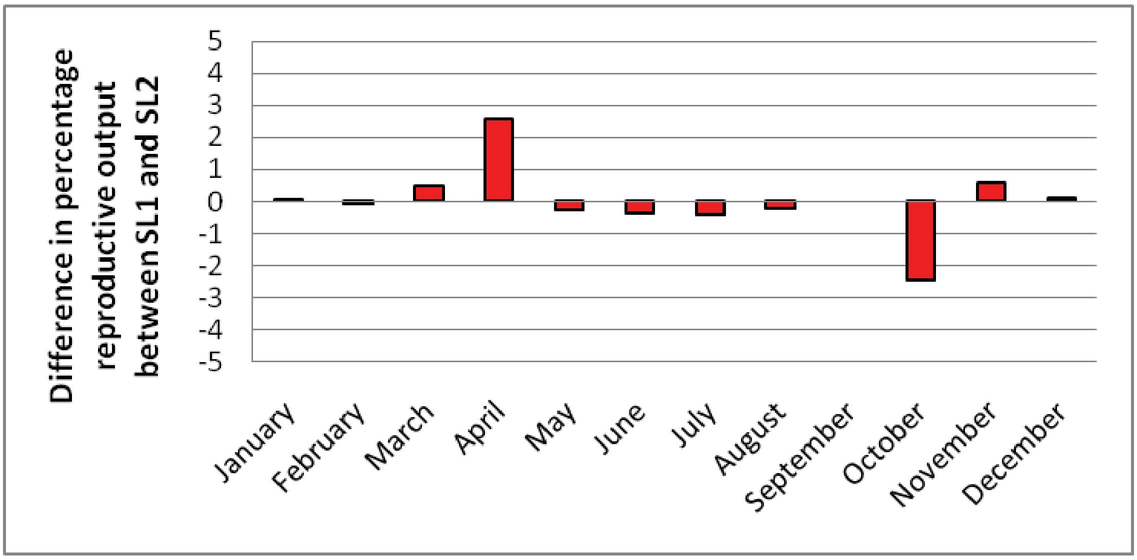


Figure 9.4 Difference in percentage reproductive output among communities. Percentage reproductive output each month for community at Location SL1 minus that for the community at Location SL2. Reproductive data are summarised for colonies sampled from autumn 2008 and autumn 2010.

Conclusions:

Multiple periods of reproduction by coral communities at Scott Reef

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. 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. 2009a). Although there is only limited sampling over this latitudinal gradient, current evidence suggests a breakdown in participation in the spring spawning with increasing latitude; there is minimal participation at Barrow Island and no evidence of participation at Ningaloo Reef (Rosser 2005), the Houtman Abrolhos Islands (Babcock et al. 1994) or Rottnest Island (Crane 1999). Biannual spawning has been documented on several other reefs around the world, but the timing on north-west Australian reefs is most similar to that on reefs off Singapore (Oliver et al. 1988; Guest et al. 2005; Mangubhai and Harrison 2008).

Patterns of biannual spawning by populations of the same species are either a consequence of individual colonies spawning at different times of the year, or some individuals spawning twice a year. Individual colonies of biannual spawners at Scott Reef appear to be reproducing consistently either in autumn or spring, with few exceptions. 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).

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.

10. PATTERNS OF RECRUITMENT FOR CORAL COMMUNITIES AT SCOTT REEF

Summary

Larval supply of scleractinian corals at Scott Reef following the autumn mass spawning events was quantified from 1996 to 2010. Settlement plates were deployed out at six locations on Scott Reef during the spawning event, two years before, and up to twelve years after the mass bleaching event in 1998, which caused a decrease in coral cover of between 75 and 90% across the entire reef system. Following the bleaching, coral settlement was drastically reduced at all locations, with observed settlement rates over the following four years only 3% of that seen in pre-bleaching years. Small increases in recruitment occurred over the following eight years, up to 15% of pre-bleaching levels in 2006. Recruitment rates reached pre-bleaching levels in 2008, almost ten years after the bleaching event. In 2008, 2009 and 2010 recruitment rates were above or similar to that seen in pre-bleaching years. Acropora *was the dominant group making up 86% of recruits over all years. Recruitment rates were spatially variable at the scale of locations, with a consistent pattern of relatively high recruitment at SL1 and SS2 and low recruitment at SL4 and SS1. These data support the premise that as an isolated reef system, Scott Reef depends largely on self-seeding, and therefore recruitment rates are highly vulnerable to large scale disturbance of the local adult community.*

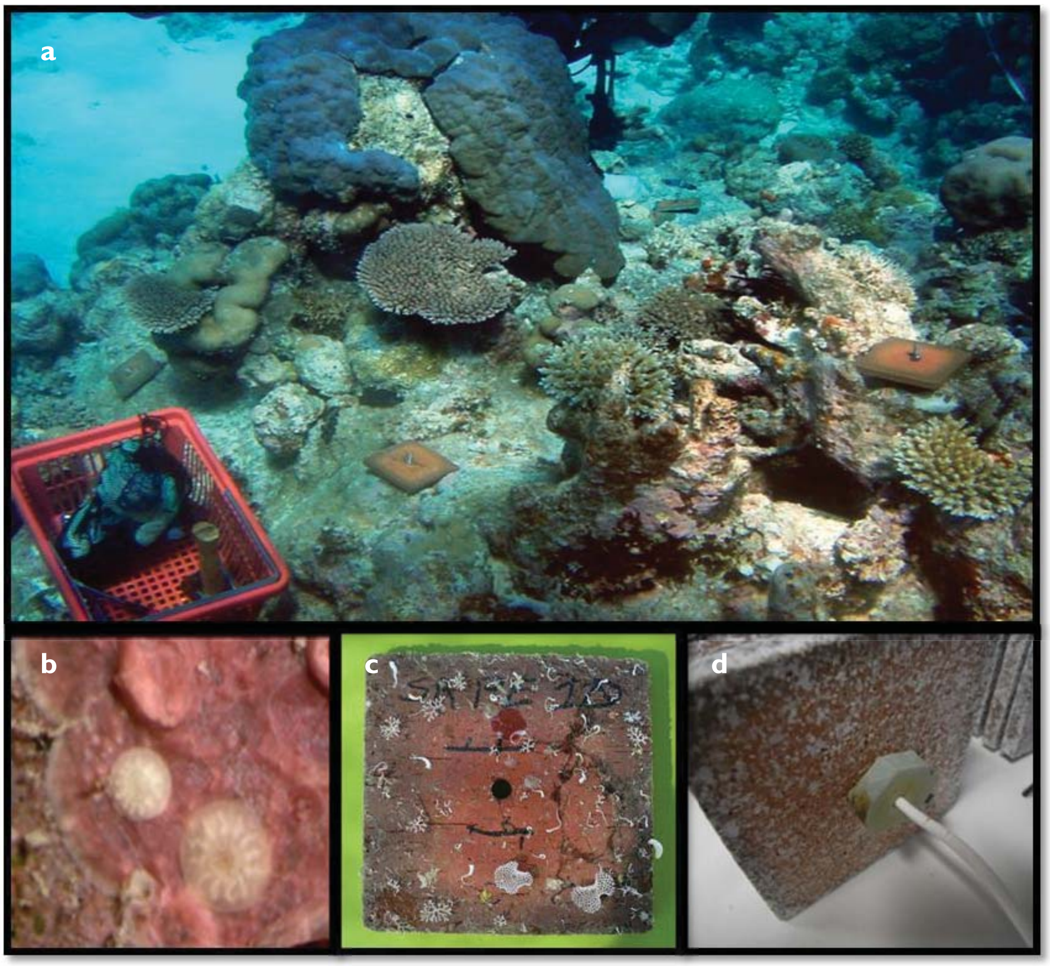


Figure 10.1 a) Coral settlement plates deployed on the reef slope. b) Live coral spat. c) Settlement plates removed from the water. d) Bleached settlement plates prepared for census.

Introduction

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

Effective management of coral reefs requires an understanding of how the scale and severity of different disturbances affect the demographic processes that underlie replenishment and recovery, such as the supply of sexual recruits. Populations of many species on coral reefs may be self-replenishing, as indicated by local stock-recruitment relationships (Hughes et al. 2000; Mora and Sale 2002) and growing evidence of short-distance dispersal of larvae (Ayre and Hughes 2000; Whitaker 2004; Nishikawa and Sakai 2005). As a consequence, replenishment of a reef system following locally intense disturbances may be seriously hindered by the lack of local brood-stock to supply new recruits. This is particularly important for reef systems that through isolation by distance or flow of currents from neighbouring reefs, receive little larval supply from outside. Predictions of coral community resilience and recovery require our understanding of how local disturbances affect the supply and recruitment of larvae.

Here we investigate how a severe mortality event affected the larval supply and recruitment of scleractinian corals at an isolated reef system. Rates of sexual recruitment were quantified from two years before and up to 12 years following a catastrophic thermal bleaching event that killed more than 75% of corals across the entire reef system. Our results show that to understand the resilience of reefs to disturbances requires the quantification of important demographic parameters, such as recruitment, in addition to the changes in coral cover and community structure.

Methods

The rate of coral recruitment was quantified during ten mass spawning events in autumn between 1996 and 2010 (years 1996 to 1999, 2002, 2003, 2006, 2008, 2009 and 2010) at the reef-slope monitoring locations. At each of five locations at north and south Scott Reef, six terracotta recruitment plates (110mm x 110mm x 10mm) were deployed at each of three sites separated by 50m on the 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) four weeks (± 4 days) prior to the predicted mass coral spawning in autumn and collected eight weeks later (± 5 days) (Figure 10.1). After collection, the recruitment plates were bleached and the coral recruits identified to one of four taxonomic groups (Family *Acroporidae*, *Pocilloporidae*, Poritidae or Others) according to (Babcock et al. 2003), using a dissecting microscope (Figure 10.2). In 2010 the autumn mass spawning was split between two spawning events. At Location SL1, one set of tiles captured the first spawning in March, and another replicate set of tiles was laid to capture the spawning in April. In order to compare the 2010 spawning effort to previous years, the recruit counts at locations where only one event was captured were standardised according to the ratio at SL1 between the second spawning event, and the two events combined.

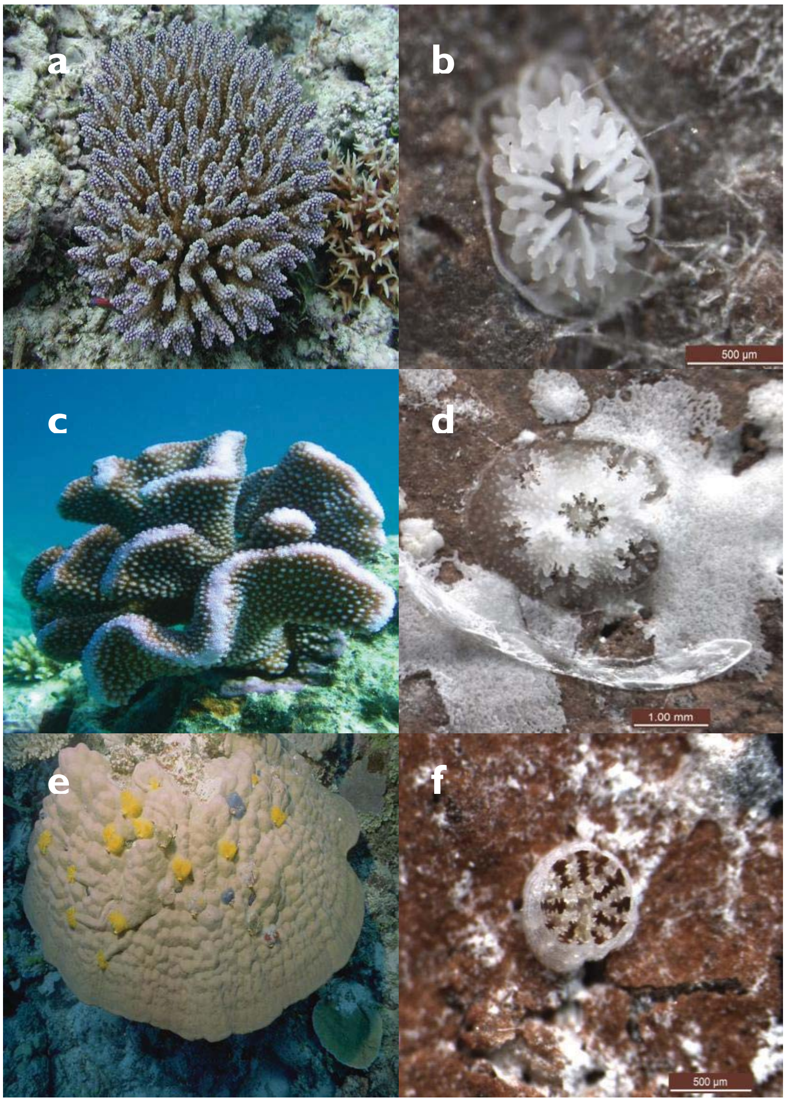


Figure 10.2 (a) Adult *Acropora* colony; (b) *Acropora* recruit; (c) *Pocillopora* adult colony; (d) *Pocillopora* recruit; (e) *Porites* adult colony; (f) *Porites* recruit.

Results

As a result of the 1998 bleaching event, all hard corals we observed to a depth of 20 m had expelled their zooxanthallae and bleached. Within a year of the bleaching, coral cover decreased by between 74 to 89% across the entire Scott Reef system. Following this mass mortality of hard corals, a dramatic reduction in recruitment was seen at all the reef slope locations studied across the Scott Reef system. The observed recruitment rate decreased by 97% over all locations, with mean recruits plate^{-1} year $^{-1}$ falling from 39.1 (±12.6 SE) in the pre-bleaching years, to 1.3 (±0.2 SE) over the following four years (Figure 10.3). In 1999 and 2002, there was almost complete recruitment failure at Scott Reef, with only 0.25 (± 0.1 SE) coral recruits plate^{-1} yr^{-1} averaged across all monitoring locations. Recruitment levels remained low for eight years following the bleaching, with average recruit numbers still at only 15% of pre-bleaching levels in 2006. In 2008, 2009 and 2010 however, recruit numbers were similar or higher than that seen in 1996 and 1997 at the reef slope locations studied, with recruits tile^{-1} year^{-1} at 70.42 (±14.9 SE), 60.05 (±6.3 SE), and 44.02 (± 5.5 SE) respectively (Figure 10.3).

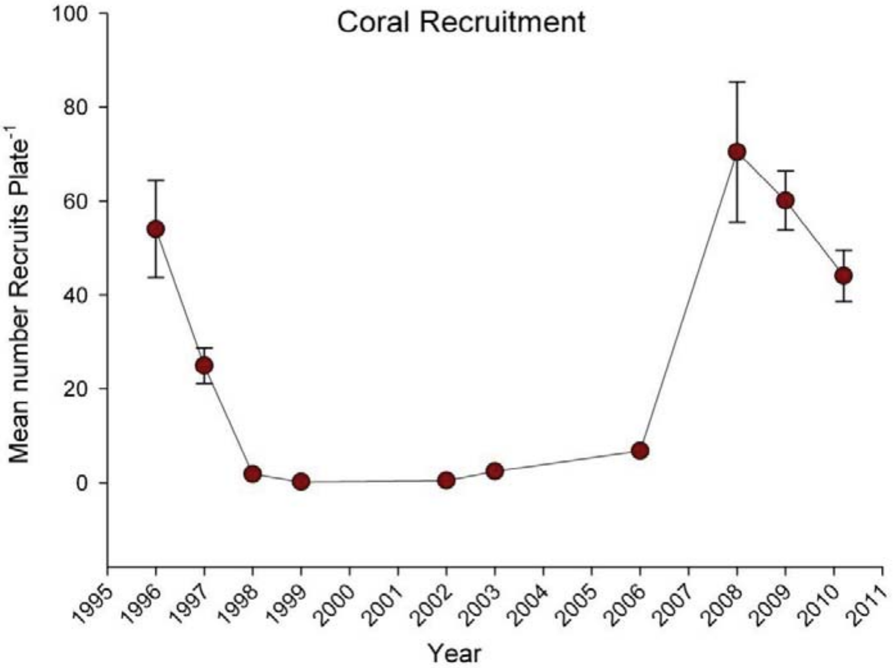


Figure 10.3 Mean number of Coral Recruits per Recruitment Plate per Year-1 (± S.E) at Scott Reef across all monitoring locations.

Variation between locations:

Recruitment was highly variable between locations at Scott Reef. In years of good recruitment, SL1 and SS2 between them account for between 59 - 92% of the total recruits captured on the tiles each year (early post bleaching years are excluded as total numbers were too low) (Figure 10.4). SL1 in particular had massive spikes in recruit numbers in 1996, 1997 and 2008 (Figure 10.5), with mean recruits plate^{-1} 255.5 (25.2 SE), 82.77 (14.17 SE) and 354.33 (51.46 SE) respectively (Figure 10.6), up to tenfold higher than the other locations in those years (Figure 10.4). Other locations such as SS1 and SL4 consistently received a low proportion of the recruits, together receiving between 4-12% of total recruit numbers each year.

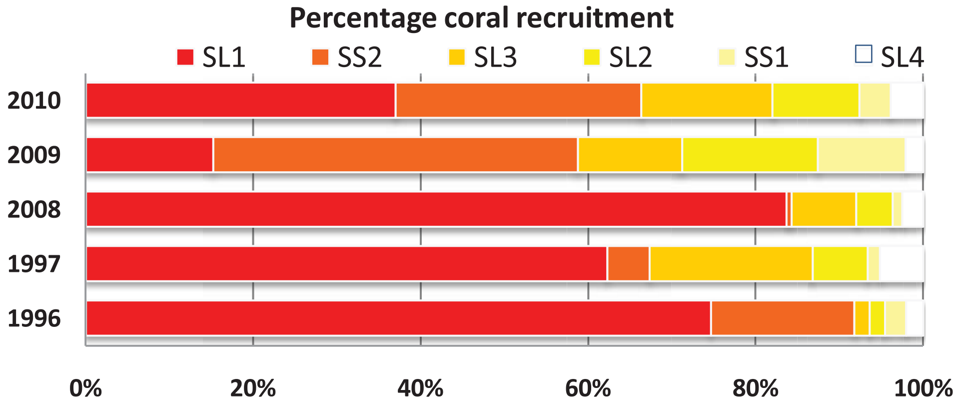


Figure 10.4 Proportion of Coral Recruits settled to experimental plates at each Reef Slope Location per Year. (Early post-bleaching years are excluded as total recruit numbers are too low). See Location Map Figure 1.2.1.

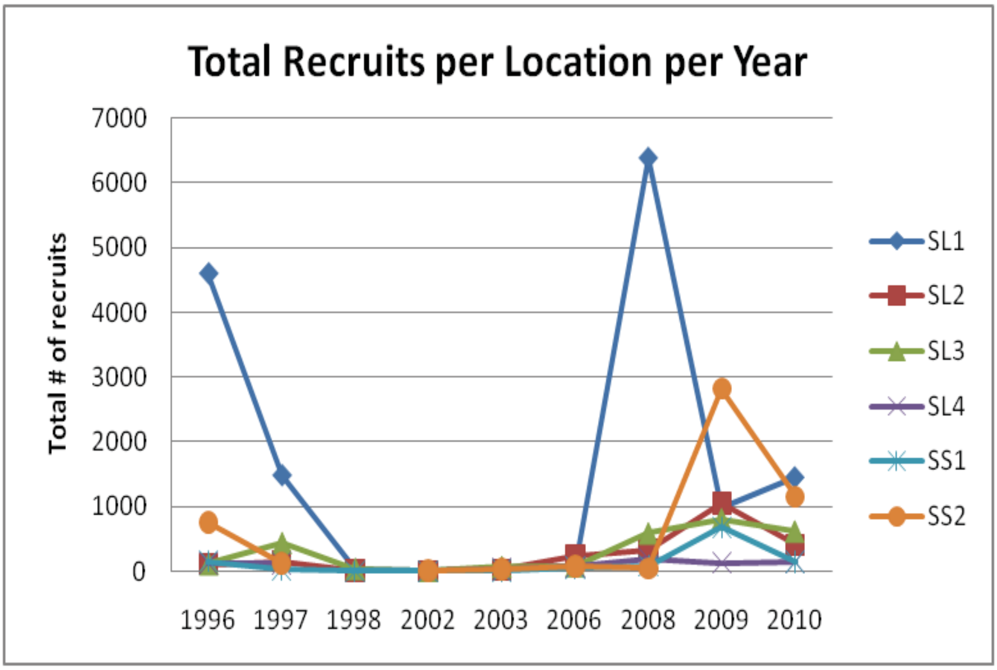


Figure 10.5 Total number of Recruits found on recruitment plates per Location per year. This axis was used to clearly indicate the large peaks in recruitment rates at SL1 in 1996 and 2008 and at SS2 in 2009, and the very low recruitment post bleaching1998-2008. The data is shown in more detail in Figure 10.6 below, See Location Map Figure 1.2.1.

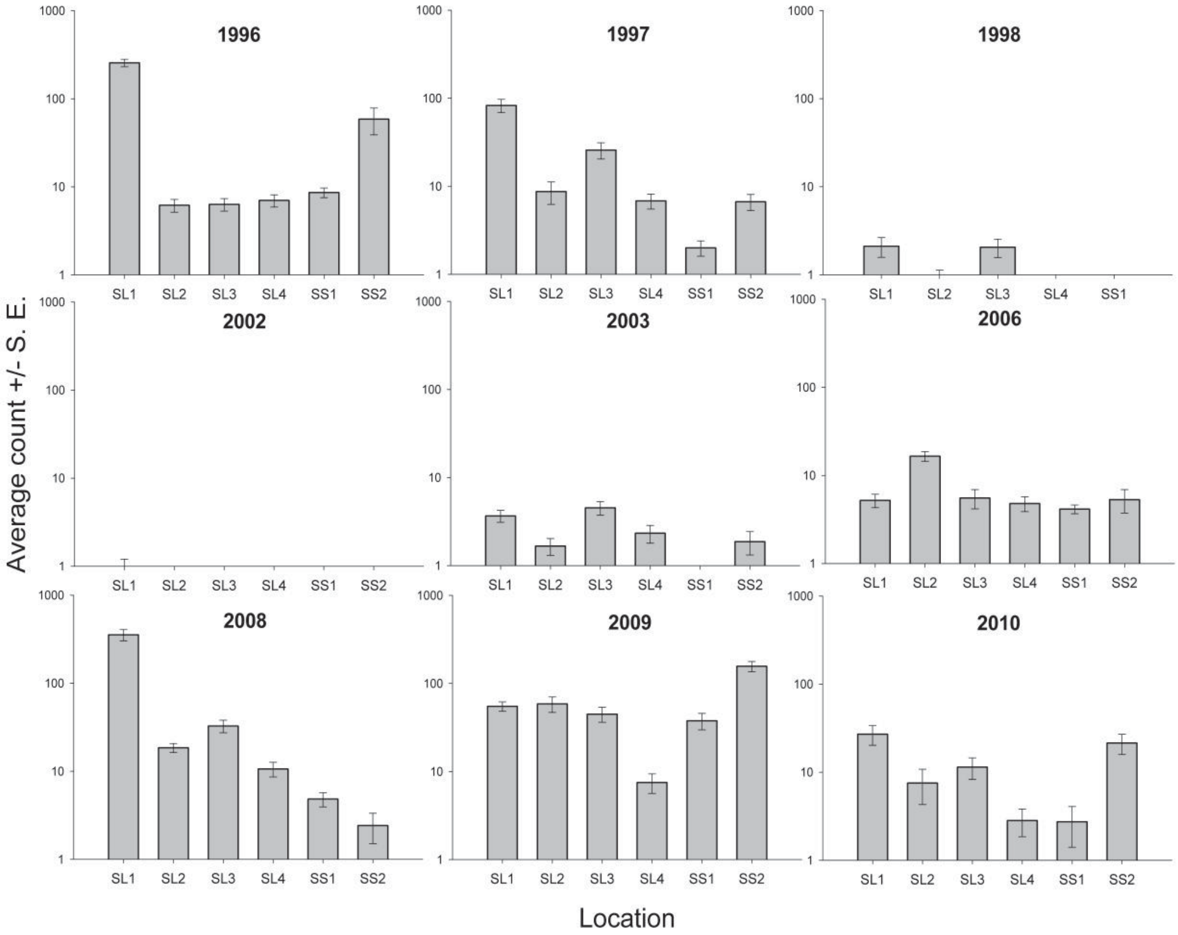
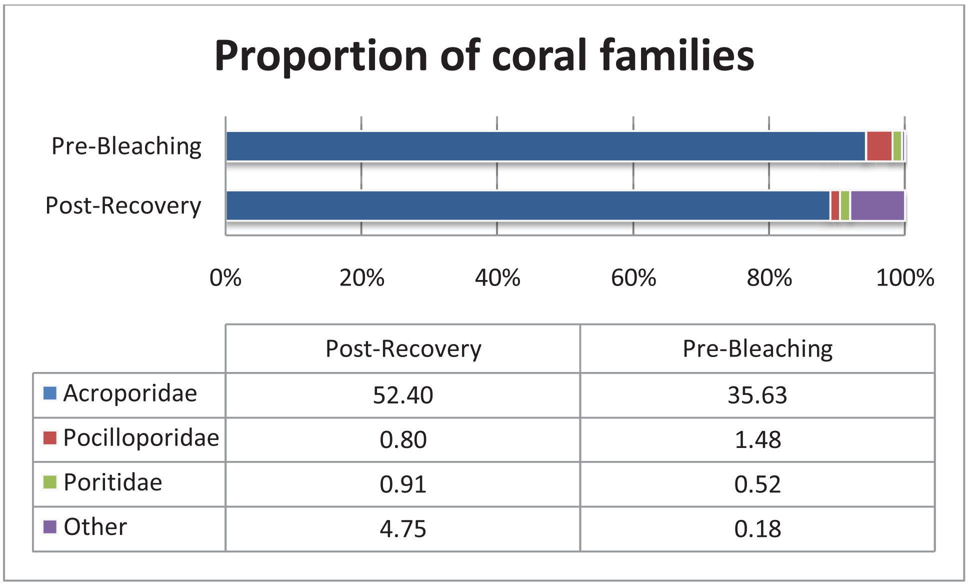


Figure 10.6 Mean Recruits per Recruitment Plate for each Location and Year surveyed, shown on a Log(10) axis. See Location Map Figure 1.2.1.

Coral Families:

The average proportion of each identifiable coral family was calculated for the pre-bleaching years 1996 and 1997 and the post-recovery years 2008 - 2010. In both pre-bleaching and post-recovery years the family *Acroporidae* made up 88-94% of total recruits (Figure 10.7). The families *Pocilloporidae* and Poritidae make up only a small proportion (1-3%) of the recruits captured during the mass spawning events in both periods, however these families are known to spread their reproductive effort over numerous months of the year (Harrison et al. 1990; Richmond and Hunter 1990; Tanner 1996; Fan et al. 2006). The number of recruits from coral families grouped as "Others" is slightly higher in Post-recovery years, however the recruits of these families are unable to be consistently separated at the age of 1 month, therefore we cannot identify the coral families responsible for this slight increase.



	Post-Recovery	Pre-Bleaching
🟦 Acroporidae	52.40	35.63
🟥 Pocilloporidae	0.80	1.48
🟩 Poritidae	0.91	0.52
🟪 Other	4.75	0.18

Figure 10.7 The Proportion of each identifiable coral family (*Acroporidae*, *Pocilloporidae*, Poritidae and Others on the recruitment plates (Average per plate) for Pre-bleaching (1996-1997) and Post-recovery (2008-2010) Years, across all reef slope locations surveyed at Scott Reef. The horizontal bars represent the proportion of all recruits represented by each coral family, with the number (average per plate) listed in the table below.

Discussion

Recovery of communities devastated by catastrophic disturbances is usually facilitated by the arrival of new individuals onto the reef (Caley et al. 1996; Connell et al. 1997; Nystrom and Folke 2001). For reef systems that do not receive significant sexual recruits from outside, replenishment depends largely on the surviving adult colonies as brood-stock (Smith 2005). Scott reef is situated more than 240km from its nearest neighbouring reef, and studies on the velocity and complexity of surface currents in the region suggest larval transport times of at least 30 days between reef systems (Cresswell and Peterson 1993), longer than the optimal larvae competency periods for most species (Ayre and Hughes 2000; Nishikawa et al. 2003; Baird 2004). Therefore, Scott Reef is expected to rely mostly on self seeding (Gilmour et al. 2009a; Underwood et al. 2009).

Due to the scale and severity of the 1998 bleaching, adult brood-stock was severely diminished across the Scott Reef system. For the surviving adults, reduced colony size through partial mortality would cause lower per capita reproductive output (Hall and Hughes 1996), and re-allocation of energy reserves to the repair and re-growth of injuries, rather than gamete production (Glynn 1993; Baird and Marshall 2002; Ward et al. 2002). Additionally, fertilisation rates of gametes may be reduced due to lower colony densities (Oliver and Babcock 1992; Omori et al. 2001). The lack of connectivity with unaffected reefs, and the spatial scale of the disturbance, meant that recruitment was slow to return to pre-bleaching levels at Scott Reef. However, after the initial slow increase up to 2006, the number of sexual recruits increased dramatically in 2008 and remained at or above pre-bleaching levels for the following three years. This return to high recruitment levels lagged slightly behind the increase in adult colony number and size seen in the size frequency data of scleractinian corals at most locations surveyed at Scott Reef. For *Acropora*, an increase in small adult colonies to levels close to that seen before the bleaching is seen by 2003-2004, but not in large adult colonies until 2006-2008. The sudden increase in sexual recruits recorded in 2008 may indicate a critical mass reached in terms of adult colony abundance and/or fecundity required to facilitate high levels of fertilisation and larval survivorship (see Oliver and Babcock 1992; Hughes et al. 2000; Omori et al. 2001).

Variation between locations:

There is high variation in recruitment at the location scale on Scott Reef. In years of good recruitment, certain locations receive a much higher proportion of recruits. Of our six studied locations, SL1 received up to tenfold higher recruit numbers than other locations in many years. Evidence of the 2008 spike in recruitment at SL1 can also be witnessed in the size frequency demography of *Acropora spicifera* corals at that location (see Chapter 7 Figure 7.3), where a strong cohort of recruits can be seen in the following two years. In years where recruitment is not particularly high at SL1, there is a peak at SS2.

Difference in adult coral cover between locations does not sufficiently explain the variation in recruitment between locations. High recruitment at SL1 may be due to the local oceanographic conditions during the larval dispersal period, where there is some evidence that currents could carry larvae from other locations to the inner west hook of south Scott reef where they become entrained in an eddy (Steinberg et al. 2006b). We hypothesise that in years when the larvae do not become entrained at SL1, they move further out and cause an increase in recruitment at SS2. SL4 consistently receives low numbers of recruits during mass spawning. This may be partly due to low *Acropora* cover at this site compared to other locations, depending on the scale of self-seeding at Scott Reef. Alternatively, low larval supply to this location during mass spawning due to current and tidal movements may be a contributing factor to the low cover of *Acropora* seen at SL4 compared with other locations at Scott Reef. Variable larval input plays an important role in shaping local adult populations (Gaines and Roughgarden 1985; Caley et al. 1996).

11. PATTERNS OF CORAL RECRUITMENT FOR DEEP-WATER COMMUNITIES IN THE SOUTH-LAGOON.

Summary

Recruitment to the deeper waters of the South Scott Lagoon (41-56m) was surveyed over five approximately ninety day periods from April 2008 to February 2010 (depths and survey times for each location and period are shown in Table 11.1). A strong peak in recruitment was seen during the Feb-May survey period in 2009 corresponding with the Autumn mass spawning observed on the shallow reef, Mean recruits per plate for the Feb-May 09 period were 31.7 (±4.2 SE) compared with an average of 4.08 (±0.6 SE) for the other periods (Figure 11.3). However such a peak was not observed during the April-July 2008 period, which also included an autumn mass spawning event. The orientation of coral recruits on the recruitment plates was seen to differ between the shallow and deeper-water reef. In the deeper lagoon, 80% of recruits settled on the top surface of the plates, with 5% on the underside and 5% on the sides (Figure 11.4). In the shallow reef, most recruitment is seen on the underside of plates (44% Underside part, 30% Sides, 24% Top). *Acroporidae* was the dominant family identified on recruitment plates at both the shallow reef and the deep-water lagoon. However on the deeper-water plates, *Acroporidae* make up less than 50% of total recruitment, compared with almost 90% in the shallow-water plates (Figure 11.5). On the deeper-water plates there is a much higher proportion of recruits classified as 'Others', which includes all families other than *Acroporidae*, *Pocilloporidae*, and Poritidae, (41%) compared with the shallow water plates (5%).

Introduction

Recently there has been much speculation about the ability of deeper-water coral communities to act as refugia for shallow reefs following severe disturbance (See reviews by Lesser et al. 2009; Bongaerts P. 2010). In theory, deep-water communities are better protected from disturbances that affect shallow reef areas, such as bleaching and cyclones, and therefore may be able to act as brood-stock for a recovery. Relatively little is known about the connectivity between deep and shallow coral communities, and the potential for deep reefs to provide a viable reproductive source following disturbance (Bongaerts P. 2010). Scott Reef provides an opportunity to explore this hypothesis. Due to the good water quality at Scott Reef, the deeper-waters of the south Scott Lagoon (40-70m) maintain an extensive hard coral community containing a subset of the shallow reef slope coral species (Gilmour et al. 2009b). This deeper-water community is relatively protected from bleaching and cyclones, the major disturbances experienced at Scott Reef, and was far less affected by the 1998 bleaching than the shallow coral communities. The extremely low recruitment we observed on the shallow reef for ten years following the bleaching however, suggest that this deep reef may contribute little to the larval supply on the shallow reef, at least during the period of the autumn mass spawning. To better understand the connectivity between the deep and shallow coral communities of Scott Reef, more information is needed about the patterns of spawning, larval supply, and recruitment in the deeper reef communities.

Here we investigate the pattern of coral recruitment throughout the year from March 2008 to February 2010 at 11 locations between the depths of 40-60m in the deeper-water coral community of south Scott Lagoon (survey periods can be seen in Table 11.1). We compare recruit numbers, the proportion of each identifiable coral family, and orientation on the recruitment plate with that found in our recruitment study on the shallow reef slope at Scott Reef.

Methods

In addition to the main recruit survey, in 2008-2010 recruitment plates were attached to instrumentation (Figure 11.1) deployed at eleven sites (6 replicate plates per site) in the deeper-water of the south Scott Lagoon (Figure 11.2). These instruments were left positioned on the substrate at depths of between 41 and 56 meters, for five approximately ninety day periods from April 2008 to February 2010 (depths and survey times for each location and period are shown in Table 11.1). These tiles were then bleached, and processed in the same manner as the shallow reef recruitment tiles. Coral recruits were identified to one of four taxonomic groups (Family *Acroporidae*, *Pocilloporidae*, Poritidae or Others) according to Babcock and Baird (2003), using a dissecting microscope.

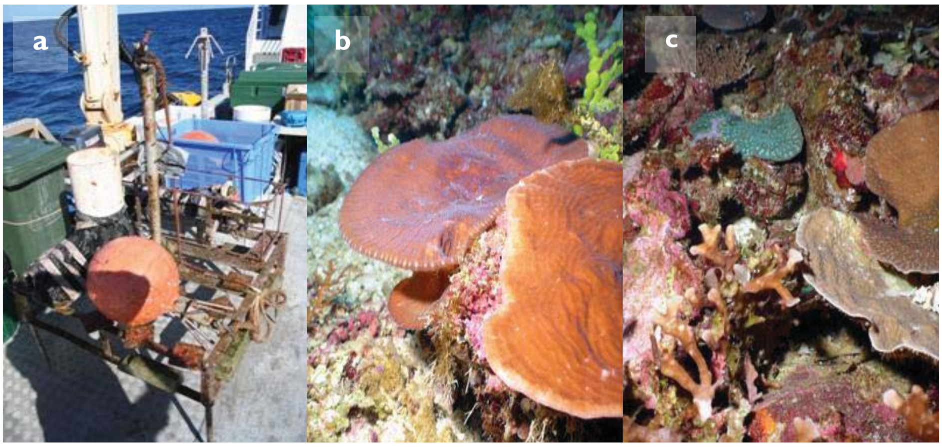


Figure 11.1 a) Deep-water observational equipment with attached recruitment plates following retrieval. b+c) Photos of the Deeper-water coral community at south Scott Reef taken by ROV.

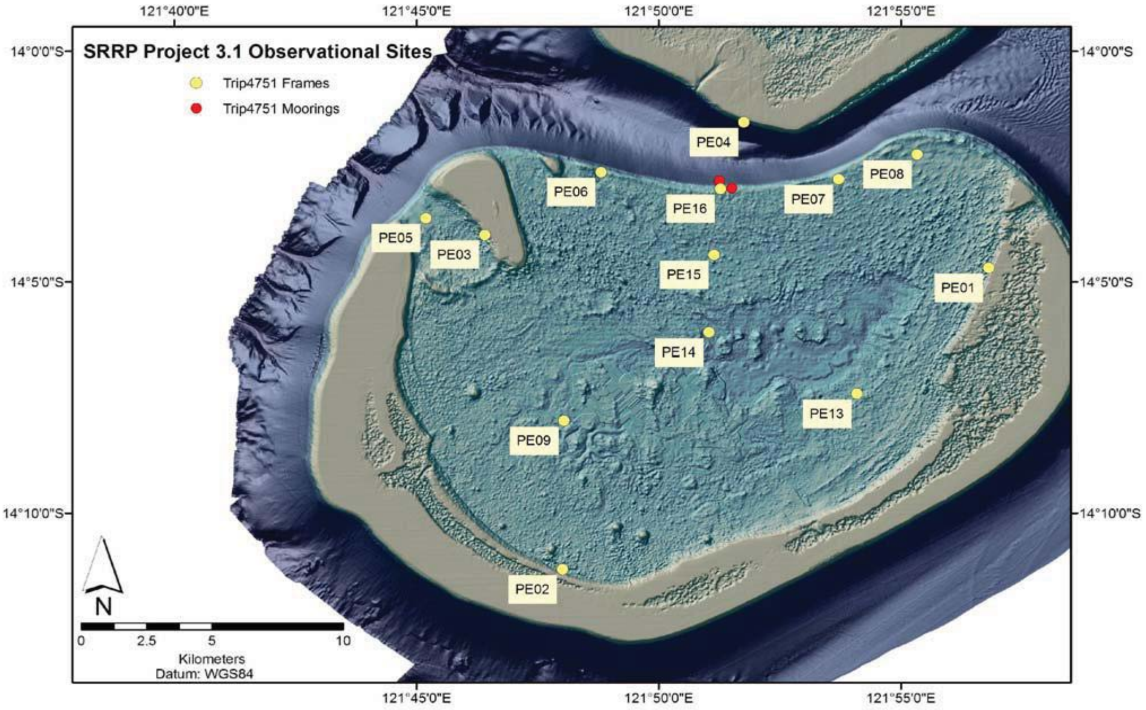
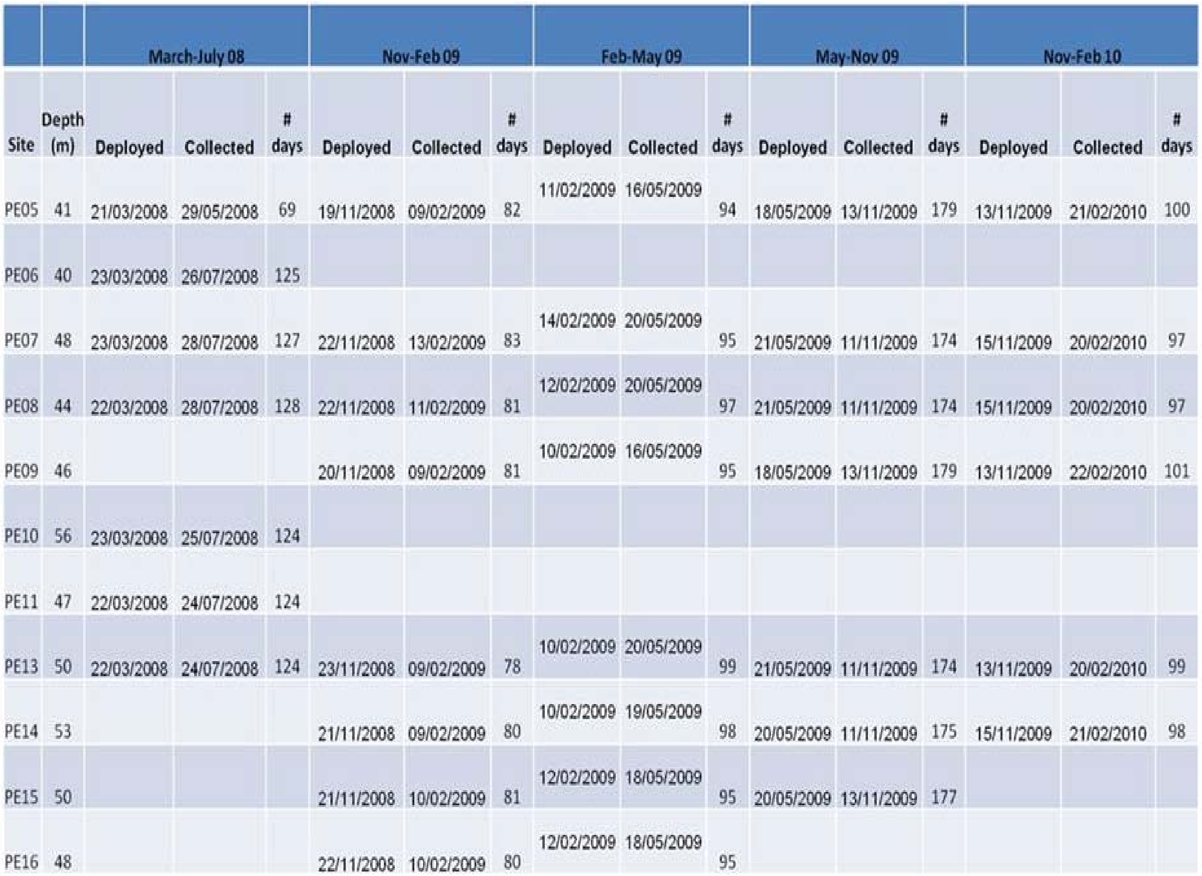


Figure 11.2 Location of deeper-water observational sites at south Scott Reef Lagoon

Table 11.1 Deeper-water lagoon sites: Depths, deployment and collection dates and number of days in the water for each survey period. For location of sites refer to Figure 11.2.



		March-July 08			Nov-Feb 09			Feb-May 09			May-Nov 09			Nov-Feb 10		
Site	Depth (m)	Deployed	Collected	# days	Deployed	Collected	# days	Deployed	Collected	# days	Deployed	Collected	# days	Deployed	Collected	# days
PE05	41	21/03/2008	29/05/2008	69	19/11/2008	09/02/2009	82	11/02/2009	16/05/2009	94	18/05/2009	13/11/2009	179	13/11/2009	21/02/2010	100
PE06	40	23/03/2008	26/07/2008	125												
PE07	48	23/03/2008	28/07/2008	127	22/11/2008	13/02/2009	83	14/02/2009	20/05/2009	95	21/05/2009	11/11/2009	174	15/11/2009	20/02/2010	97
PE08	44	22/03/2008	28/07/2008	128	22/11/2008	11/02/2009	81	12/02/2009	20/05/2009	97	21/05/2009	11/11/2009	174	15/11/2009	20/02/2010	97
PE09	46				20/11/2008	09/02/2009	81	10/02/2009	16/05/2009	95	18/05/2009	13/11/2009	179	13/11/2009	22/02/2010	101
PE10	56	23/03/2008	25/07/2008	124												
PE11	47	22/03/2008	24/07/2008	124												
PE13	50	22/03/2008	24/07/2008	124	23/11/2008	09/02/2009	78	10/02/2009	20/05/2009	99	21/05/2009	11/11/2009	174	13/11/2009	20/02/2010	99
PE14	53				21/11/2008	09/02/2009	80	10/02/2009	19/05/2009	98	20/05/2009	11/11/2009	175	15/11/2009	21/02/2010	98
PE15	50				21/11/2008	10/02/2009	81	12/02/2009	18/05/2009	95	20/05/2009	13/11/2009	177			
PE16	48				22/11/2008	10/02/2009	80	12/02/2009	18/05/2009	95						

Results

Although the survey periods were not the same throughout the year, it can be seen that there is a peak of recruitment in the Feb-May 09 survey period, corresponding with the autumn mass spawning. Mean recruits per plate for the Feb-May 09 period were 31.7 (±4.2 SE) compared with an average of 4.08 (±0.6 SE) for the other periods (Figure 11.3). Interestingly, there is not a peak in the April-July 08 period, which also included an autumn mass spawning event. This may be due to lower recruitment in the deep-water lagoon in 2008 compared to 2009, a missed spawning event if the deeper-water corals spawn on a different night to the shallow community, or a dramatic difference in post-recruitment mortality due to different survey periods. In 2008 plates were deployed only 5-6 days before the autumn spawning, and were collected almost four months later, whereas in 2009, plates were deployed approximately one month prior to the spawning and collected two months after. Recruit numbers per tile during the other survey periods were low (<5). The spawning of three species of deep-water corals (Montastraea cavernosa, Montastraea franksi, and Diploria strigosa) at the same time as the mass spawning of nearby shallow reef species has been directly observed in the Gulf of Mexico (Vize 2006).

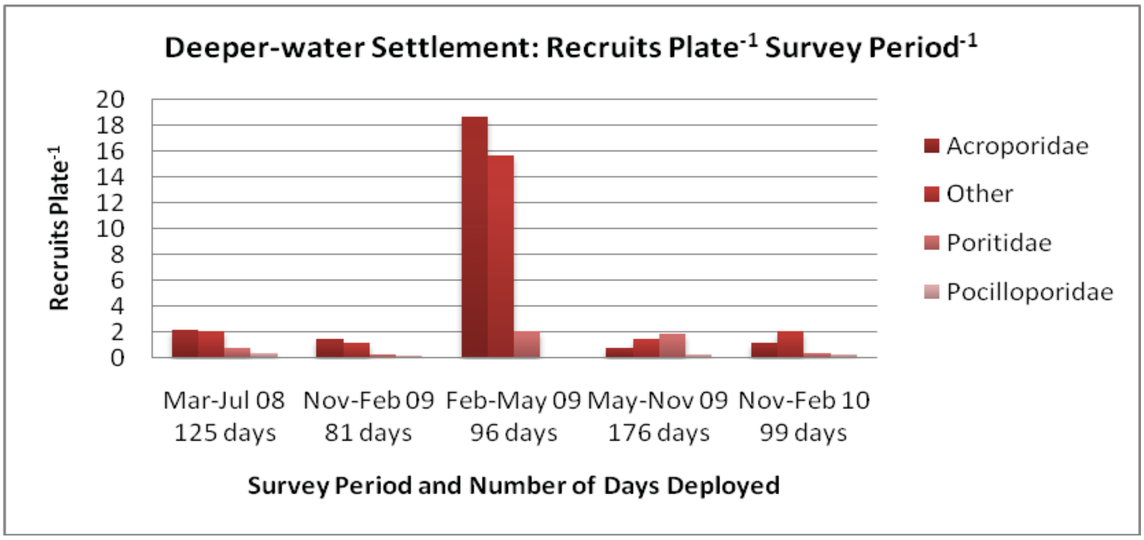


Figure 11.3 Recruitment at the Deeper-water sites at south Scott Reef Lagoon: Mean number of Recruits Plate^{-1} Survey Period^{-1}

Orientation on the recruitment plates:

In the deeper lagoon, 80% of recruits settled on the top surface of the plates, with 5% on the underside and 5% on the sides (Figure 11.4). In the shallow reef, most recruitment is seen on the underside of plates (44% Underside part, 30% Sides, 24% Top). Coral larvae recruitment selection has been found to be strongly influenced by light (Babcock and Mundy 1996; Mundy and Babcock 2000) and Ultraviolet Radiation levels (Kuffner 2001; Gleason et al. 2006). At shallow depths (<12 m), coral recruits are typically found on cryptic or vertical surfaces, but at greater depth or low light conditions, recruitment is typically higher on horizontal or exposed surfaces (Babcock and Mundy 1996; Edmunds et al. 2004).

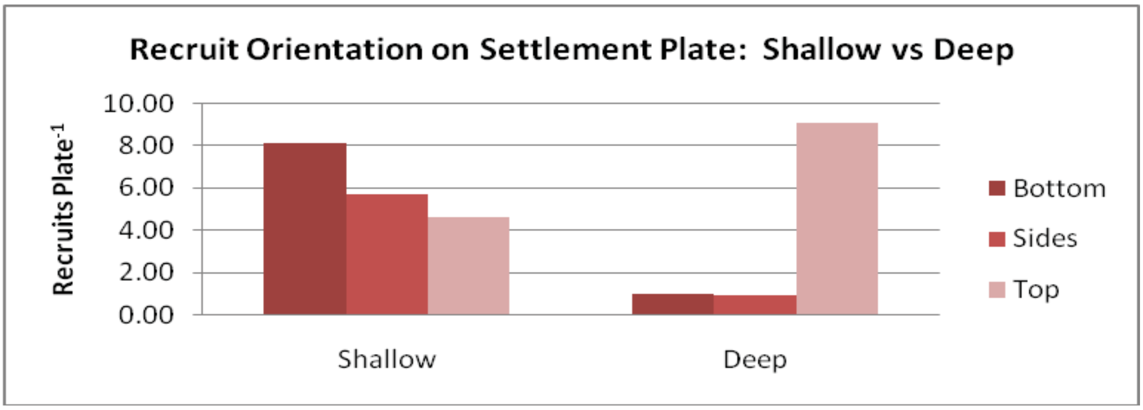
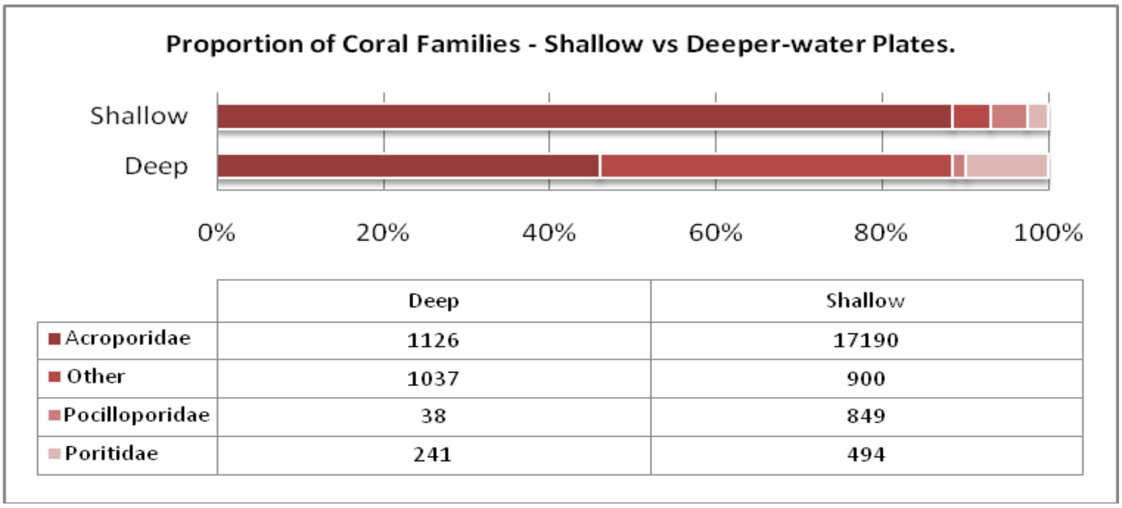


Figure 11.4 Recruit orientation on recruitment plates (Average number of recruits plate^{-1} over all surveyed years) at the shallow reef slope (Shallow) and the deeper-water lagoon at Scott Reef (Deep). Surveyed years for the shallow reef recruitment plates were 1996-2010, and 2008-2010 for deep reef recruitment plates.

Coral Families

Acroporidae is the dominant family identified on recruitment plates at both the shallow reef and the deep-water lagoon. However on the deeper-water plates, *Acroporidae* make up less than 50% of total recruitment, compared with almost 90% in the shallow-water plates (Figure 11.5). Most of the *Acropora* recruits are seen on the deeper-water plates during the Feb-May 09 period (autumn mass-spawning), with lower numbers during the rest of the year. On the deeper-water plates there is a much higher proportion of recruits classified as Others, which includes all families other than

Acroporidae, *Pocilloporidae*, and Poritidae, (41%) compared with the shallow water plates (5%). The high proportion of 'Other' recruit families during the autumn mass spawning period on deeper-water plates compared to shallow-water plates suggests that there may be a number of coral species that settle in the deep lagoon that are not settling in high numbers on the shallow reefs.



	Deep	Shallow
■ Acroporidae	1126	17190
■ Other	1037	900
■ Pocilloporidae	38	849
■ Poritidae	241	494

Figure 11.5 Comparison of the proportion of coral families seen on recruitment plates on the shallow reef slope and the deeper-water lagoon at Scott Reef. Bars represent the proportion of total recruits for each family (colour coded below), the table shows the total counts.

Coral larvae are capable of actively selecting their preferred recruitment substrate, using a number of different cues. Babcock and Mundy (1996) found that corals with deeper-water distributions selected recruitment substrate with lower light levels, and Baird (2003) found that the coral larvae of a number of zone-specific species strongly preferred recruitment plates conditioned at the depth of their parental habitat. Therefore coral larvae show a strong tendency to settle within the depth zone of their parental distribution. Combined with the short distance larval dispersal seen in some species (Underwood et al. 2007b), this seriously diminishes the potential for deep reef communities to supply sufficient propagules to repopulate a shallow reef. Connectivity between deep and shallow reefs is likely to be restricted to depth generalist species, which represent only about 25% of diversity (Bongaerts P. 2010).

12. FISH REPRODUCTION AND RECRUITMENT AND HABITAT USE OF THEIR JUVENILES

Summary

*The number of recently settled coral reef fish recruits was surveyed at Scott Reef in crest, mid-slope and lower slope habitats at six locations between 2009 and 2010. As there were many intervening months during which recruitment was not surveyed, earlier fish recruitment data (1995 to 1997) was also analysed. Demographic data were also obtained in April and October 2008 in order to age fish, back calculate their time of settlement and determine their reproductive status. Initial analyses indicate that a large proportion of bicolour damselfish (*Chromis margaritifer*) spawn around April, with a potential peak in settlement occurring in July, although some settlement occurs over several months of the year. The 1995 and 1997 fish recruitment data also indicate that* Chromis margaritifer *recruits throughout the year, but the greatest numbers occur in autumn and spring when water temperatures are rising and monsoonal storm fronts and associated strong wind and waves are least. The juveniles of different fish species tended to settle among different micro-habitats and reef zones, with the bicolour damselfish settling predominantly onto bare substrates in the shallower reef crest zone, whereas scaly damselfish juveniles display a preference for soft corals in the deeper slope zone. These data further highlight the often specific relationship between some fish and coral species.*

Introduction

Reproduction in reef fishes typically involves the production of either demersal or pelagic eggs and the subsequent hatching into a planktonic larval phase that can last from 9 to over 100 days depending on the species (Leis 1991). In many of the smaller conspicuous families of reef fishes such as the damselfishes, females produce demersal eggs in nests that are usually built and guarded by males before the larvae hatch into the pelagic environment (Meekan et al. 1993; Robertson et al. 1999). For larger reef fishes, however, reproductively mature adults often take part in paired or group spawning in which males fertilise buoyant planktonic eggs released by females (Domeier and Colin 1997). Within the surgeonfish family (Acanthuridae), this spawning activity can involve spectacular mass group spawnings in which large numbers of fish migrate to an area of the reef at specific times and form spawning groups characterised by individuals moving rapidly amongst the clouds of gametes released by both males and females (Figure 12.1)(Robertson 1983; Domeier and Colin 1997). Although the subsequent pelagic larval stage generally represents a period when larvae can disperse to distant reefs, there is mounting evidence of active behaviour in which they are able to sustain swimming speeds greater than the surrounding currents and use their senses in order to orientate themselves to reefs (Leis 2006). This implies some degree of retention of larvae to natal reefs is likely.

Figure 12.1 Spawning aggregations of parrotfish (foreground) and surgeonfish (background) gather in the late afternoon on the top of the tide. Pairs split off from the group and fertilization occurs in a brief intense frenzy near the surface.

While some species of tropical coral reef fish spawn throughout the year, the timing of spawning and reproduction is often coupled with seasonal patterns of water temperature or productivity and with monthly changes in moon phase and tidal range, thus invariably coinciding with the most favourable conditions for larval survival and growth (Johannes 1978; Cushing 1987; Doherty and Williams 1988; Robertson et al. 1999). The degree to which patterns of spawning and recruitment are seasonal diminishes towards the equator as seasonal changes in environmental conditions such as water temperature become less. On the Great Barrier Reef, recruitment of most fish species occurs during summer when water temperatures are at their peak (Russell et al. 1977; Talbot et al. 1978; Williams and Sale 1981; Milicich et al. 1992; Milicich and Doherty 1994). In contrast, most species of reef fish in the Caribbean spawn during months when water temperatures are minimal (Munro et al. 1973). The timing of these important reproductive events for fishes is currently unknown at Scott Reef.

As in many terrestrial ecosystems, coral reefs are composed of spatially subdivided populations that are connected via the movement of individuals. In the marine realm, the maintenance of such connections requires the movement of individuals as pelagic larvae (coral and fish) or as wide roaming adults (fish) in the water column. Many organisms, including coral reef fishes, utilise a wide variety of habitats that provide essential resources such as food, shelter from predators and sites for reproduction at different stages of their life cycle (Schmitt and Holbrook 2000; Syms and Jones 2001; Wilson et al. 2008). While certain fish species are more targeted in their resource requirements (specialists), and compete for and defend such resources, other species are more general in their resource requirements and share a range of habitats with other species (generalists). As coral reef habitats exposed to disturbance become degraded there is often a loss of fish species with specialist resource requirements and increases in others that have wider niche breadths, as has been demonstrated in the present study of fish communities at Scott Reef and at Indo-Pacific reefs elsewhere (Wilson et al. 2008). To enhance our understanding of resilience of fishes at Scott Reef and the pronounced changes in fish species composition that have occurred there since the 1998 bleaching, it is important to understand the particular habitat requirements of the juveniles of these species and assess the extent to which their nursery habitats are being provided in the post-bleaching environment at Scott Reef.

Materials and Methods

Study area and sampling regime

This study was conducted at Scott Reef (14˚S 122.5˚E) and the Rowley Shoals (17˚ 7'S 119˚ 36' E). These are isolated oceanic reef systems that rise from *ca* 400m depth along the continental shelf between north-western Australia and the south coast of west Timor, Indonesia (Figure 12.2). Scott Reef is comprised of north and south Scott Reefs and the Rowley Shoals is comprised of three atolls; Mermaid, Clerke and Imperiuse Reefs.

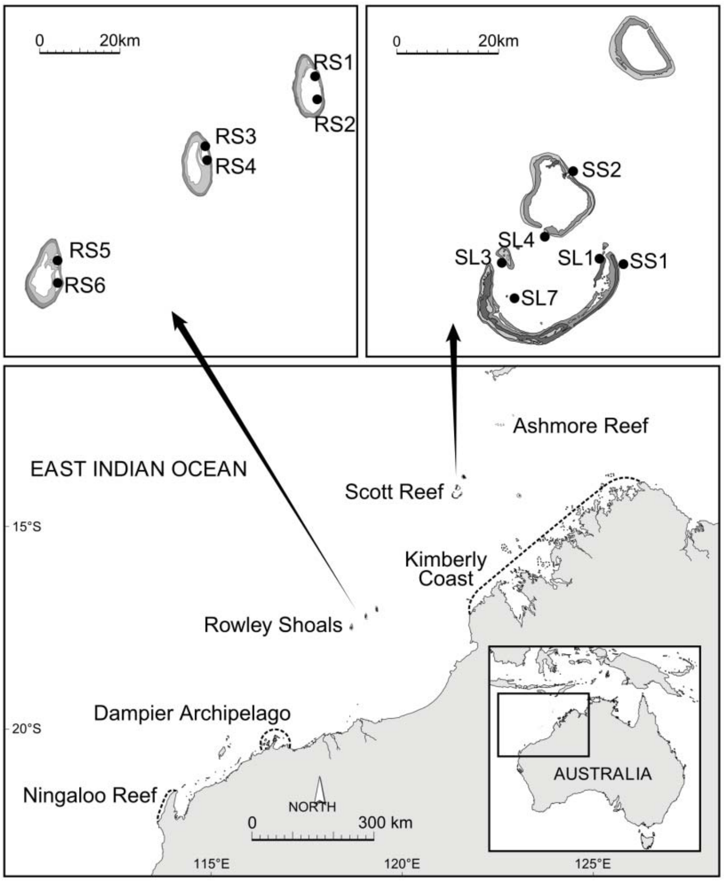


Figure 12.2. Map of north-west Australia showing sites where *Chromis margaritifer* were sampled at the Rowley Shoals and Scott Reef.

Fish collection

In April 2008, 580 *C. margaritifer* were collected on SCUBA using a combination of hand nets, barrier nets and clove oil from six sites at both Scott Reef and the Rowley Shoals (Figure 12.2). On average, 45 individuals were collected per site (sample sizes ranged from 32 to 53), and replicate sites were sampled on each reef. Seven months later (October 2008), 98 recruits (15-30 mm) were collected from three sites at Scott Reef (SL1, SL3, SS2) and one site at the Rowley Shoals (RS3), with average samples sizes of 25 individuals per site.

Fish processing, reproductive staging, otolith preparation and analysis

The earbones of fish, known as otoliths, contain a vast amount of information on the life history of individual fish. Growth rings within these otoliths are used to age fish in much the same way as the reading of growth rings in trees and important early life history events such as the date of hatching, length of larval life and date of settlement back to the reef can be determined.

Fish collected in April and October 2008 were measured to the nearest 1 mm total length (TL), fork length (FL) and standard length (SL), and weighed to 0.1 mg total weight (TW). The sex of each *C. margaritifer* that was considered large enough to reproduce (> 45 mm TL) was recorded when its gonad could be identified macroscopically as either an ovary or a testis. Gonads were assigned to one of the following eight stages after (Wallace and Selman 1981): I-Virgin; II-maturing virgin/resting adult; III-developing; IV-partially developed; V-pre-spawning; VI-spawning; VII-spent and VIIIrecovering spent. The pair of sagittal otoliths was extracted by opening the otic bulla from under the operculum. Otoliths were then cleaned of adhering tissues, washed in freshwater and stored dry in envelopes prior to processing. One of the pair was weighed to within 0. 1 mg and mounted over the edge of a glass slide using thermoplastic glue and oriented internal face up, rostrum outside the glass and the core inside the edge of the glass following the method of Secor *et al*. (1991). The protruding portion of the otolith was ground off using 9, 3 and 1 µm lapping film. The otolith was then mounted on a new glass slide so that it sat upright on its cut edge, in the centre of the slide. The upright portion was then ground on the same series of lapping films to produce a thin transverse section that contained the core. The number of increments on each preparation 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. 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 (Figure 12.4). Pre-settlement age (PLD) was determined by counting the number of increments (days) between hatching (first increment) and settlement. Dates of settlement were back-calculated by subtracting the number of post-settlement increments from the date of capture. Fifty percent of otoliths were re-read and the increments in all of otoliths viewed were unambiguous. A settlement date for each individual was calculated by subtracting the number of post-settlement increments (growth rings between the settlement mark and the edge of the otolith) from the date of capture. Settlement date was converted to the lunar calendar by determining the number of days until the nearest full moon, with values negative during waxing stages and positive during waning stages. Mean daily water temperature was overlapped on settlement frequency distributions; we used water temperature data recorded by in situ Odyssey loggers that recorded water temperature every 30 minutes throughout the study.

The back-calculation process assumes that somatic growth is directly related to otolith growth (Bagenal 1978). This assumption is usually validated through the demonstration of a relationship between the otolith size and body length.

Fish recruitment surveys

Underwater visual surveys by SCUBA divers were used to estimate of numbers of recruit fishes along permanent transects (50 × 1 m) at Scott Reef and the Rowley Shoals between 1995 and 1997 and at Scott Reef on surface supplied breathing apparatus (SSBA) between 2009 and 2010. Surveys at Scott Reef were carried out at three locations (SS1, SS2 and SS3) positioned on the outer reef slope and four locations (SL1, SL2, SL3 and SL4) positioned on the inner reef slope. At the Rowley Shoals surveys were carried out at one outer-slope site at each of the three reefs (RS1, RS2 and RS3). At each location, three permanently marked 50 m transects were positioned parallel to the reef crest in water depth ranging between 6 - 9 m, each separated by a distance of 10 to 20 m. In 2009, three 50 × 1 m long permanent transects were established along the reef crest (*ca* 3 m depth) and mid-slope (*ca* 6m depth) further up the slope and adjacent to the three lower slope (*ca* 9m depth) transects. Recently settled recruits were identified by their small size and juvenile colouration patterns. The identification of each species, total length (nearest 5 mm) and microhabitat association was recorded for each individual. The authors are experienced at visually surveying fish assemblages and also at estimating fish lengths accurately, their estimates of fish length were validated by using artificial fish figurines as part of their training process.

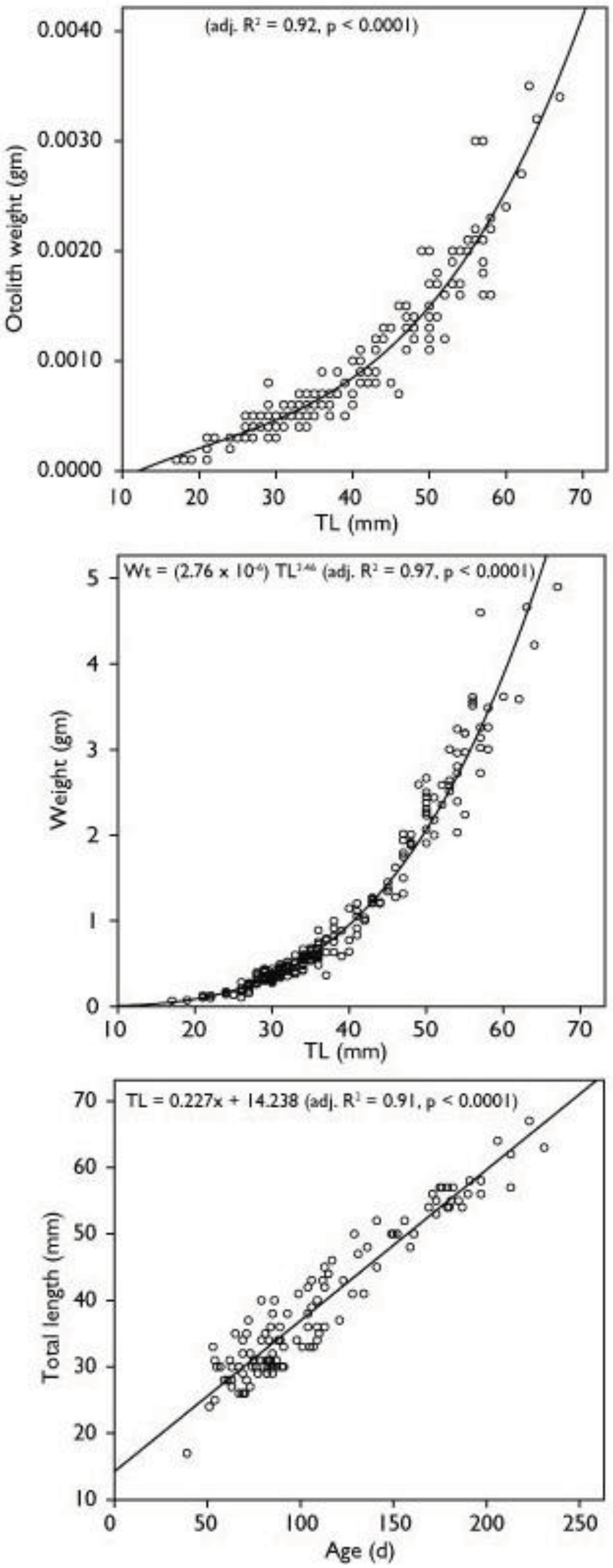


Figure 12.3 Otolith weight at length (a) weight at length (b) and length at age (c) relationships for the damselfish *Chromis margaritifer* at Scott Reef derived from samples collected during April and October 2008

Results and Discussion

Aspects of early life history and demographic parameters

A total of 691 post settlers of *Chromis margaritifer* were collected, 365 from Scott Reef and 326 from the Rowley Shoals. Their lengths (TL) ranged from 18 to 75 mm, with a mean (±SE) of 55.1 (11.7) at Scott Reef and 52.9 (13.5) at the Rowley Shoals. There was a highly significant cubic relationship (Adj. $R^2 = 0.92$, $p < 0.0001$) between otolith weight and total length of fish (Figure 12.3). Young-of-the-year, *C. margaritifer* had typical weight-total length relationship of the form: $W = (2.76 \times 10^{-6}) TL^{3.46}$, (Adjusted $R^2 = 0.97$, $p < 0.0001$). We aged otoliths from 223 individuals and the estimated post-settlement age ranged from 3 d (21 mm TL) to 191 d (67 mm TL) (Figure 4.6.3.1). The general model of age-length relationship was $TL = 0.227 \times Age + 14.238$, (Adjusted $R^2 = 0.91$, $p < 0.0001$).

Pelagic larval duration and settlement patterns

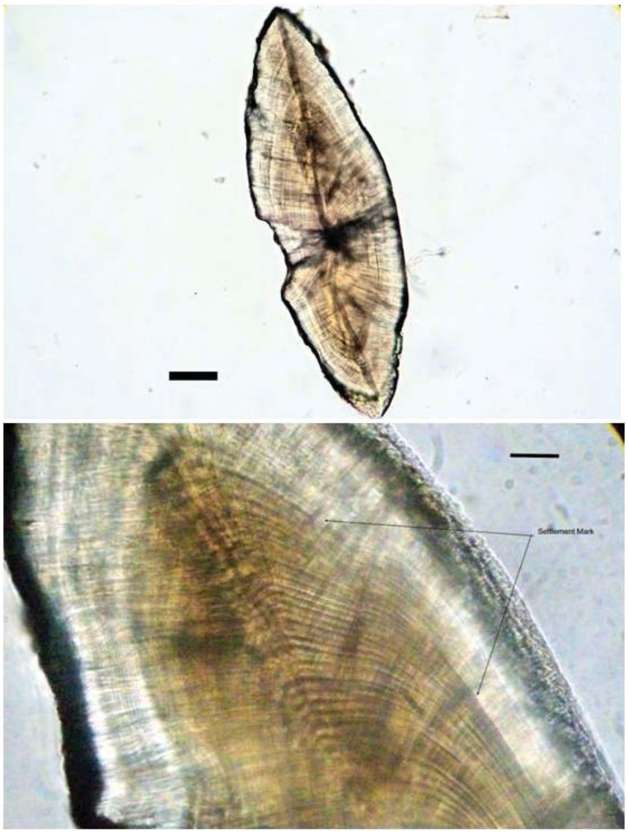


Figure 12.4. Photomicrographs of sagittal otoliths of newly settled bicolour damselfish *Chromis margaritifer* showing (a) daily growth rings (67 day old fish) and (b) pre-settlement increments and settlement mark at 37 days (59 day old fish). Scale bar in (a) = 100 µm and (b) 20 µm.

The estimated planktonic larval duration (PLD) of fish pooled across locations, ranged from 26 to 42 d at Scott Reef ($\bar{x}$ = 34.2 ±0.36 SE) and 28 to 42 d at the Rowley Shoals ($\bar{x}$ = 35.8 ±0.40 SE), and did not vary between the two reef systems. The mean and range of PLDs estimated for *C. margaritifer* at Scott Reef and the Rowley Shoals was longer than at two Pacific Ocean locations (Table 12.1).

Table 12.1. Regional comparison of the pelagic larval duration (PLD) in days of *Chromis margaritifer* and the 'gap traversed' that larvae are required to travel to the nearest large reef system.

Region	Mean PLD (± 1 S.D.)	Range	*n*	Reference	Gap (km)
GBR	30.4	27-33	5	Thresher *et al.* (1989)	< 50
Palau	33.2 (2.1)	30-36	10	Wellington & Victor (1989)	100
Scott Reef	34.2 (4.0)	26 to 42	125	Present study	180
Rowley Shoals	35.8 (4.0)	26 to 42	98	Present study	350

From the derived length-age relationship and the estimated number of days until a fish settled (PLD), settlement of *C. margaritifer* occurred when they were between 20.1 and 23.5 mm TL (data not shown). Although there are no data on the maximum ages for *C. margaritifer*, the maximum reported size for this damselfish is 90 mm (TL), 15 mm shorter than our longest fish. Back calculation of these dates for *Chromis margaritifer* at Scott Reef and the Rowley Shoals show that settlement occurs throughout the year, but peaks did occur in October and July when water temperatures were *ca* 28˚C (Figure 12.5).

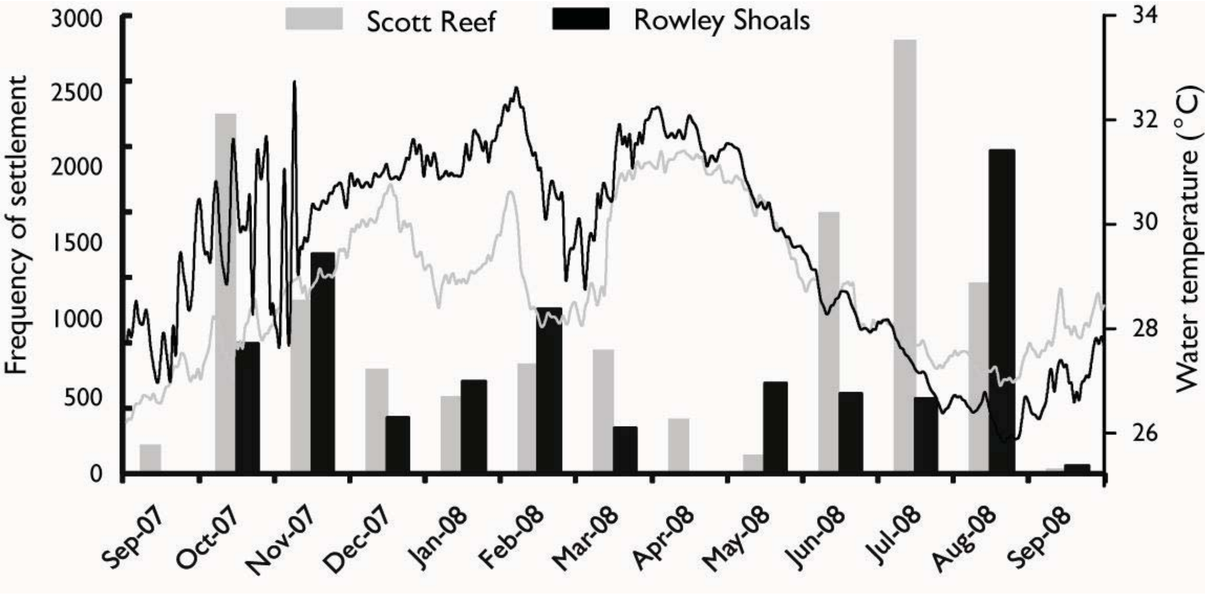


Figure 12.5 Comparison of settlement months for *Chromis margaritifer* at Scott Reef and the Rowley Shoals as determined by back calculation of settlement dates from otoliths collected in April and October 2008. An instantaneous mortality rate of 0.1 d^{-1} has been applied. Water temperature is recorded at 6 to 9m depth.

Fish recruitment surveys carried out at Scott Reef on five occasions between February 2009 and May 2010, show that numbers of *C. margaritifer* recruits were recorded on most occasions but were much higher in April and October 2009 (Figure 12.6).

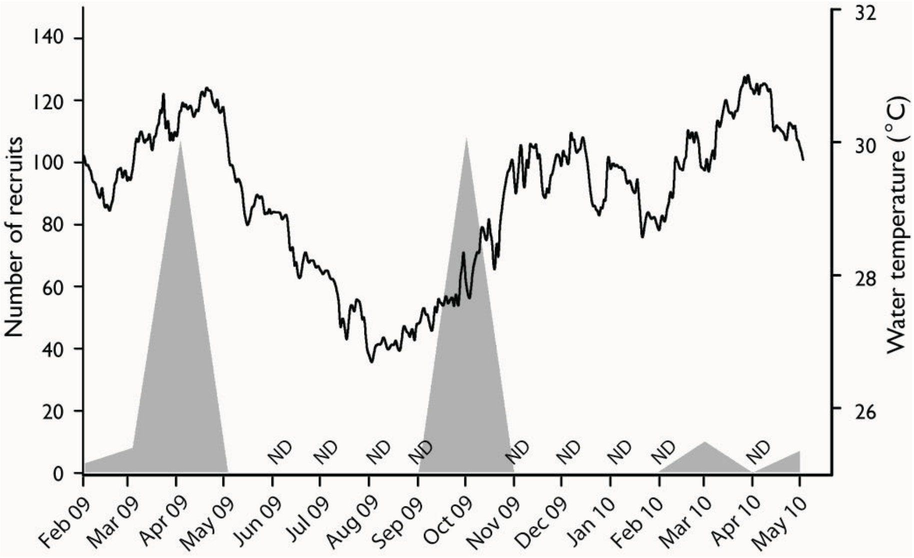


Figure 12.6. Plot showing number of *Chromis margaritifer* settlers (< 30 mm TL) through time at Scott Reef (indicates monthly peaks in settlement) with water temperature (6 to 9m depth) on the z axis. Data derived from recruitment surveys. ND = no data.

As there were many intervening months during which recruitment was not surveyed, earlier fish recruitment data (1995 to 1997) was also analysed. These data also indicate that this species recruits throughout the year, but the greatest numbers occur in autumn and spring when water temperatures are rising and monsoonal storm fronts and associated strong wind and waves are least (Figure 12.7). The greater number of *C. margaritifer* recruits at the Rowley Shoals than at Scott Reef on all but one occasion, presumably reflects the relatively larger population size of this species at the Rowley Shoals. The very high number of new recruits from all fish species at the Rowley Shoals in May 1996 was mainly due to a strong recruitment of the yellow-striped fairy basslet *Pseudanthias tuka* (Figure 12.7).

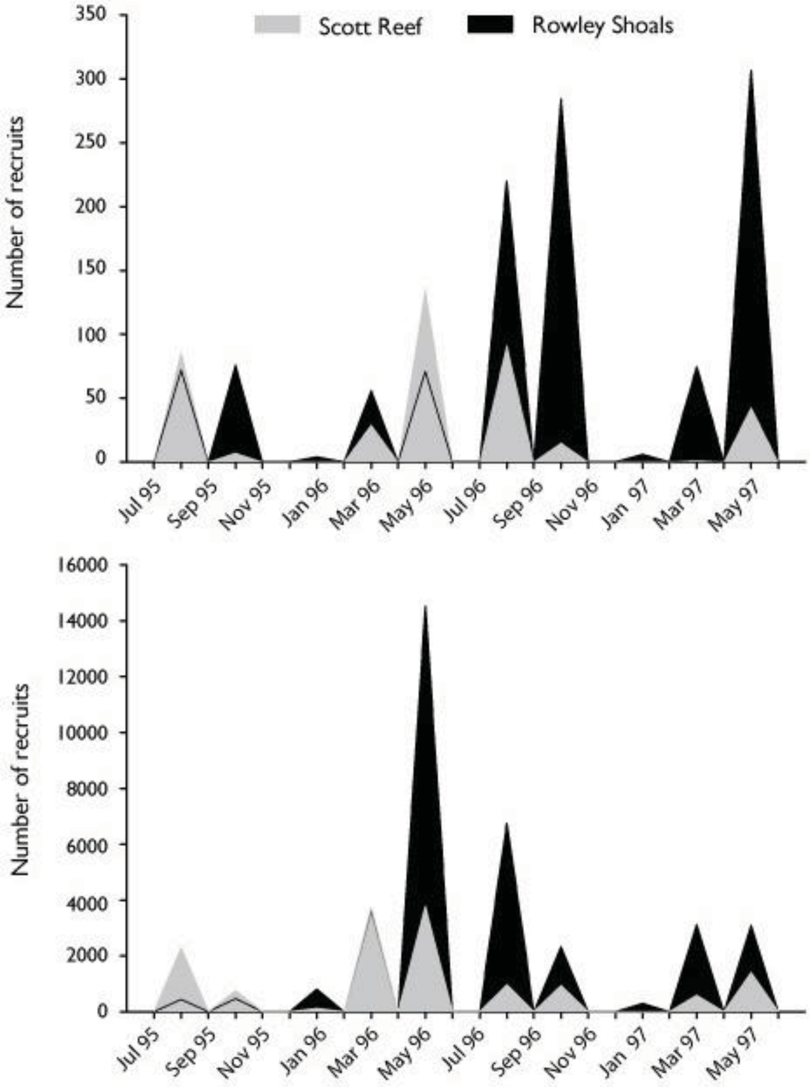


Figure 12.7. Plot showing numbers of recently settled *Chromis margaritifer* (< 30 mm TL) at Scott Reef and the Rowley Shoals and also total numbers of fish recruits from all species (Data derived from 1995-97 recruitment surveys).

The influence of the moon on reproductive activity of marine fishes is well known and is a particularly evident in nest-tending damselfishes (Taylor, 1984). Although an increase in sample size is required to confirm any trends, the frequency of egg hatching for *C. margaritifer* increased as the full moon approached before declining over the full moon and increasing again to the quarter moon (Figure 12.8). Such a peak in activity several nights before the full moon has been recorded elsewhere and is thought to reflect tidal patterns (high tidal amplitude) better suited for larvae to be transported away for the immediate environs of the reef and thus avoid being preyed upon (Johannes, 1978; Robertson et al. 1993). The inferred pattern of fish spawning at Scott Reef also contrasts to some degree with that at Ningaloo Reef, where numbers of recently hatched damselfish larvae peaked just prior to the full moon during summer neap tides (McIlwain, 2002). However, in that fringing reef system, neap tides were suggested to promote the transport of larvae out of the reef lagoon and away from the reef. The pattern of settlement at Scott Reef also appeared related to the lunar date, with a maximum frequency of settlement attained during the quarter moons (Figure 12.8). From the available data, there were no clear lunar hatching or settlement patterns at the Rowley Shoals.

These initial observations suggest that, similar to most coral populations at Scott Reef, there is evidence that fish spawning may also peak in autumn and spring when water temperatures are high and wind speeds low. In contrast to corals, however, which spawn after the full moon when tidal movement is small, fish spawn mainly just prior to the full moon or just after, when tides are large.

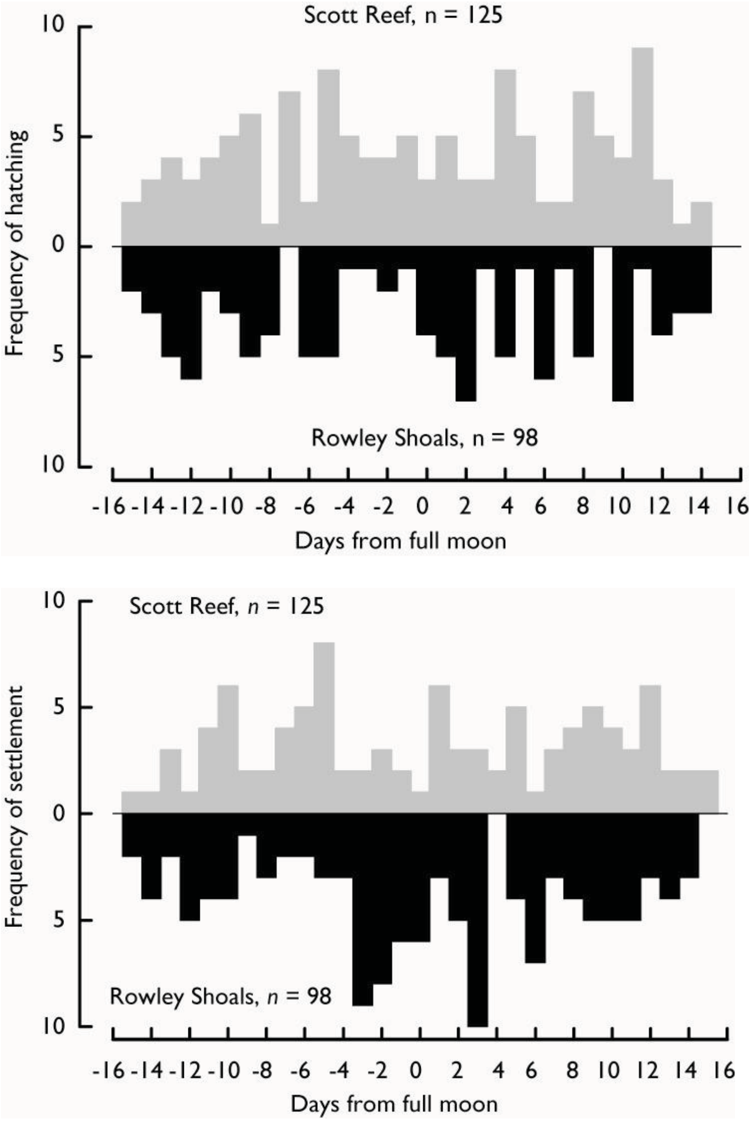


Figure 12.8. Hatch and settlement frequency distributions obtained from back calculations of 223 sagittal otoliths of *Chromis margaritifer*. Zero represents full moon; -15 and 15 represent the previous and following new moons, respectively. Fish were collected between April and October 2008.

Reproductive stages of maturity

The ovaries of the majority of female *C. margaritifer* collected at Scott Reef in April 2008 were at stages V (pre-spawning) and VI (spawning) in their reproductive cycle (Figure 12.9). Ovaries of females at the Rowley Shoals were evenly dispersed among stages IV (partially developed) to VI. The high occurrence of spawning female bicolour damselfish at Scott Reef in April 2008, and of *Pomacentrus lepidogenys* in October 2008, provides further evidence that spawning occurs during autumn and spring when water temperatures are high.

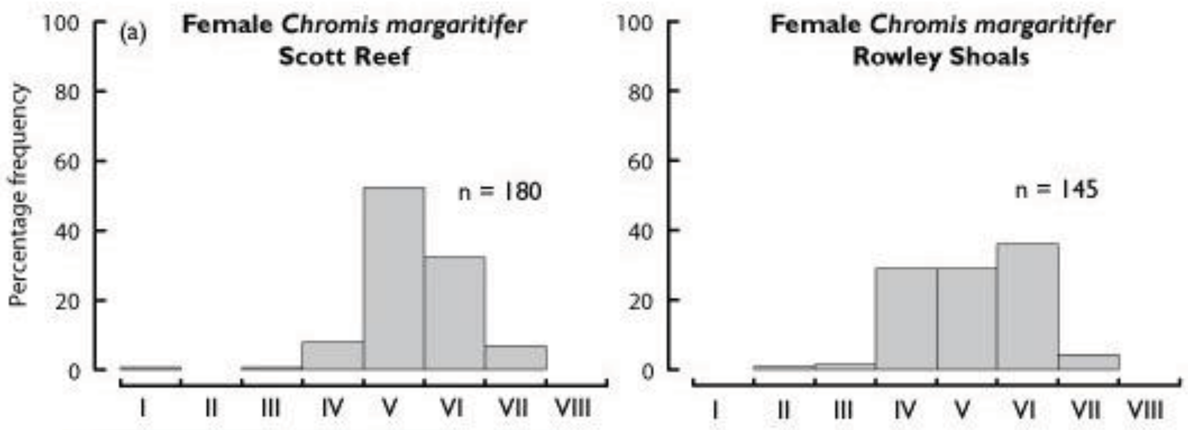
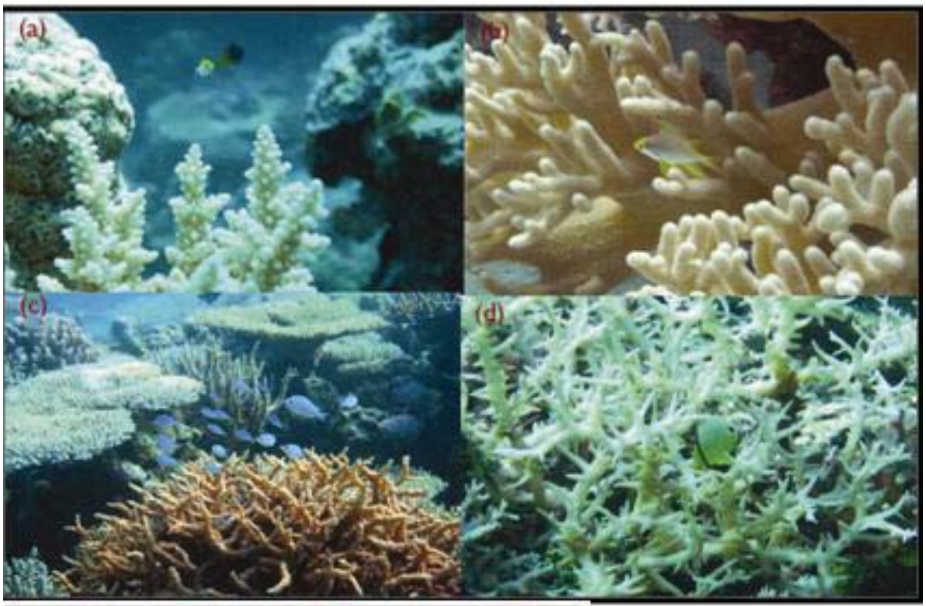


Figure 12.9. (a) Percentage frequencies of occurrence of sequential stages in female ovary development in *Chromis margaritifer* caught at Scott Reef and the Rowley Shoals in April 2008 and (b) photo of a ripe spawning stage VI ovary in a female *Chromis margaritifer*. n = sample size.

Fish nursery habitats

Reef fish species at Scott Reef use a wide variety of habitats as recruitment sites including both hard and soft corals (Figure 12.10). Surveys of fish recruitment at Scott Reef reveal how the juveniles of various fish species partition the use of different habitat types among reef zones. New recruits of the bicolour damselfish *Chromis margaritifer* were predominantly associated with encrusting coral and bare reef in the shallow (< 3m) crest zone (Figures 12.10, 12.11a). Although < 10% of their recruits were recorded in the lower-slope zone (6 to 9m), the numbers of adults recorded in LTM surveys have increased through time at this depth, and this species is now a diagnostic species of the post-bleached fish community at Scott Reef. This suggests an increased availability of the encrusting coral and bare habitat in the shallow reef-crest that are used as recruitment habitats, followed by the movement of individuals down the reef slope as they increase to adult size. In contrast, recruits of the scaly damsel *Pomacentrus lepidogenys* were predominantly associated with soft corals along the mid-slope (6 m) but particularly the deeper lower-slope zones (Figure 12.11b). Young recruits of the Philippines damselfish *Pomacentrus philippinus* were strongly associated with overhanging ledge type habitats in both mid and lower slope reef zones (Figure 12.11c).



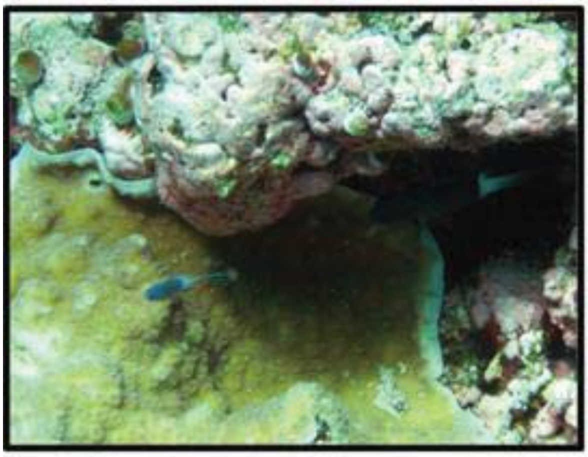


Figure 12.10. Juvenile fish habitats at Scott Reef. Newly settled damselfish sheltering among (a) *Acropora* (b) soft coral and (c) *Acropora* and (d) juvenile butterflyfish among a colony of *Seriatopora hystrix*. All fish rush to shelter in their preferred habitats at the slightest disturbance. A newly recruited bicolour damselfish associated with encrusting coral.

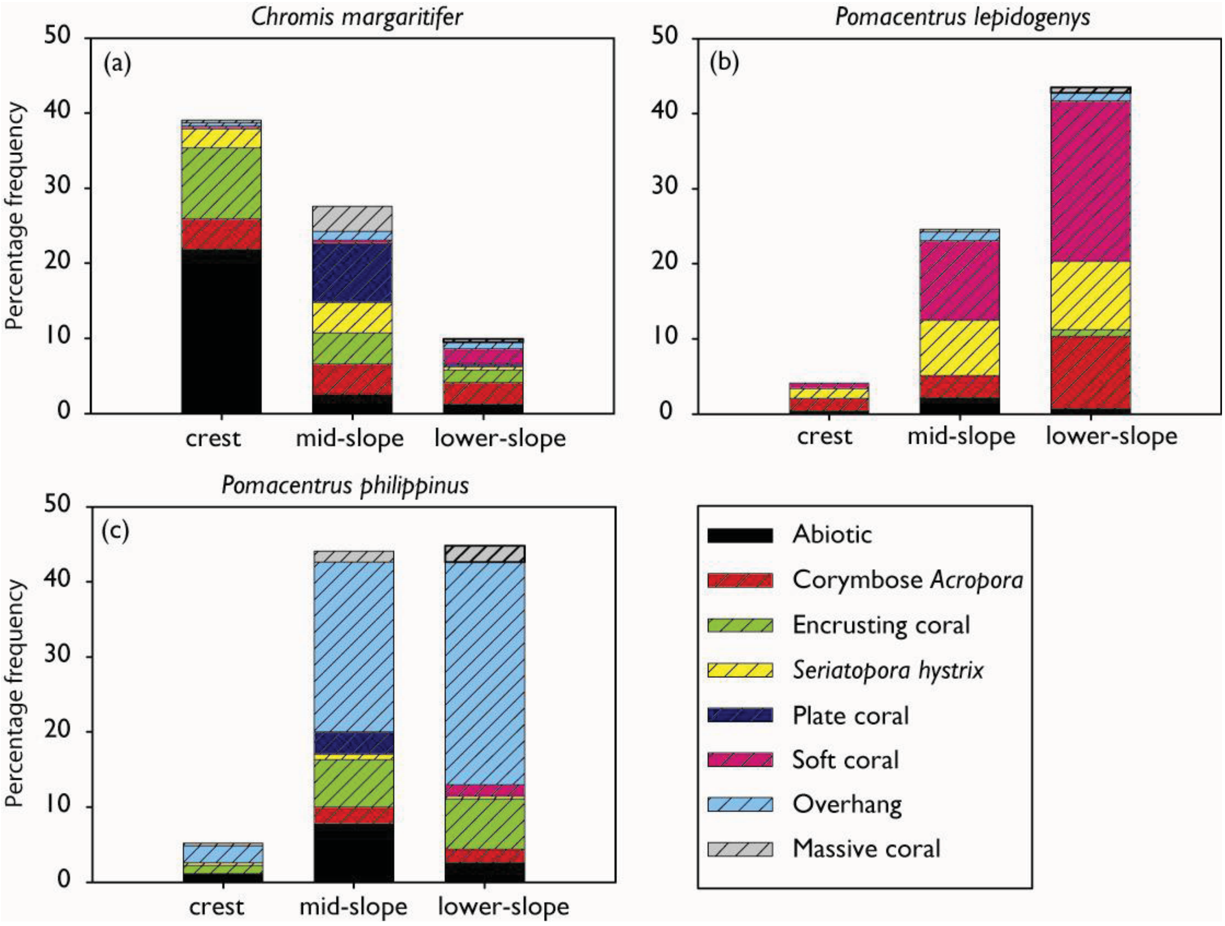


Figure 12.11. Frequency histograms depicting benthic micro-habitat associations of recently settled (< 30 mm) individuals of three pomacentrid species at Scott Reef from data collected between February 2009 and May 2010. Depth zones along reef: crest (3 m); mid-slope (6 m) and lower-slope (9 m).

Knowledge gaps of fishes at Scott Reef

The description of fish recruitment patterns at Scott Reef, in conjunction with measures of environmental variation and microhabitat use of juvenile fish, together provide an insight into aspects of the early life histories of fishes at Scott Reef and complement the large amount of reproductive data collected for corals. However, in order to understand why the fish communities at Scott Reef are not as resilient to disturbances as other reef systems, more data are required to identify the potential environmental and habitat-related drivers of spawning and recruitment of fishes in this system. Furthermore, as genetic analyses have already shown that the recovery of coral and fish populations at Scott Reef is largely based on recruitment from within the reef itself, a sound understanding of the factors promoting successful reproduction and recruitment of fishes is necessary. Additional fish recruitment data from other emergent reef systems in the region (Ashmore Reef and the Rowley Shoals), will also show whether patterns at Scott Reef are specific to that system or are influenced by processes operating at wider scales. This requirement is particularly timely owing to the coral bleaching event at Scott Reef in 2010 and the forecast of a severe bleaching over the 2010-2011 Indian Ocean bleaching season. Following the 2010 coral bleaching at Scott Reef, some fish species were obviously immediately impacted by the sudden changes in their preferred habitats, while other species appeared unaffected (Figure 12.12). Fish recruitment data collected at Scott Reef between 2009 and 2010 can be used to determine whether juvenile fishes utilise different microhabitats as they increase in size (ontogenetic shifts).

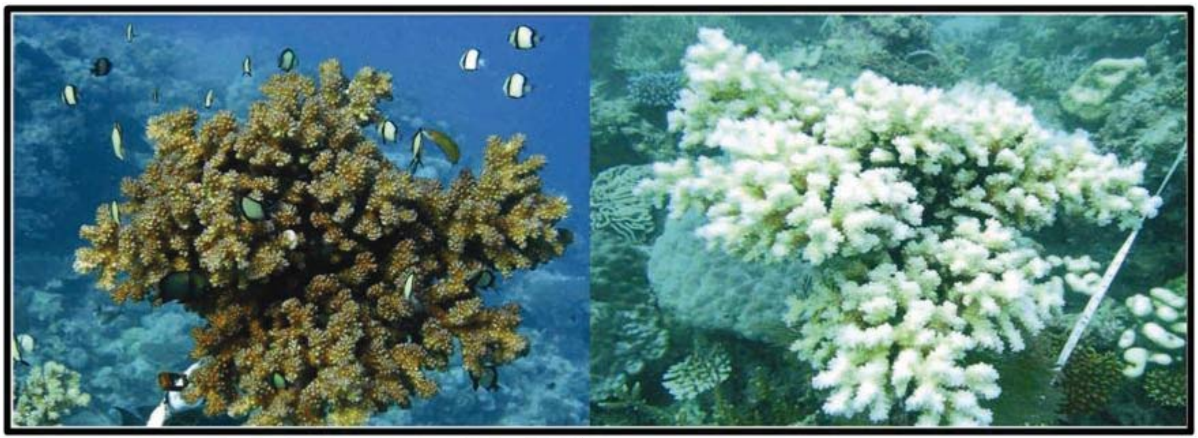


Figure 12.12. A colony of *Pocillopora* hosting resident damselfish (*Dascyllus reticulatus*) at Scott Reef in March 2010 and the same colony again after the May 2010 bleaching and the damselfish have disappeared from the colony. A predatory hawkfish sits perched amongst a bleached colony of its preferred *Pocillopora* from which it launches its attacks on other fish.

13. WATER TEMPERATURE AND SEDIMENTATION REGIMES AT SCOTT REEF

Introduction

Mass coral bleaching is the most severe and widespread disturbance at Scott Reef since the start of monitoring in 1994. In 1998, extreme sea-water temperatures caused mass-mortality of hard and soft corals and the impacts were so severe that they also caused major changes to the fish communities across Scott Reef. The effects of the mass-bleaching in 1998 are still evident today. High water temperatures outside the tolerance range of corals interfere with coral reproduction and feeding, reduce zooxanthellae numbers and reduce zooxanthellae photosynthesis (Coles and Brown 2003). Elevated sedimentation rates have also been identified as a cause of decline in coral cover and diversity on coral reefs around the world (Bellwood et al. 2004). Increased sedimentation rates can result in the smothering of corals, abrasion of coral tissue, reduced sexual recruitment and growth, lower coral growth rates and excess energy expenditure (Rogers 1990; Crabbe and Smith 2005). In some settings, however, certain coral species have been shown to tolerate high sediment loadings (Woolfe and Larcombe 1998) and others use sediments as a source of food, thus benefitting coral health (Rosenfeld et al. 1999; Anthony 2000). As it is often difficult to separate causes of reef decline (Dubinsky and Stambler 1996), long-term research monitoring is important to understand and separate the most significant impacts in particular regions. Monitoring of water temperature across different regions of the reef is necessary in order to identify and understand the cause of future coral mortality, as was the case with the 2010 coral bleaching event. We present physical data associated with the coral reef communities developing at Scott Reef, an isolated atoll system in the north-east Indian Ocean.

Methods

Study area and sampling regime

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

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 (cm^{-2} d^{-1}) = (Weight of sample / Area of trap entrance) / Duration (d)

Calculation of sedimentation rate in this manner allows for cross-study comparisons. A restricted number of samples (one from each location in October 2008) were also studied with a scanning electron microscope (SEM) to determine the mineral composition of various particles within the samples. Samples were analysed for total carbon (TC) content by heating at 1400˚C in an oxygen-enriched atmosphere so that the carbon in the sediment was converted to CO^2 gas. This was carried through drying and particulate removal stages to an IR cell for measurement against standards. A subsample was treated with a 50% Nitric acid solution that reacted with the inorganic carbon (TIC) content only to produce CO^2 gas. This was removed by heating and drying and the residue organic carbon (TOC) was then analysed as for the total carbon and the inorganic carbon content of the sample was calculated by difference.

Data analysis

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

Results and Discussion

Water temperature

Although not as severe as the event in 1998, mass-bleaching also occurred at Scott Reef between March and May 2010 (Chapter 3). The bleaching event coincided with the 2009-2010 El Niño-Southern Oscillation (ENSO) warming conditions and sustained sea surface temperatures above 31˚C (Figure. 13.1). The NOAA Bleaching Watch issued for Scott Reef on 18 February 2010 was upgraded to a Bleaching Warning on 22 March 2010, and to a Bleaching Alert Level 1 (≥ 4 Degree Heating Weeks) on 12 April 2010 (Figure 13.1). This is the first bleaching alert for Scott Reef since NOAA began this programme in 2000.

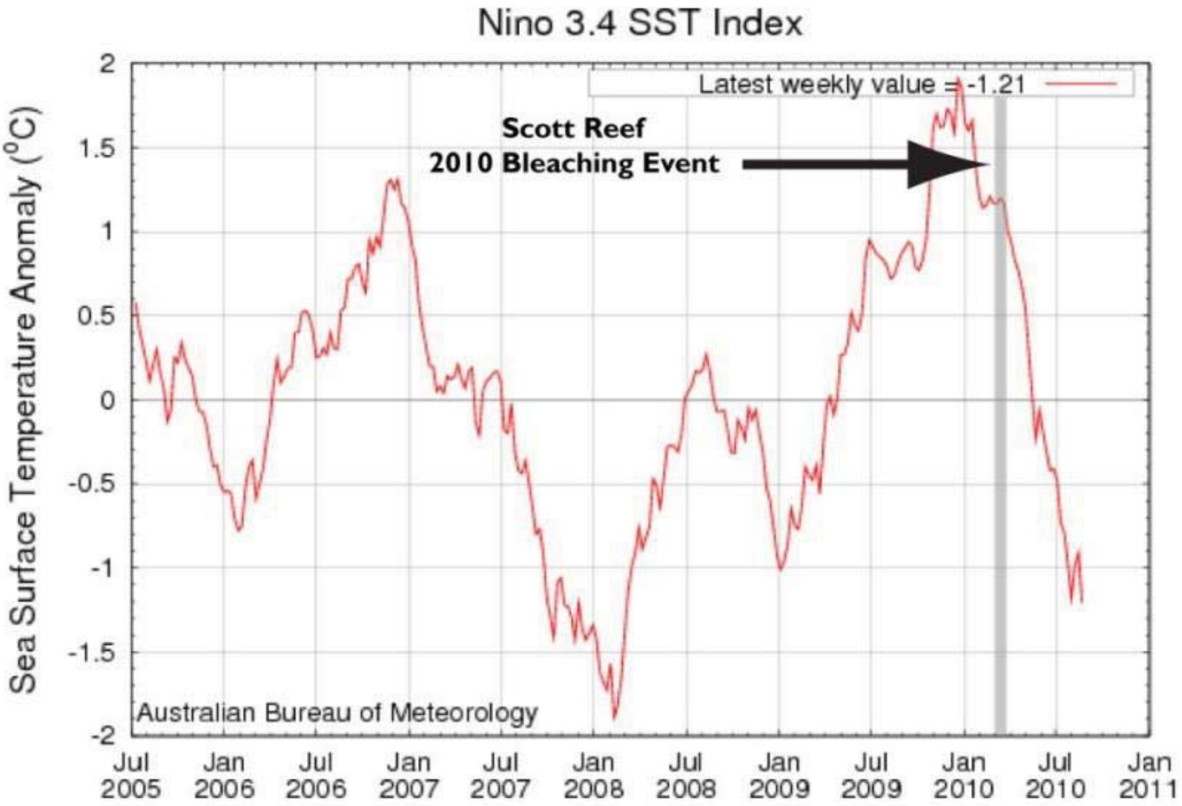


Figure 13.1. El Niño-Southern Oscillation (ENSO) monitoring graph issued by the Australian Bureau of Meteorology showing the peak in the Nino 3.4 SST index in December 2009 and the period of bleaching at Scott Reef between March and May 2010. Monthly values > +0.8 indicate typical El Niño conditions.

Water temperatures at Scott Reef climbed to over 31˚C between March 25 and April 12 2010 and reached 32˚C at SS1 on the exposed eastern edge of north Scott where coral bleaching was moderate to severe (Figure 13.2). Temperatures at most locations showed two peaks during this period with each occurring during either side of the March spring tide, *i.e.* when water movement was lower. Variation in daily temperature range among locations during this period was probably related to the influences of tidal movement and distance to the deep-channel between north and south Scott Reefs and/or distance to oceanic water on the western side of Scott Reef (Figure 13.2). Water temperature at the most southern location on the inner side of south Scott (SL2) where water circulation is low tended not to range more than1˚C in a 24h period, whereas temperatures at locations with high tidal influence and short distances to oceanic input (SL3 and SL4) exhibited wide ranges > 1˚C in a 24 h period (Figure 13.3). The higher water temperatures at Scott Reef during this period also coincided with a period of low wind "doldrum" conditions (Figure 13.4) which has been shown to have an influence on rising water temperatures associated with coral bleaching events (Miller et al. 2009).

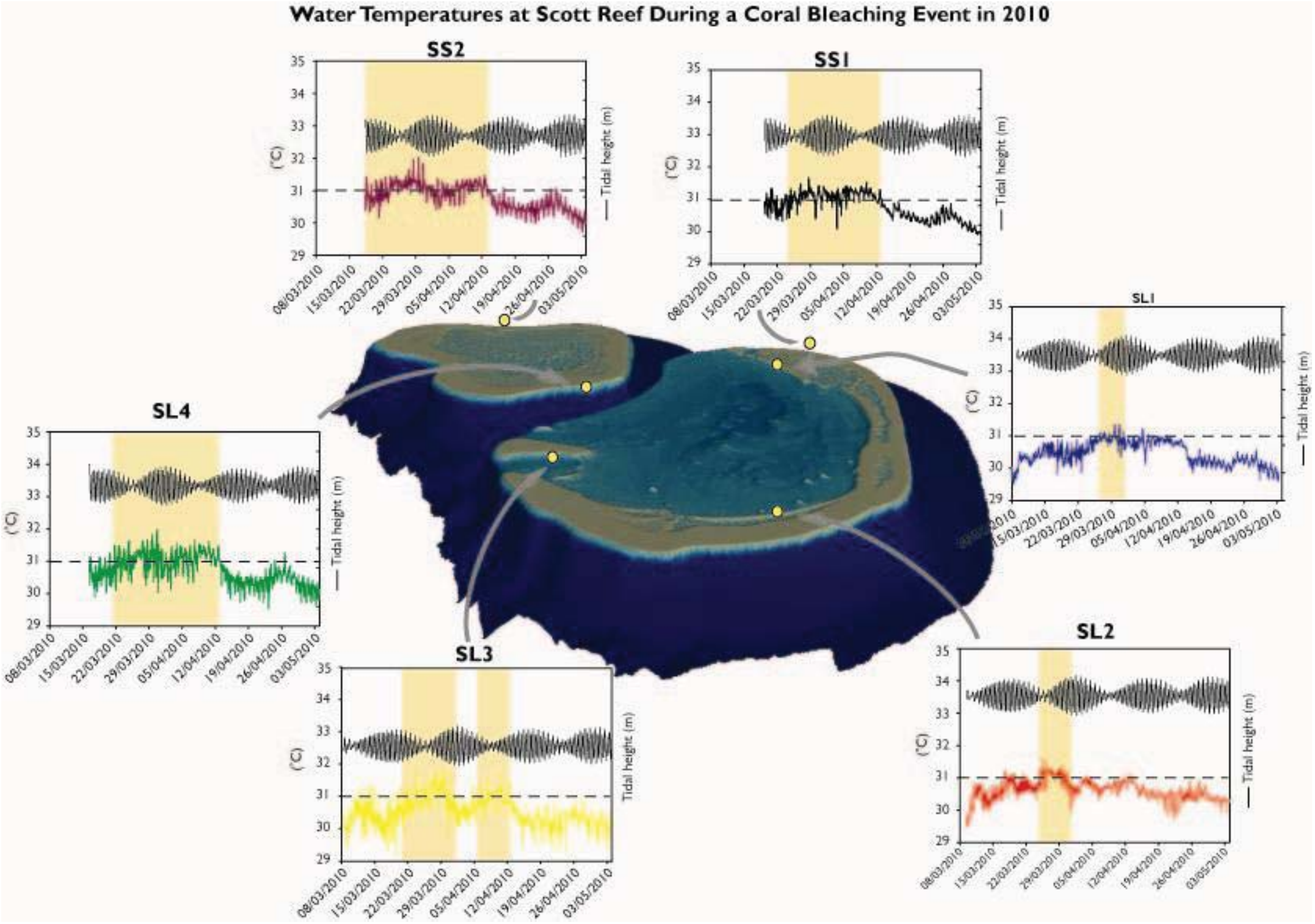


Figure 13.2. Water temperatures during the 2010 coral bleaching event at Scott Reef varied with distance to the deep-channel between north and south Reef and with distance oceanic influence. Inner lagoon locations (SL1 and SL2) recorded temperatures at or just below 31˚C whereas other locations closer to deeper-water showed more extreme ranges both above and below 31˚C.

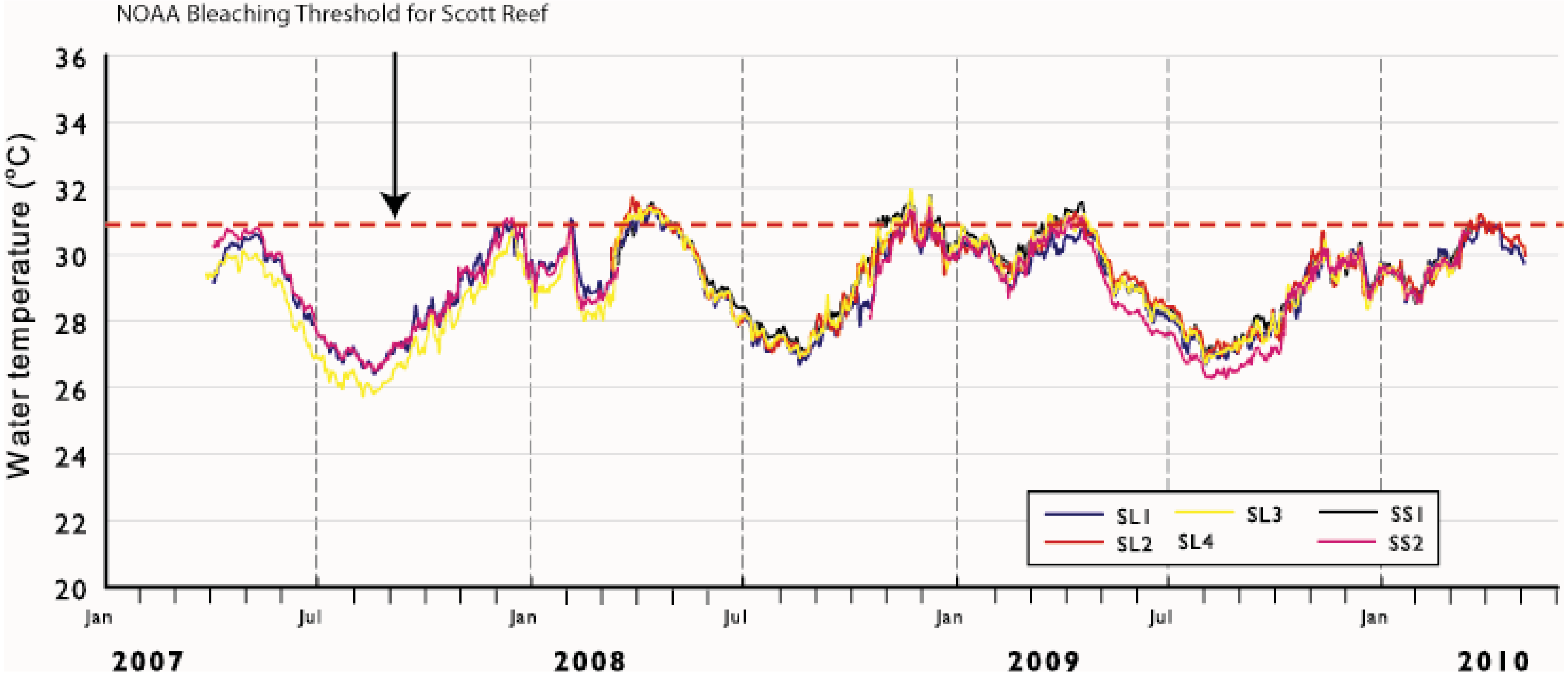


Figure 13.3. Average daily water temperatures recorded at six locations at Scott Reef between April 2007 and May 2010. The NOAA bleaching threshold represents a calculated value that is 1˚C above the maximum mean monthly sea surface temperature at Scott Reef. Temperature loggers deployed at Scott Reef record temperature at 6 to 9m below the surface.

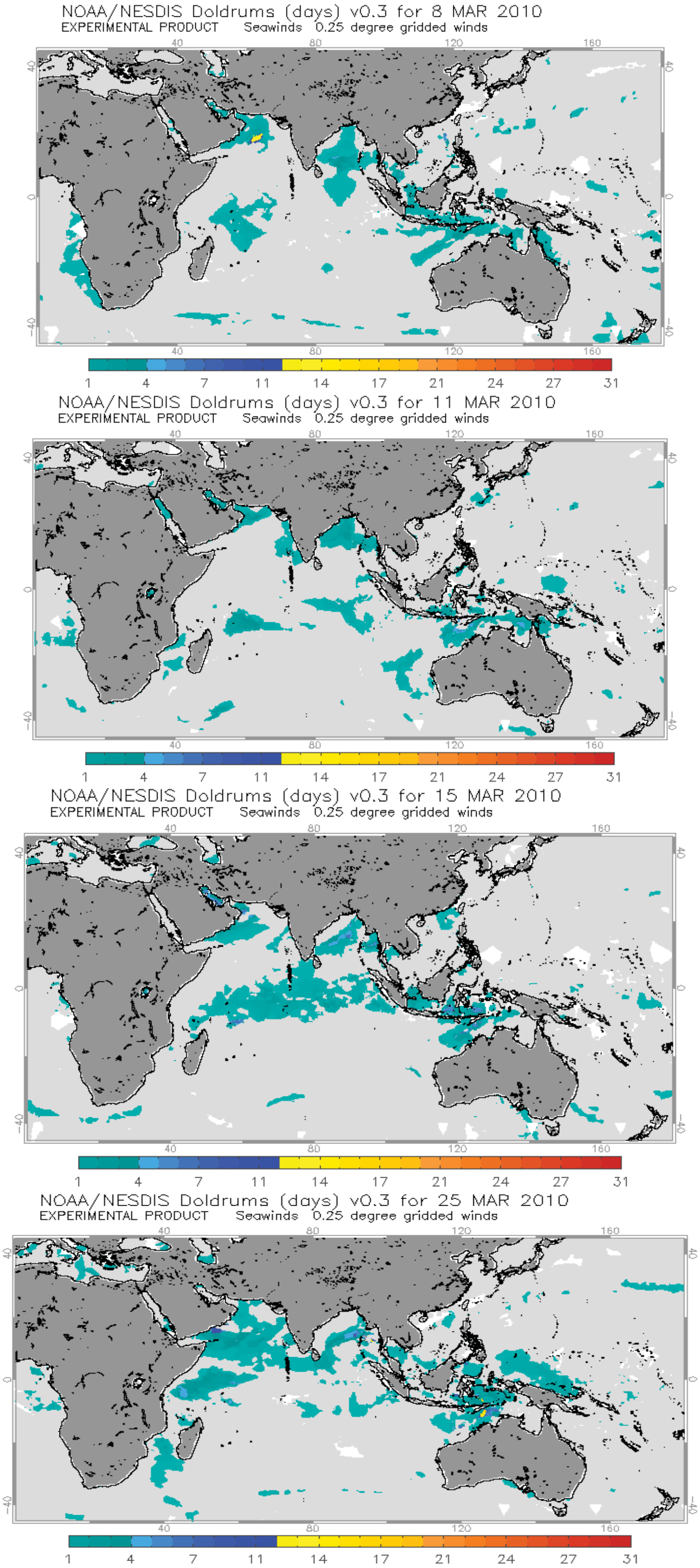


Figure 13.4. Windless “doldrum” conditions experienced during the 2010 bleaching event at Scott Reef and across the northern Indian Ocean where bleaching also occurred in early 2010.

Sedimentation regime

Sedimentation rate

Sedimentation rates in shallow (6 to 9 m) water depths at Scott Reef differed significantly among seasons ($P < 0.05$) and locations ($P < 0.001$) but not among years and all interactions were significant (Table 13.1). In terms of main effects the mean square was far greater for location (0.22) than for season (0.06), however the highest mean square was recorded for the interaction between year and season (0.39). Mean sedimentation rates tended to be lower than 2 mg cm^{-2} d^{-1} at all locations, particularly at SL1 and SL2 (Figure 13.5). However, sediment rates greater than this were recorded at certain locations when exposed to seasonal onshore winds. For example, rates at SL3 and SL4 are greater during the summer periods when these locations are exposed to frequent westerly winds, whereas the highest rates at SS1 and SS2 are recorded during the autumn through spring period when easterly winds are onshore at the eastern outer reef edge.

Particle size distribution

Three-way ANOVA showed that mean sediment grain-size differed significantly among years, seasons and locations (all $P < 0.001$) and there were significant interactions between these factors (Table 13.1) The mean squares were greatest for the main effects of time of year (2.11) and location (0.43) than for the interactions. Mean grain size was consistently smallest (*ca* 50 µm) at the most protected location where water circulation is least (SL2) and was over 200 µm at SL3 and SS2 during the seasons when these locations were exposed to onshore winds, *i.e.* summer in the case of SL3 and winter in the case of SS1 and SS2 (Figure 13.6).

Small sediment grain size (clay and silt) characterised (> 80%) the most protected lagoon location (SL2) in all seasons due to the lower water circulation regime at this location from a small influence of tides and a greater protection from winds (Figure 13.7). In contrast, at locations more exposed to seasonal winds larger grain sizes contributed > 60% to sediments such as during the summer period at SL3 when westerly winds dominate and in winter on the east side of the reef when easterly winds are onshore.

Table 13.1. Mean squares (MS) and their significance levels (*P*) for ANOVAs of the sedimentation rate and sediment size in summer, autumn and spring at six locations at Scott reef between 2008 and 2010. df, degrees of freedom. Bold face indicates significant results.

		Sedimentation rate		Sediment size	
	df	MS	*P*	MS	*P*
Year	1	0.01	0.751	2.11	**< 0.001**
Season	2	0.06	**< 0.05**	0.28	**< 0.001**
Location	5	0.22	**<0.001**	0.43	**< 0.001**
Year × season	2	0.39	**<0.001**	0.05	0.097
Year × location	5	0.08	**<0.001**	0.09	**< 0.01**
Season × location	10	0.26	**<0.001**	0.07	**< 0.01**
Year × season × location	8	0.15	**<0.001**	0.11	**< 0.001**
Residual	124	0.01		0.02	

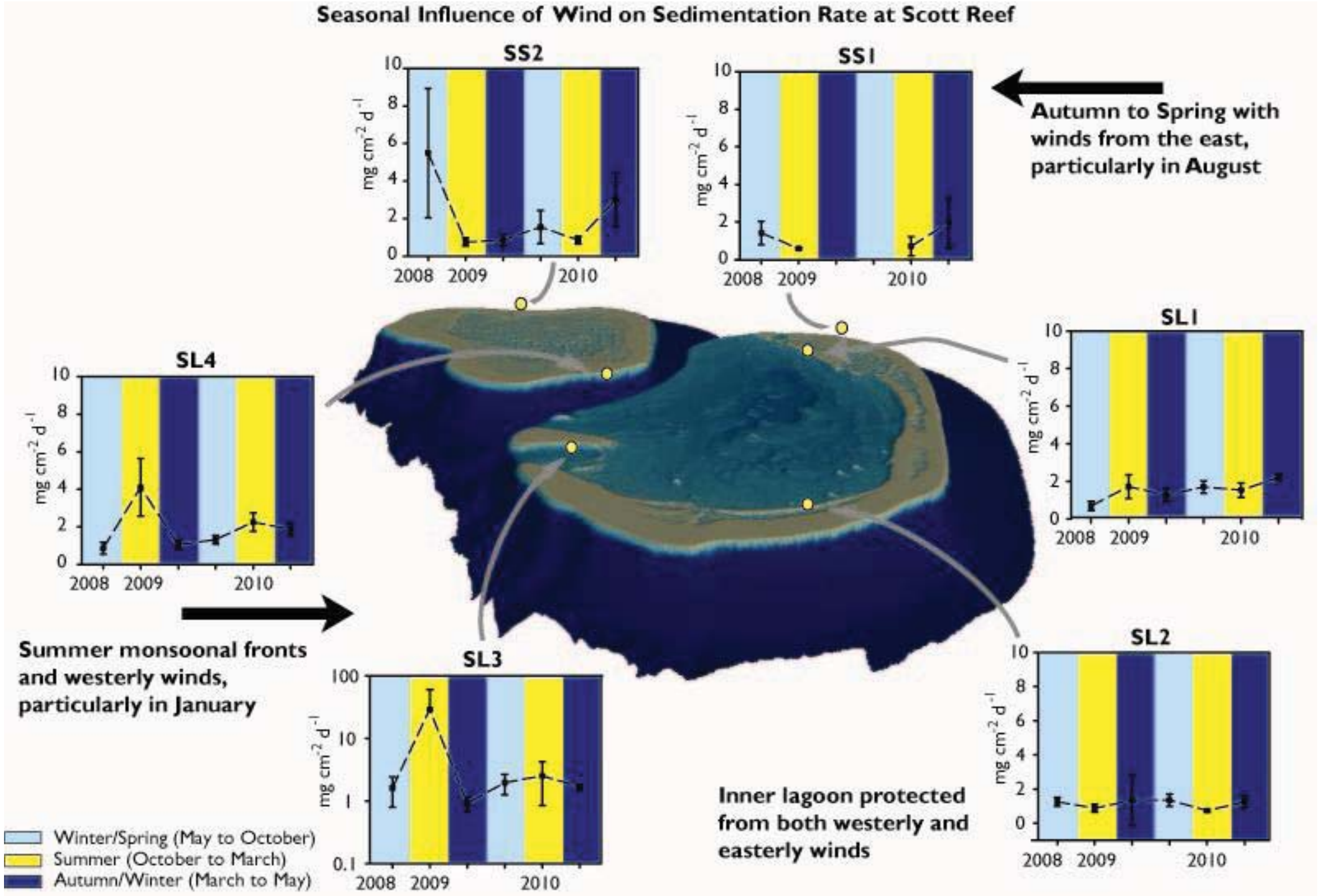


Figure 13.5 Variation in mean sedimentation rates across regions at Scott Reef that differ in their tidal water movement and wind and wave exposure. Locations within the protected inner reef where exposure and tidal circulation are least such as SL2 have low rates throughout the year whereas more exposed locations have higher rates, particularly in the seasons when they are exposed to the predominate wind directions, i.e. summer on the western side of the reef (SL3 and SL4) and autumn through spring on the eastern side of the reef (SS1 and SS2).

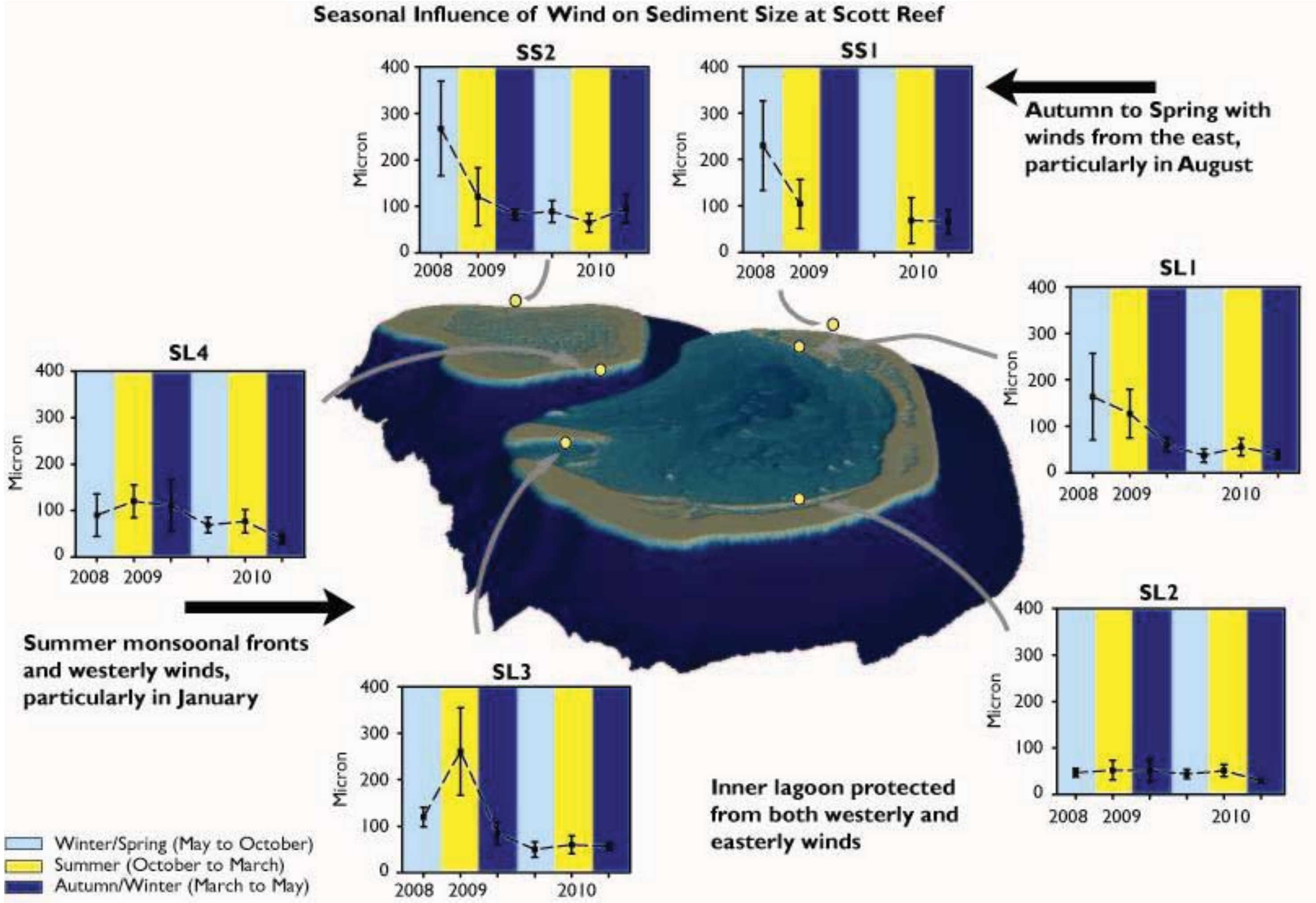


Figure 13.6 Variation in mean sediment size across regions at Scott Reef that differ in their tidal water movement and wind and wave exposure. Locations within the protected inner reef where exposure and tidal circulation are least such as SL2 have low medium size throughout the year whereas more exposed locations have larger mean sizes, particularly in the seasons when they are exposed to the predominate wind directions, i.e. summer on the western side of the reef (SL3 and SL4) and autumn through spring on the eastern side of the reef (SS1 and SS2).

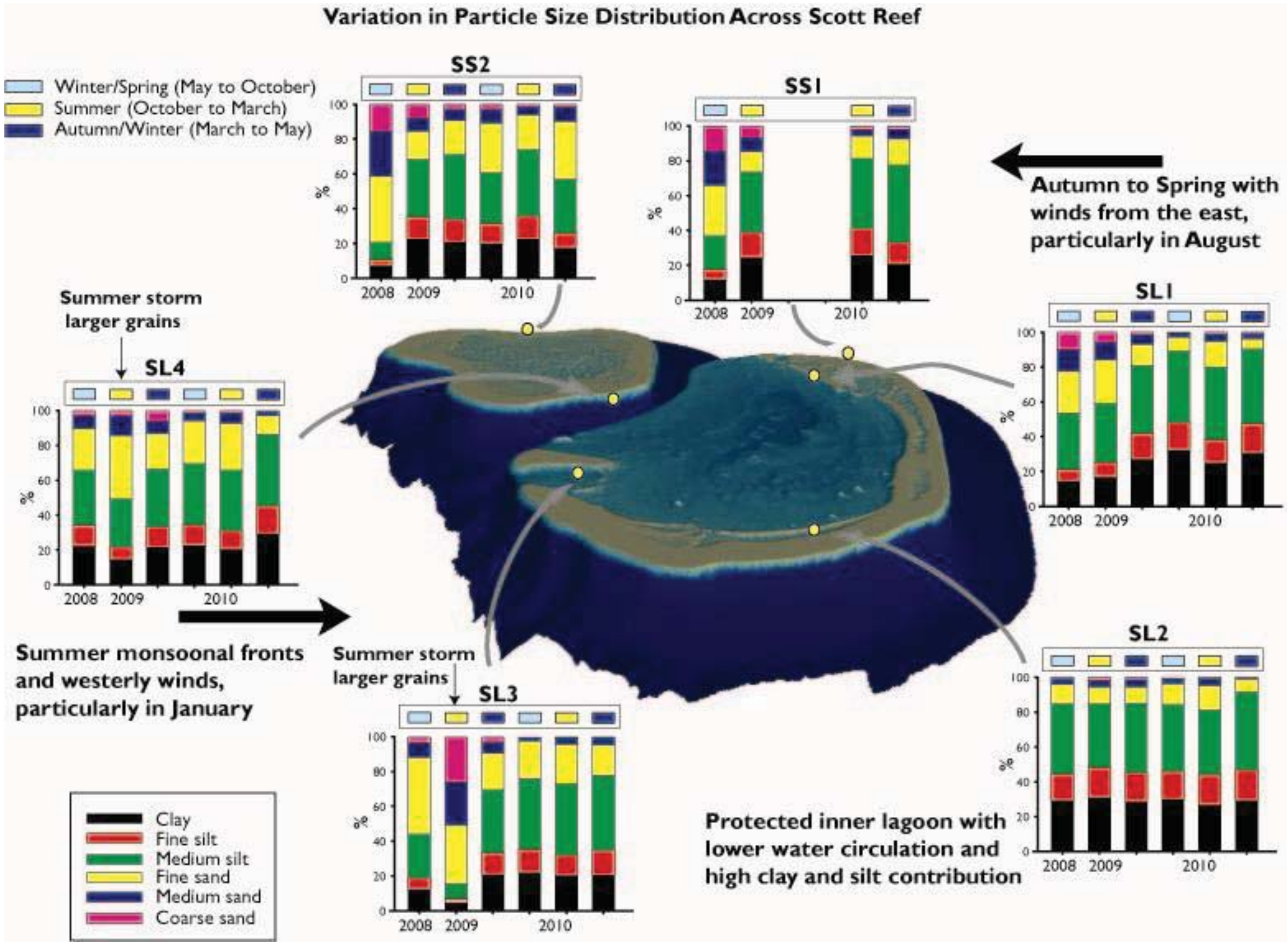


Figure 13.7 Variation in particle size distribution across regions at Scott Reef that differ in their tidal water movement and wind and wave exposure. Locations within the protected inner reef where exposure and tidal circulation are least such as SL2 have high clay and silt contributions throughout the year whereas more exposed locations have higher concentrations of sand sized particles, particularly in the seasons when they are exposed to the predominate wind directions, i.e. summer on the western side of the reef (SL3 and SL4) and autumn through spring on the eastern side of the reef (SS1 and SS2)

Comparisons with other regions

The mean sedimentation rates at Scott Reef between May 2008 and May 2010 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 summer, 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 summer 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. 2005b) and in coastal waters of Hawaii (Bothner et al. 2006) and Mexico (Fernandez and Perez 2008). For example, rates during the dry season in Mexico were 6.8 to 73.5 mg cm^{-2} d^{-1} whereas during the wet season they reached 147.6 cm^{-2} d^{-1} (Fernandez and Perez 2008). The height of wind-induced waves is thought to largely control patterns of suspended sediment on the GBR and thus largely influences the conditions for these coral communities (Larcombe et al. 1995).

Significance of variation in particle size

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

The total contribution of carbon to the sediment samples at all locations at Scott Reef was small (*ca* 12%) and was almost entirely composed of inorganic carbon with only a slight contribution of organic carbon (Table 13.2). SEM analyses demonstrated that the sediment was mostly calcium based.

Table 13.2 Percentage contributions of total carbon (TC), total inorganic carbon (TIC) and total organic carbon (TOC) in a single sediment trap sample from each of the six locations at Scott Reef in October 2008.

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

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