

Appendix F24

Gilmour et al. 2013a

Long-term Monitoring of Shallow Water Coral and Fish
Communities at Scott Reef 2012



BROWSE FLNG DEVELOPMENT
Draft Environmental Impact Statement

EPBC 2013/7079
November 2014

Long-term monitoring of shallow water coral and fish communities at Scott Reef 2012



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REPORT PRODUCED FOR
WOODSIDE ENERGY LTD
AS OPERATOR OF THE
BROWSE LNG DEVELOPMENT

**PERTH
2013**



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This report should be cited as:

Gilmour et al 2013;. Long-term monitoring of shallow water coral and fish communities at Scott Reef 2012; for Woodside Energy Ltd as Operator of the Browse LNG Development. Australian Institute of Marine Science, Townsville. (64pp)

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Revision History

Rev 0 5th November 2013

Rev 1 10th November 2014

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Preamble

Background and Scope of Works

The Australian Institute of Marine Science (AIMS) undertook field work at Scott Reef in November 2012 to monitor benthic and fish communities in accordance with an on-going Co-investment Agreement with Woodside Energy Ltd (WEL). The Scott Reef Research Project (SRRP) has been running for the past 15 years, and as such, provides one of the longest running and most comprehensive studies of coral reef ecosystems, and valuable insights into tropical coral reef ecology.

The scope of the most recent field trip ('SRRP 2012') included on-going long-term monitoring of shallow water coral and fish communities, as well as deployment of temperature loggers and sediment traps. All data collection was completed at Scott Reef in November 2012 as outlined in the co-investment contract, of which the analyses and results are presented herein.

1. Executive Summary

The coral communities at Scott Reef have been impacted by two disturbances between monitoring surveys in 2010 and 2012 - a moderate bleaching event and a severe monsoonal storm. These disturbances affected a subset of sites and coral groups, but the cumulative effect was to reduce mean cover of hard and soft corals at monitoring sites (9 m depth) across Scott Reef for the first time since the mass bleaching in 1998. The impact of the storm in 2012 was so severe at the Inner West Hook and at the Channel between North and South Reef that communities returned to a similar cover and structure as that following the mass bleaching in 1998. The impact was far less at Inner East Hook, but still caused small decreases in coral cover and killed approximately 80% of the most susceptible corals (Acroporidae). At all other locations, there had been small increases in the cover of hard and soft corals since 2010, although these increases were less than expected due to the combined effect of bleaching and storm disturbances.

Since the mass-bleaching in 1998, the fish community at Scott Reef has undergone significant changes in composition and remains different to the assemblage prior to the disturbance. Here we extend this long-term dataset to describe the progression of the fish community between October 2010 and 2012. Of particular note is the decline of carnivorous and planktivorous fishes, which decreased in abundance by 33% and 38% respectively since 2010; there was also a sharp increase of 82% in abundance of detritivores and 18-year record densities of corallivores, in line with the near full recovery of the coral community. Planktivorous fishes were largely composed of damselfishes (Pomacentridae) that also markedly declined in abundance by 35% from the 2010 surveys. Despite this decline, damselfishes have a long history of instability at Scott Reef, a feature that is most likely attributable their life history traits, high recruitment variability and status as prey species on coral reefs. The same cannot be said for the carnivores, which have switched from being a very stable group at Scott Reef to recent reductions from previous surveys in 2010 of 11% and a further 33% in this most recent survey. Considering that Scott Reef fishes may rely strongly on self-replenishment, a reduction in reproductive adults threatens the integrity of stocks within the ecosystem. On-going traditional fishing in the region may be a possible explanation for the decline in this group. Future surveys should collect additional abundance and size-structure information for this important group to address the likely causes of their decline.

2. A summary of disturbance at Scott Reef: 1994-2012

In the last 20 years, by far the most significant disturbance to have impacted monitoring locations (9 m depth) at Scott Reef was the mass-bleaching of corals in 1998, and all subsequent changes at the reef have been interpreted in the context of that disturbance (Figure 2.1). The mass bleaching was due to extremely high water temperatures through March and April 1998. The cumulative Degree Heating Weeks (DHW) for the period, a measure of the temperature stress issued by NOAA (NOAA), reached 13.3 °C week⁻¹. The mass bleaching killed most of the shallow water (< 20 m) corals at Scott Reef, causing relative decreases in cover of between 70 and 90% (Figure 2.1, Gilmour *et al.* 2013). Recovery from the mass bleaching was slowed by cyclones in 2006 and 2007, but by 2008 many of the coral communities were recovering well. Further recovery was again slowed by an outbreak of disease and a second, but less severe, coral bleaching in 2010 (Gilmour 2011). However, by the end of 2010 most coral communities had largely recovered from the mass bleaching in 1998 and were sustained by high rates of coral recruitment (Gilmour *et al.* 2013).

Since 2010, there have been two significant disturbances at Scott Reef that have contributed to a mean reduction in cover of hard and soft corals between 2010 and 2012- a moderate coral bleaching in 2011 and a severe storm, probably in early 2012. There was also a moderate coral bleaching in February 2013, but its effects were not captured in the most recent quantitative monitoring survey in October 2012. In 2010, water temperatures at Scott Reef were higher than normal from February to April, and again in December (Figure 2.1A, Gilmour *et al.* 2011). Prolonged periods of high water temperatures lead to NOAA issuing a Bleaching Alert Level I for Scott Reef during March 2010, given cumulative Degree Heating Weeks (DHW; °C week⁻¹) of $4 \leq \text{DHW} < 8$, and Bleaching Warnings ($0 < \text{DHW} < 4$) were issued in December 2010, and again from December 2011 to February 2012. A Bleaching Alert Level I ($4 \leq \text{DHW} < 8$) was issued during February 2013, with a prolonged period of heating from January to May. The bleaching event in March 2010 affected approximately 5% of corals, primarily from a subset of families (e.g. Fungiidae, Pocilloporidae) and locations (e.g. Outer South, Outer North reef) (Figure 2.2, Gilmour *et al.* 2011). The effects of the more recent temperature anomalies have not been directly quantified, but qualitative observations also suggested that around 5% of colonies, from a subset of coral families and locations, had bleached during December 2011 and/or in February 2013.

At least three cyclones have impacted Scott Reef since monitoring commenced in 1994, but there have been no apparent impacts in recent years (Figure 2.1B). However, a monsoonal storm caused significant damage to the reef and its coral communities. The storm probably occurred in early 2012 and was responsible for mean decreases in the cover of hard and soft corals at Scott Reef between 2010 and 2012 (Figure 2.1C); the first since the mass-bleaching in 1998. The cover of hard corals in 2012 was reduced to 36.7%, similar to that in 2008, and the soft corals reduced to 2.5%, similar to that shortly after the mass-bleaching in 1998. However, these mean changes were driven primarily by large decreases in cover of the most susceptible corals at the locations most exposed to the monsoonal storm (Figure 2.1D & E).

Monsoonal storms occur predominantly during the summer months, and produce strong winds and waves from a westerly direction. Consequently, coral communities on the outer western edge of Scott and Seringapatam Reefs are sparse, and typically have a cover of < 5%. Of the inner slope communities, those most exposed to the recent monsoonal storm were at the Inner West h Hook and the Channel locations (Figure 2.2A), where there were relative decreases in cover of hard and soft corals of 55 to 75%, between 2010 to 2012 (Figure 2.2). At these locations, the storm damaged the reef structure and overturned massive boulders and coral bommies. The most fragile corals (e.g. Acroporidae, Pocilloporidae) were severely impacted, having relative decreases in cover of >75%, but all coral groups were affected; the relative cover of soft corals decreased by between

55% and 75%, and even the massive and encrusting corals decreases by between 15% and 50% (Figure 2.2). The community at the Inner East Hook location was also impacted by the storm, decreasing in cover by a few percent. However, only the most fragile corals were affected at the Inner East Hook, with relative decreases in cover of Acroporidae by 35% and Pocilloporidae by 16%, while all other groups of corals increased between 2010 and 2012.

The coral communities at the Inner Lagoon, and at the outer slope locations on the eastern side of South Reef, North Reef and Seringapatam, were comparatively sheltered from the effects of the monsoonal storm in 2012 (Figure 2.2). The cover of hard corals at the Inner Lagoon increased by approximately 10% between 2010 and 2012, as this community was worst affected by the outbreak of disease and bleaching in 2010 (Figure 2.1). The increases in coral cover at the Inner Lagoon were primarily Acroporidae, Pocilloporidae, and the Echinopora and foliose corals unique to this community; massive corals and soft corals are rare (Figure 2.2). By comparison, at the outer slope communities (Outer South, Outer North, and Outer Seringapatam) there were smaller increases in cover of soft corals (< 1%) and hard corals (1-5%), which were mostly the Acroporidae and/or Pocilloporidae (Figure 2.2). At the outer slope communities, there were small decreases (< 2%) in the cover of encrusting and massive corals, either due to their being concealed from view by the growth of other corals, or being impacted by the bleaching event in 2011.

To compound environmental disturbances at Scott Reef, on-going traditional fishing by Indonesian fishers in the MOU Box (est. 1974) has likely contributed to observed reductions in commercially important invertebrates (e.g. trepang and trochus), reef sharks, and potentially reef fish. Shark populations in particular are over exploited at Scott Reef compared to reefs located to the south at the Rowley Shoals (Meekan *et al.* 2006). Previous reports from Scott Reef observed that there had been an increase in some families of reef fish such as emperors, coral trout, and groupers, which might be indicative of a reduction in piscivores and sharks (Gilmour *et al.* 2010); this process is known as 'predator release'. However, more recent declines in carnivorous fish species at Scott Reef might be at least partially attributable to pressure from traditional fishers switching from shark species to other more readily available fish such as a range of emperors, red bass, and coral trout, as observed in Australian Fisheries Management Authority (AMSA) creel surveys. These patterns are not uncommon throughout coral reef ecosystems worldwide, and may be indicative of a practice known as 'fishing down food webs', where once higher order predator stocks have been depleted, meso-predators, and finally herbivores are systematically removed (Pauly *et al.* 1998). Overfishing is one possible explanation for the recent declines in these higher level trophic groups at Scott Reef.

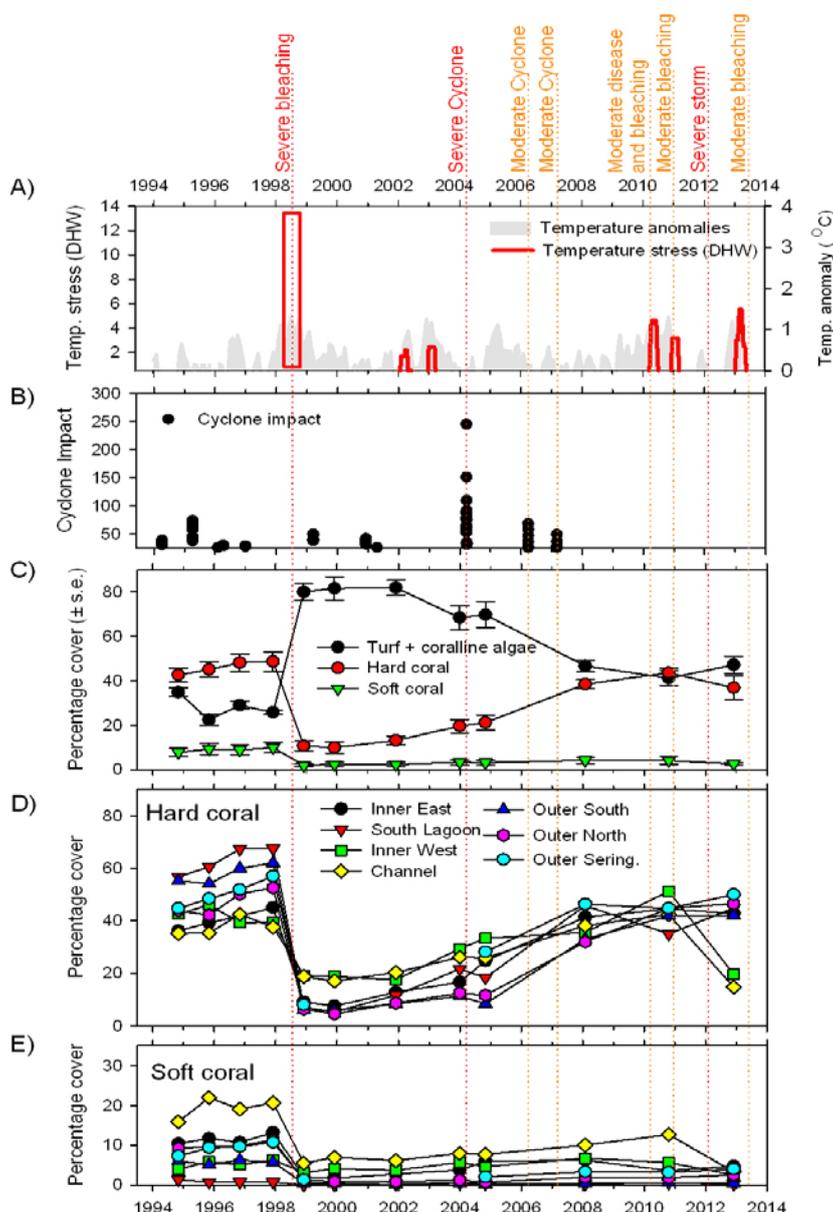


Figure 2.1 Disturbances and changes to coral communities at monitoring location (9 m depth) at Scott Reef. A) Temperature stress is measured by temperature anomalies and Degree Heating Weeks (DHW). DHW $>4^{\circ}\text{C week}^{-1}$ are indicative of coral bleaching and of $>8^{\circ}\text{C week}^{-1}$ indicative of severe coral bleaching and mortality. Severe bleaching occurred in 1998 and moderate bleaching in 2010, 2011 and 2013. Associated with the bleaching event in 2010 was a moderate outbreak of coral disease. B) Cyclone exposure at Scott Reef. The exposure index incorporates the distance of the cyclone from Scott Reef and its central pressure. Severe cyclone damage occurred in 2004, and moderate cyclone damage in 2006 and 2007. A severe monsoonal storm affected Scott Reef in early 2012. C) Mean changes in the cover of hard corals, soft corals and turfing and coralline algae at locations across Scott Reef. There were consistent increases in mean coral cover following the mass bleaching in 1998, until the decreases in hard and soft corals following the severe storm in 2012. Changes in the cover of C) hard and D) soft corals varied among the locations across Scott Reef, mainly due to their exposure to disturbances. By 2010, hard corals at most locations had recovered from the mass bleaching in 1998, whereas soft corals at most locations had not. Hard corals at the Inner Lagoon were worst affected by the outbreak of disease and bleaching in 2010; both hard and soft corals at the Inner West and Channel locations were worst affected by the severe storm in 2012, and those at the Inner East location were moderately affected.

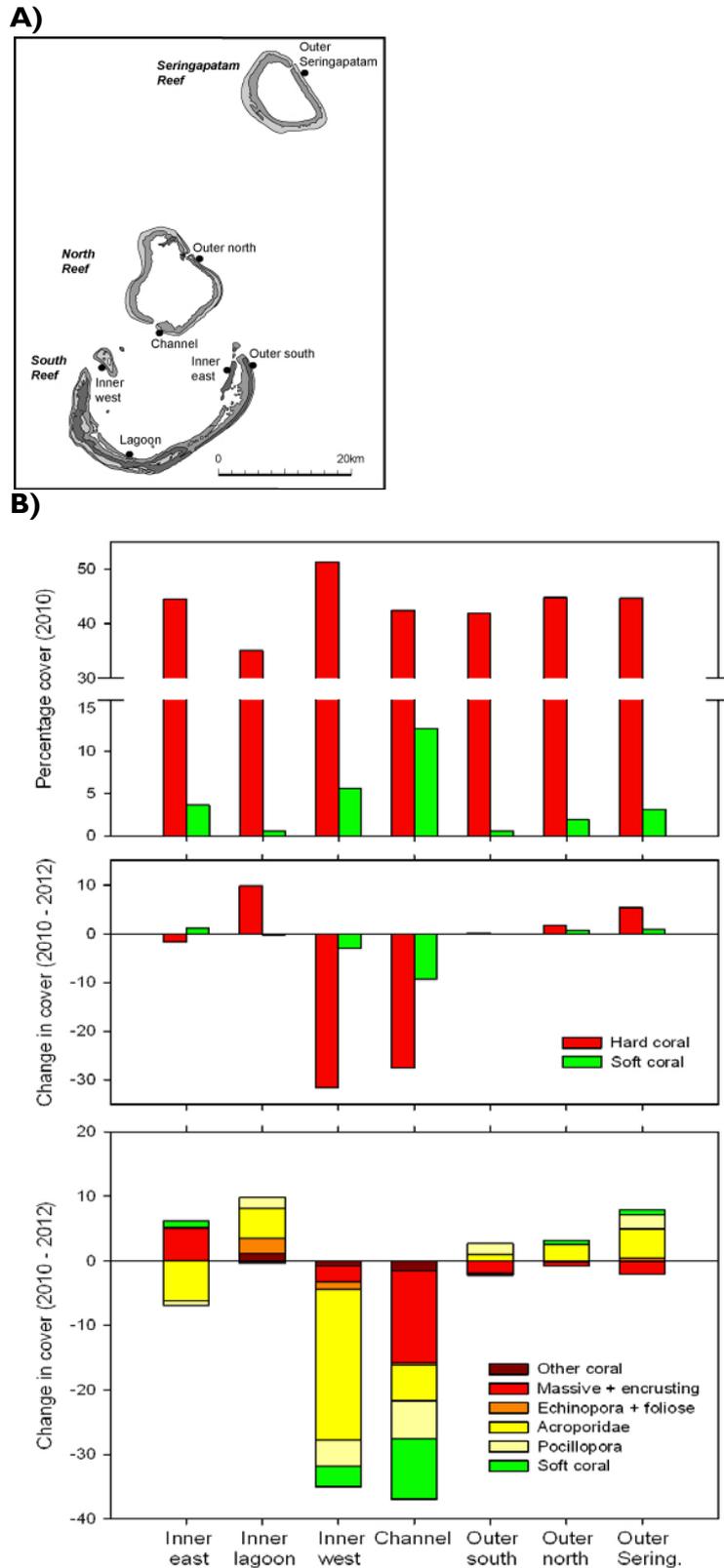


Figure 2.2 A) Long-term monitoring locations (9 m depth) at Scott Reef and B) the changes in coral communities between 2010 and 2012, following exposure to a moderate bleaching event and a severe storm.

3. Long-term monitoring of coral communities

3.1 Introduction

Coral reefs are dynamic ecosystems that have adapted to variation in habitat conditions and exposure to disturbances over a variety of spatial and temporal scales. The influence of routine habitat conditions on the distribution and structure of coral communities has been widely documented (Fabricius *et al.* 2012; Done 1982; Woesik van and Done 1997; Ninio and Meekan 2002; van Woesik *et al.* 1999). Against these background conditions, coral communities are structured by acute disturbances of varying severity. Acute disturbances (e.g. cyclones, bleaching, crown-of-thorns outbreaks) occur periodically, with corresponding cycles of recovery (Reichelt *et al.* 1990; Miller 2002; Done 2010). Among these disturbances, tropical cyclones are historically one of the most important drivers of change (Dollar and Tribble 1993; Connell 1978; Hughes 1989; Bythell *et al.* 2000). Cyclones tend to have highly localised and selective impacts that influence species diversity and structural complexity of reefs (Glynn *et al.* 1998; Done 1992; Connell 1978; Karlson and Hurd 1993). Recently, global warming has exposed coral reefs to disturbances that are more frequent, severe and widespread (Hoegh-Guldberg *et al.* 2007; Hoegh-Guldberg 1999; Harvell *et al.* 2002). In particular, reefs are now exposed to coral bleaching and outbreaks of disease that can impact communities over broad spatial scales, and evidence suggests the severity of monsoonal storms and tropical cyclones may also be increasing. Predictions of an increased frequency and severity of disturbances have led to concerns about the resilience of coral reef communities to this increased disturbance regime (Hoegh-Guldberg 2004; Hughes *et al.* 2003).

Assessing the resilience of coral communities to changing regimes of disturbance requires long-term data over large spatial scales. Recovery of impacted areas will be driven by either regrowth of remnant corals (Gleason 1993; Kayanne *et al.* 2002; van Woesik *et al.* 2011) or recolonisation through recruitment from unaffected areas (Schuhmacher *et al.* 2005; Golbuuet *et al.* 2007; Graham *et al.* 2011; McClanahan *et al.* 2012). As such, the spatial scale and frequency of disturbance determines reef resilience and differences in recovery trajectories have been attributed to reef isolation (Graham *et al.* 2006; Ledlie *et al.* 2007) and disturbance frequency (Cheal *et al.* 2010; Baker *et al.* 2008). Communities that return to previous levels of coral cover within years to decades after impact may be considered resilient (Smith *et al.* 2008; Golbuu *et al.* 2007; Done *et al.* 2010); however, the return to a prior percentage cover alone is a low criterion for recovery. Of greater relevance to the restoration of reef-building capacity, structural complexity and biodiversity is the degree to which the structure of coral communities is restored (Adjeroud *et al.* 2009; van Woesik *et al.* 2011, Hughes 2003; Done 1992). In this study, we monitor spatial and temporal changes in the structure of coral communities at Scott Reef over 19 years, through regimes of disturbance of varying scale and severity, and assess the extent to which communities return to their pre-disturbance states through time. We synthesise biological and environmental data and examine the degree to which routine habitat conditions, disturbance regimes and coral life histories influence the resilience of communities.

3.2 Methods

3.2.1 Study sites

Scott Reef is a large atoll-like reef system on the edge of the continental shelf, 270 km from the mainland of north-western Australia (Figure 3.1). The system consists of South Reef, North Reef and Seringapatam Reef. Benthic communities and habitat conditions were studied at seven locations (Figure 3.1) on the reef-slope (≈ 9 m) habitat at all reefs. Outer-slope locations were on the eastern

side of South Reef (Outer South East), North Reef (Outer North East) and Seringapatam Reef (Outer Seringapatam). Inner-slope locations were adjacent to the West Hook (Inner South West) and East Hook (Inner South East) at South Reef, at the lagoon at South Reef (South Lagoon), and the channel between South and North Reef (Channel).

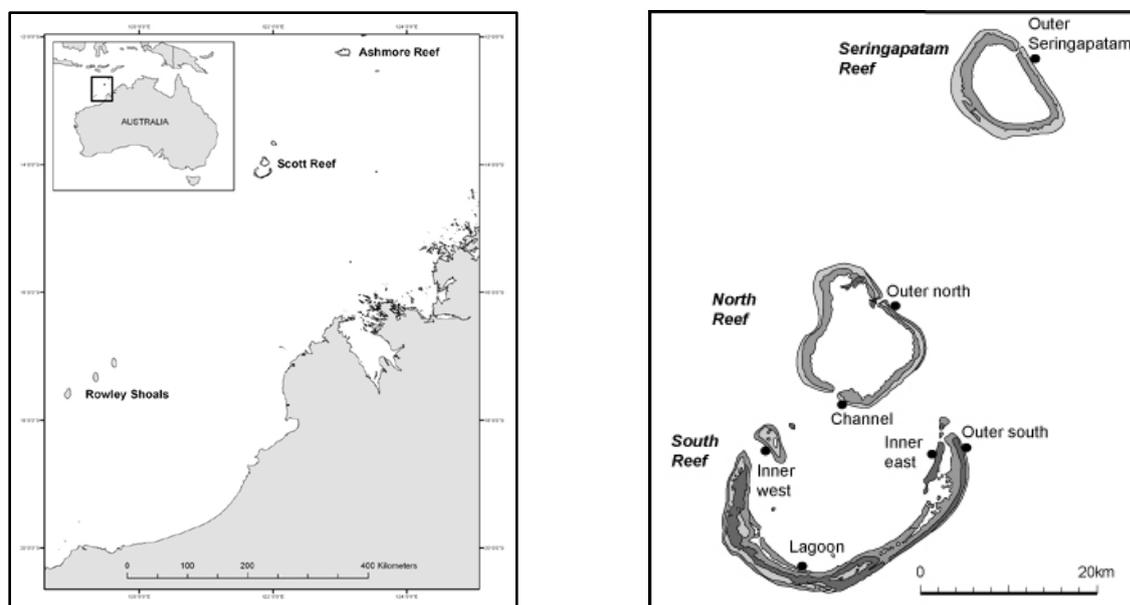


Figure 3.1 Position of Scott Reef off north-western Australia and the location of study sites. Study sites are at seven locations across the three reefs, at the inner and outer reef slope habitat (≈ 9 m depth). Outer Seringapatam = SS3, Outer north = SS2, Channel = SL4, Inner west = SL3, Inner east = SL1, Outer south = SS1, Lagoon = SL2.

Benthic Communities

At each of the seven locations across Scott Reef (Figure 3.1), benthic communities were sampled at three replicate sites. Sites were separated by approximately 300 m, and each consisted of 250 m of permanent transects marked at 10 m intervals. Most sites were surveyed annually between 1994 and 1999, and then in 2003 to 2005, 2008, 2010 and 2012. During each survey, a tape was laid along the permanent transect and a video or camera used to capture an image of the benthic community at a distance of between 30 and 50 cm from the substrata. Images were analysed using point sampling technique and benthic groups identified to the lowest taxonomic resolution achievable by each observer (Jonker *et al.* 2008).

From these data, the most meaningful insights into the impacts of disturbances and the resilience of communities were obtained when the coral assemblages were divided among benthic groups according to taxa (i.e. family, genus), reproductive mode (brooders, spawners) and growth form (encrusting, massive, corymbose, foliose, tabulate, branching) (Table 3.1). A total of 52 genera of hard coral were recorded at Scott Reef, but the nine most abundant genera accounted for 97% of total hard coral cover. In instances where genera were low in cover or difficult to distinguish, they were grouped to the family level. Alternately, rare genera were grouped according to growth forms that distinguished their response to disturbances. Rare groups were defined by having $< 3\%$ cover at any study location, during any survey. Growth forms were also used to further divide the three most abundant genera (*Isopora*, *Acropora*, and *Porites*).

Benthic communities were compared by multivariate analyses using the software PRIMER (Clarke and Warwick 2001). Percentage cover data were square-root transformed to reduce the influence of dominant groups but to retain the major differences in community structure according to relative

abundances. Specific comparisons among communities in space or time were investigated by calculating Bray-Curtis measures of dissimilarity. Changes in community structure were illustrated using two-dimensional plots of non-metric multidimensional scaling (nMDS). The benthic groups that characterised communities during a survey period, or distinguished communities between periods, were identified using the SIMPER procedure in PRIMER. Whether groups characterised or distinguished communities was based on: 1) their percentage contribution to dissimilarity among communities within a period, or between periods within a community, 2) whether they were consistently represented within a group (S/SD [S]), and 3) their changes in percentage cover (Clarke and Warwick 2001).

The scale at which community structure varied spatially (sites) and temporally (years) was investigated using cluster analysis and dendrograms, and tested using the SIMPROF procedure in PRIMER. Over the entire survey period (1994 to 2012), there was considerable variation in community structure among the seven locations across Scott Reef, but very little variation among the replicate sites within each location (Figure 3.2). Consequently, data are presented at the location level throughout the Results, with associated variances derived from site replication.

Table 3.1 Benthic groups used to describe changes in structure of coral assemblages at locations across Scott Reef. The majority of groups were common in most communities during one or more periods, with the exception of groups that characterised the South Lagoon community at South Reef.

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

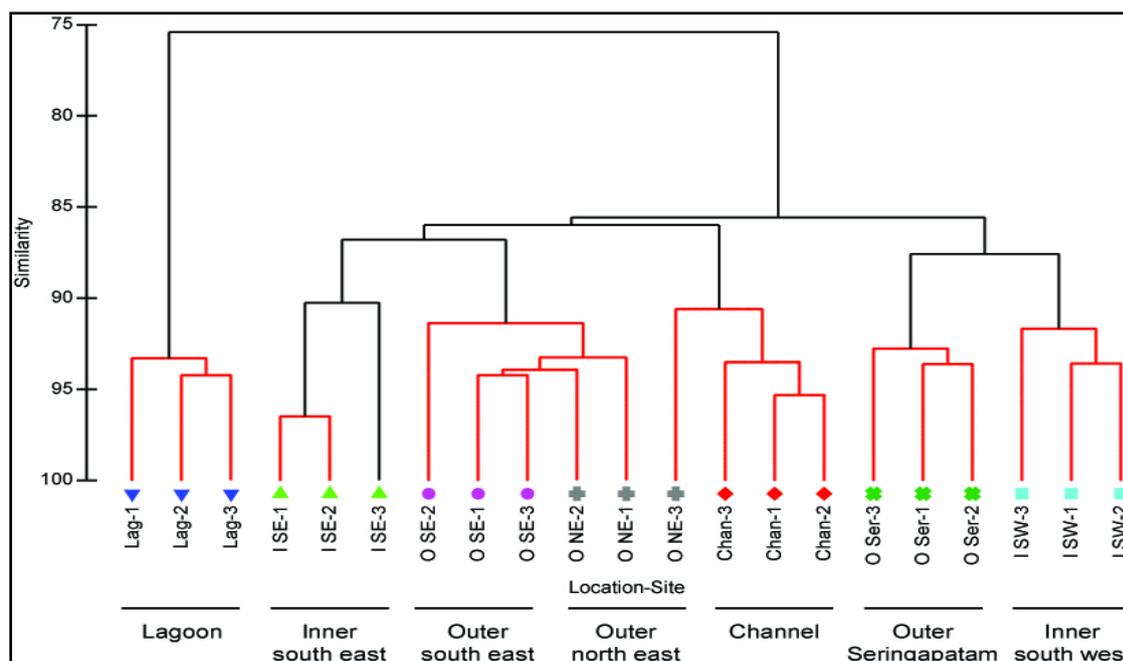


Figure 3.2 Spatial variation in the structure of coral communities from 1994 to 2012. Replicate sites ($n = 3$) consistently grouped within locations. Locations are: the South Reef Lagoon (Lag), Inner South East (I SE), Outer South Reef (O SE), Outer North Reef (O NE), the Channel between North and South Reef (Chan), Outer Seringapatam Reef (O Ser), and Inner South West (I SW) (Figure 1). Sites linked by red lines are not significantly different, according to the SIMPROF procedure. Data are Bray Curtis similarities for square-root transformed percentage cover of benthic groups (Table 1).

Spatial and temporal variation in habitat conditions

Differences in environmental conditions among locations were investigated by quantifying variation in the physical parameters predicted to have the greatest influence on biological communities (Table 3.2). Multi-parameter water quality loggers were deployed at, or adjacent to, the inner slope locations from March 2008 to April 2009 (Brinkman *et al.* 2010).

On the current trip, long-term temperature loggers were also deployed at 9 m to monitor ongoing changes in water temperature at a number of locations (Inner east, Lagoon, Inner west, Channel, Outer south, Outer north, Outer Seringapatam, North lagoon, and Seringapatam lagoon). Loggers were attached to star pickets at the beginning of the first transect. Salinity, fluorescence, turbidity and Photosynthetically Active Radiation (PAR) were quantified using Seabird SBE16 loggers with integrated Wetlabs ECO FLNTU and ECO PAR optical sensors between May 2008 and April 2009. From these data, PAR was extrapolated for each location at 9 m depth. Water column current profiles and waves heights were also quantified using Nortek 600 kHz AWAC and Nortek 1MHz Aquapro Acoustic Doppler Current Profilers (ADCP) with wave capability. The current profilers were mounted adjacent to the water quality loggers and acoustically recorded vertical current velocities through the water column as five minute averages, every 30 minutes. Additionally, at each study location modelled indices of water mixing and cooling at the time of mass-bleaching in 1998 were calculated (Bird 2005) and *in-situ* water temperatures recorded at hourly intervals from 2006 and October 2012.

Comparative sedimentation rates were quantified using replicate ($n = 5$) sediment traps spaced at 10 m intervals along a permanent transect at each of the study locations between 2008 and 2010. Sediment traps were constructed from cylindrical lengths (700 mm) of PVC tubing with an internal diameter of 110 mm, sealed at one end and elevated above the bottom the substrata. Baffles within each trap consisted of seven 150 mm lengths of PVC tube with an internal diameter of 30 mm. Traps were changed at intervals of approximately three to four months. When recovered, the tops

of the traps were sealed and the contents (sediment and water) later processed by gravimetric settling of particulate material from a known volume of water onto a pre-weighed membrane filter. Four replicate 60 ml sub-samples were measured from the trap contents and stored frozen. Mean rates of sediment accumulation ($\text{mg cm}^{-2} \text{d}^{-1}$) were derived for each trap location for each period of deployment and seasonal averages were calculated for these estimates. Net weight of different sediment types and mean sediment size (mean micron) was measured using replicate samples taken from each location. Initially, mean sediment size was grouped into nine size classes ranging from clay to coarse sand, and then further grouped into three broad categories (clay, silt and sand). In addition to sediment traps deployed to assess sedimentation rates between 2008 and 2010, traps were also deployed at 9 m on the current trip in 2012 to collect sediment for subsequent analysis of hydrocarbons and trace metals. These sediment traps were deployed at the first three transects at Inner East, Lagoon, Inner West, Channel, Outer North, Outer Seringapatam, for recovery on the 2014 trip. Traps were attached to star pickets that were situated along the first transect at each location.

For all of the environmental parameters, data were summarised in ways that most obviously explained the spatial variation among study locations; for example, whether mean daily water temperatures in summer, or daily ranges or maximums, varied most among the locations. From this initial exploration, the contribution of parameters to variation in habitat conditions among study locations was formally investigated using Principal Components Analysis (PCA) of the normalised data in the software PRIMER. Parameter statistics that explained a low proportion of the variation among locations, and those that were highly correlated ($r > 0.9$) with another parameter that better explained variation, were excluded and the analyses repeated (Table 3.2).

The influence of spatial variation in physical parameters among locations on their benthic communities was formally explored through the BEST analysis in PRIMER. Benthic community data were used during the pre-bleaching years (1994-1997) because community structure was most likely to reflect the influence of routine habitat conditions, having not been affected by a severe disturbance for several years. The BEST analysis was conducted for the parameters measured at all locations, and repeated for the parameters measured only at the inner slope locations.

Throughout the monitoring period, coral communities at one or more locations at Scott Reef experienced elevated water temperatures and coral bleaching, extreme winds and waves generated by cyclones and storms, and an outbreak of coral disease. The severity of the elevated water temperatures was assessed as temperature anomalies and degree heating weeks (DHW), based on the sea surface temperature (SST) data for Scott Reef provided by NOAA (<http://www.ospo.noaa.gov/Products/ocean/cb/dhw/index.html>). The severity of cyclones was assessed using a metric of cyclone exposure, based on the distance of the cyclone to the reef and its central pressure (Done 1992).

Table 3.2 Parameters used to characterise routine habitat conditions at locations across Scott Reef. Six parameters were quantified at all but one (Outer Seringapatam) location and an additional nine parameters at the inner-slope locations. All data are for the long-term monitoring locations (9 m), unless stated. Summary statistics were produced for each parameter, and a reduced number used in the final analysis after removing statistics that explained a low proportion of the variation among locations, and those that were highly correlated ($r > 0.9$) with another parameter that better explained variation.

	Parameter	Initial estimate	Parameter revision	Final estimate
All locations	Temperature (July 06 to May 10)	Mean daily temperature (°C)	Excluded	
		Mean range in daily temperature (°C)	Divided among seasons; all but summer excluded	Summer range in daily temperature (°C)
	Sedimentation (May 08 to April 09)	Mean daily weight of sedimentation ($\text{mg cm}^{-2} \text{day}^{-1}$)	Divided between summer and winter months	Mean daily weight of sedimentation in summer and in winter ($\text{mg cm}^{-2} \text{day}^{-1}$)
		Mean sediment particle size (μm)	Excluded	
		Percentage composition of sediment particle sizes, for nine size classes ranging from clay to coarse sand (μm)	Divided between summer and winter months and size classes combined	Mean percentage of silt and clay ($<63\mu\text{m}$), sand ($63\text{-}500\mu\text{m}$) and coarse sand ($>500\mu\text{m}$), in summer and winter months
Cover of sand (Oct 94 to Oct 10)	Cover of sand on substrata each year (%)	Averaged over all years	Mean cover of sand (%)	
Inner slope locations	Current speed (Nov to May 08)	Mean current speed (ms^{-1})	Excluded	
		Maximum current speed (ms^{-1})	Included	Maximum current speed (ms^{-1})
		Range in current speed (ms^{-1})	Excluded	
	Wave height (Nov to May 08)	Mean wave height (m)	Excluded	
		Maximum wave height (m)	Excluded	Maximum wave height (m)
	Fluorescence (Mar 08 to Feb 09)	Mean chlorophyll concentration (mg/m^3) at substrata adjacent to sites (25 m to 36 m depth)	Divided between summer and winter months	Mean chlorophyll concentration (mg/m^3) in summer and winter months
	Salinity (Mar 08 to Feb 09)	Mean salinity (PSU) at substrata adjacent to sites	Excluded	
Range in mean salinity (PSU) at substrata adjacent to sites		Excluded		
Turbidity (Mar 08 to Feb 09)	Mean turbidity (NTU) at substrata adjacent to sites (25m to 36m depth)	Divided between summer and winter months	Mean turbidity (NTU) in summer and winter months	

3.3 Results

3.3.1 Routine habitat conditions and spatial variation in pre-bleaching coral communities

Habitat conditions varied among locations across Scott Reef, which influenced the structure of their coral communities in the pre-bleaching years (1994-1997). The most influential parameters were associated with varying regimes of sedimentation, water temperature, current speed, wave height, and concentrations of chlorophyll and turbidity (Table 3.3, 3.4, Supplementary Figure 1, and Appendix 1). The largest differences in habitat conditions were between the inner and outer slope locations, but there was also considerable variation among the inner slope locations (Figure 3.3).

The Outer South East and Outer North East locations were exposed to the open ocean to the east, but sheltered from monsoonal storms from the west, and had a sloping substrata with a low cover of sand. They experienced moderate variation in water temperatures, but with occasional increases in temperature at the Outer North East due to the flow of warm water out of the lagoon and over the reef flat in summer. The outer slope locations had intermediate rates of sediment deposition across a range of particle sizes, and qualitative observations indicate they experienced moderate current speeds and wave heights.

The considerable variation in habitat conditions among the inner slope locations was primarily influenced by their proximity to the sheltered lagoon in South Reef and the western side of the deep

channel between North and South Reef. By far the most sheltered location was in the South Lagoon (Figure 3.1), having the lowest maximum current speeds and wave heights in summer, a low deposition of fine particle sizes (silt, clay) and high turbidity and chlorophyll concentrations (Supplementary Figure 1). The South Lagoon experienced an intermediate temperature variation and was characterised by a fragile and moderately sloping substrata with a low cover of sand. Conversely, the Inner South West and Channel locations were the most exposed to monsoonal storms from the west and had the highest maximum current speeds and wave heights in summer. Consequently, both locations had a high cover of sand, a high deposition of larger particle sizes (sand & coarse sand), and a low concentration of chlorophyll and turbidity. In addition, they were distinguished by a large temperature range due to the flow of warm water out of north lagoon during spring tides and the flow of cool water from the deep channel between North and South Reef. The Channel location had steep substrata, whereas the Inner South West location was comparatively flat with patchy coral outcrops. Habitat conditions at the Inner South East were a mixture of those at the other inner slope locations, having intermediate values for all of the parameters measured.

3.3.2 Acute habitat conditions and temporal variation in coral communities

Over almost twenty years (1994 – 2012), acute disturbances caused impacts of varying severity to coral communities at multiple locations across Scott Reef (Figure 3.4). By far the most severe and widespread disturbance was the mass-bleaching of corals in 1998, which reduced mean (\pm s.e.) cover of hard corals from 51.6% (4.3) to 9.4% (2.6), and soft corals from 9.8% (2.4) to 1.9% (0.7). Indeed, all subsequent changes in coral communities were interpreted in the context of their recovery from the mass-bleaching, and the effect of disturbances in slowing that recovery. These subsequent disturbances included cyclones (1995, 2004, & 2007), an outbreak of disease (2009-10), coral bleaching, (2010 & 2011), and a severe storm (2012). Despite the frequency of disturbances, the mean cover of hard corals increased over consecutive surveys before reaching pre-bleaching levels in 2010 ($43.6\% \pm 1.8$ s.e.); there were also consecutive increases in the cover of soft corals, but their cover in 2010 ($4.2\% \pm 1.6$ s.e.) had only reached approximately half that prior to the mass-bleaching. The first mean decreases in coral cover since the mass-bleaching occurred in 2012 following a severe monsoonal storm, with the cover of hard corals ($37.2\% \pm 5.3$ s.e.) having decreased to a similar level as in 2008, and soft corals ($2.5\% \pm 0.6$ s.e.) having decreased to a similar level as following the mass-bleaching (1999).

Throughout the survey period, benthic communities were dominated (>90%) by hard corals, soft corals and turf and coralline algae (Figure 3.4). There were large and inverse changes in the cover of these dominant groups through periods of impact and recovery from disturbances, which were consistent at locations across Scott Reef (Figure 3.5). The substrata that became available following the loss of corals was colonised by turf and coralline algae, whereas the cover of all other benthic groups remained low (< 5%). The mass-bleaching in 1998 caused the largest reductions in coral cover and increases in turf and coralline algae, whereas all subsequent disturbances were less severe and impacts were often restricted to a subset of coral taxa and locations. The resulting changes in community structure clearly grouped according to the periods of impact and recovery from disturbances (Figure 3.5), but through these periods there was also considerable variation among locations according to their relative exposure to disturbances, their routine habitat conditions and the abundance of coral groups with different susceptibilities and life history traits (Figure 3.6).

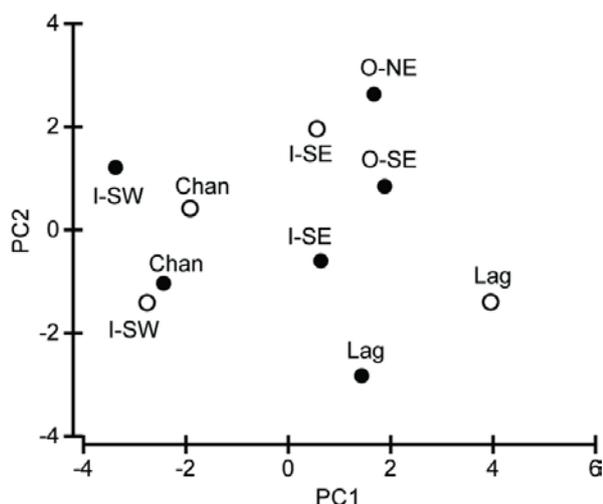


Figure 3.3 Spatial variation in habitat conditions among locations at Scott Reef. Inner slope locations at South Reef are at the Lagoon (Lag), South West (I-SW) and South East (I-SE), and between South and North Reef at the Channel (Chan); outer slope locations are on the east side of South Reef (O-SE) and North Reef (O-NE). The final analysis was based on Principal Component Analyses (PCA) of the 10 most influential physical parameters quantified at all locations (black circles), the 14 most influential parameters quantified at the inner slope locations (Table 2). PCA results are in Table 3.3.

Table 3.3 Results of principal component analysis (PCA) of variation in routine habitat conditions among locations. Analyses were conducted on normalised data from 10 physical parameters quantified at all locations, and 14 parameters quantified at inner-slope locations. More detailed parameter descriptions are in Table 3.2.

a) Habitat conditions at Scott Reef: All locations				b) Habitat conditions at Scott Reef: Inner-slope locations				
PC	Eigenvalues	%Variation	Cum.%Variation	PC	Eigenvalues	%Variation	Cum.%Variation	
1	5.22	52.2	52.2	1	9.31	66.5	66.5	
2	3.72	37.2	89.3	2	2.7	19.3	85.8	
3	0.589	5.9	95.2	3	1.99	14.2	100.0	
4	0.383	3.8	99.1					
5	9.48E-2	0.9	100.0					
<i>Eigenvectors</i>				<i>Eigenvectors</i>				
Variable				Variable				
Cover of sand	0.423	-0.106	-0.033	-0.177	0.363	0.316	0.100	-0.150
Summer sedimentation	0.419	-0.126	-0.180	-0.073	0.145	0.288	0.198	-0.247
Winter sedimentation	-0.146	0.368	-0.770	0.252	0.330	0.051	0.565	0.237
Summer silt particles	-0.399	-0.204	-0.139	0.078	-0.154	-0.321	-0.095	-0.098
Summer sand particles	0.407	0.145	-0.005	-0.382	0.150	0.327	0.010	-0.041
Summer coarse sand par	0.269	0.295	0.432	0.705	0.035	0.234	0.278	0.375
Winter silt particles	0.069	-0.509	-0.098	0.145	-0.015	-0.262	0.116	-0.405
Winter sand particles	0.009	0.518	0.045	-0.013	0.049	0.281	0.004	0.364
Winter coarse sand particles	-0.270	0.368	0.222	-0.480	-0.082	0.036	-0.530	0.340
Summer temp. range	0.386	0.158	-0.328	0.000	-0.826	0.288	0.240	-0.193
						0.264	-0.094	-0.405
						0.268	-0.236	-0.302
						-0.305	0.223	-0.029
						-0.290	0.280	-0.051

Table 3.4 Habitat conditions that best explain the variation in community structure among locations. BEST analysis conducted on ten parameters were quantified at all locations and 14 parameters at the inner-slope locations (SL1, SL2, SL3, SL4). Parameter descriptions are in Table 3.2.

a) Habitat conditions and community structure : all locations	b) Habitat conditions and community structure : inner-slope locations																																																																		
<p>Parameter numbers</p> <p>1 Summer Temperature range</p> <p>2 Summer Sediment</p> <p>3 Winter Sediment</p> <p>4 Cover of Sand</p> <p>5 Summer Silt</p> <p>6 Summer Sand</p> <p>7 Summer Course Sand</p> <p>8 Winter Silt</p> <p>9 Winter Sand</p> <p>10 Winter Course Sand</p>	<p>Parameter numbers</p> <p>1 Summer Temperature range</p> <p>2 Cover of Sand</p> <p>3 Summer Silt</p> <p>4 Summer Sand</p> <p>5 Summer Course Sand</p> <p>6 Winter Silt</p> <p>7 Winter Sand</p> <p>8 Winter Course Sand</p> <p>9 Summer Sediment</p> <p>10 Winter Sediment</p> <p>11 Maximum summer current speeds</p> <p>12 Maximum summer wave height</p> <p>13 Mean turbidity</p> <p>14 Mean Chlorophyll</p>																																																																		
<p><i>Parameters best correlated to community structure</i></p> <table border="1"> <thead> <tr> <th>#</th> <th>Corr.</th> <th>Parameters</th> </tr> </thead> <tbody> <tr><td>1</td><td>0.632</td><td>9</td></tr> <tr><td>2</td><td>0.621</td><td>8,9</td></tr> <tr><td>3</td><td>0.582</td><td>6,8,9</td></tr> <tr><td>1</td><td>0.561</td><td>8</td></tr> <tr><td>3</td><td>0.532</td><td>5,8,9</td></tr> <tr><td>2</td><td>0.507</td><td>6,9</td></tr> <tr><td>4</td><td>0.496</td><td>5,6,8,9</td></tr> <tr><td>2</td><td>0.489</td><td>6,8</td></tr> <tr><td>3</td><td>0.450</td><td>7-9</td></tr> <tr><td>2</td><td>0.432</td><td>5,9</td></tr> </tbody> </table>	#	Corr.	Parameters	1	0.632	9	2	0.621	8,9	3	0.582	6,8,9	1	0.561	8	3	0.532	5,8,9	2	0.507	6,9	4	0.496	5,6,8,9	2	0.489	6,8	3	0.450	7-9	2	0.432	5,9	<p><i>Parameters best correlated to community structure # Corr.</i></p> <table border="1"> <thead> <tr> <th>Parameters</th> <th>#</th> <th>Corr.</th> </tr> </thead> <tbody> <tr><td>4</td><td>1.000</td><td>10-12,14</td></tr> <tr><td>1</td><td>0.943</td><td>14</td></tr> <tr><td>3</td><td>0.943</td><td>6,10,12</td></tr> <tr><td>3</td><td>0.943</td><td>10,11,14</td></tr> <tr><td>3</td><td>0.943</td><td>10,12,13</td></tr> <tr><td>3</td><td>0.943</td><td>10,12,14</td></tr> <tr><td>3</td><td>0.943</td><td>10,13,14</td></tr> <tr><td>4</td><td>0.943</td><td>5,11,13,14</td></tr> <tr><td>4</td><td>0.943</td><td>5,12-14</td></tr> <tr><td>4</td><td>0.943</td><td>6,10,11,13</td></tr> </tbody> </table>	Parameters	#	Corr.	4	1.000	10-12,14	1	0.943	14	3	0.943	6,10,12	3	0.943	10,11,14	3	0.943	10,12,13	3	0.943	10,12,14	3	0.943	10,13,14	4	0.943	5,11,13,14	4	0.943	5,12-14	4	0.943	6,10,11,13
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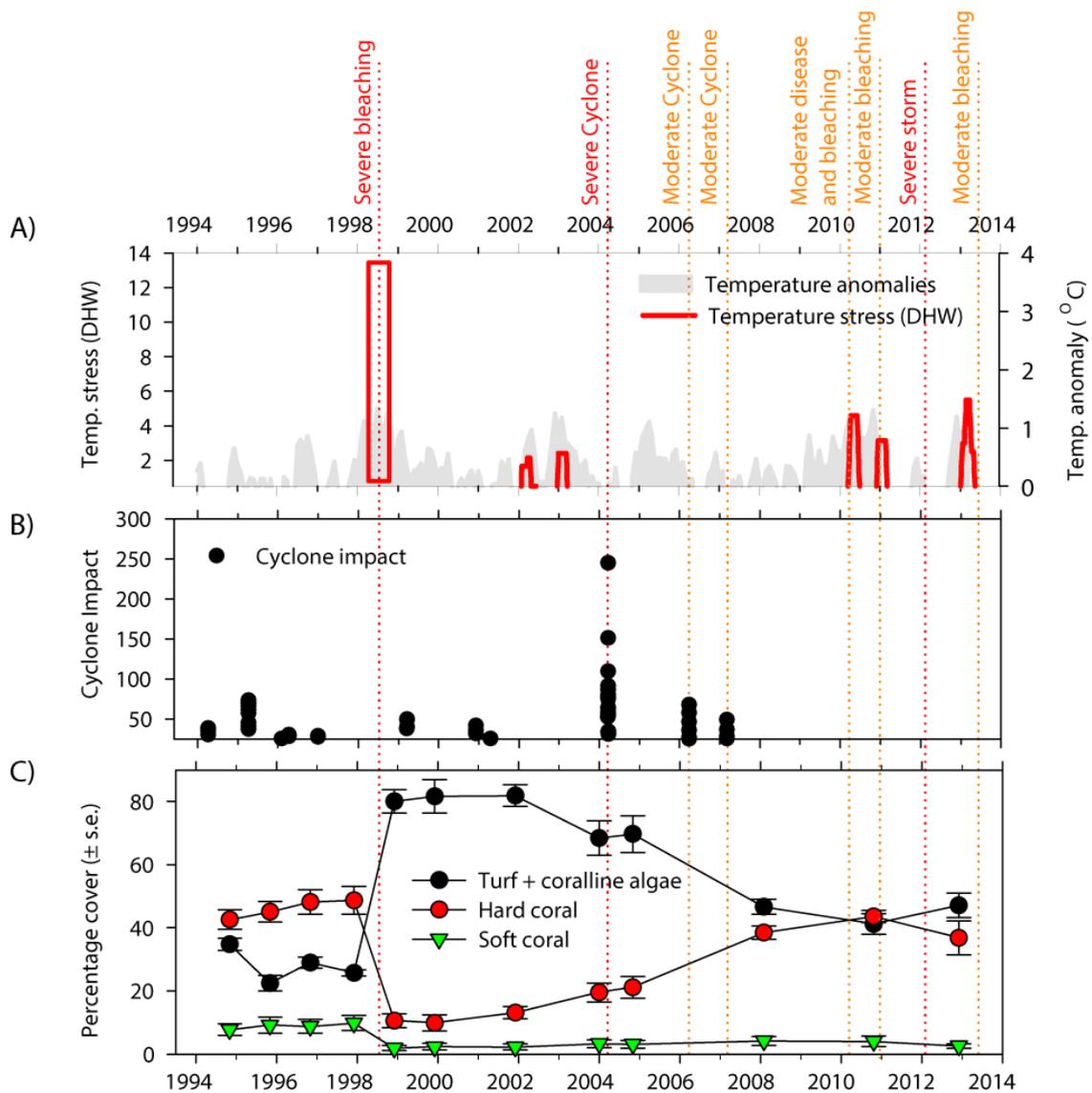


Figure 3.4 Over 18 years, acute disturbances had moderate (orange lines) or severe (red lines) impacts on coral communities at Scott Reef. A) Elevated water temperatures (anomalies) and prolonged periods of heating (Degree Heating Weeks; DHW) caused mass bleaching in 1998, and moderate bleaching in 2010, 2011, and 2013. B) Tropical cyclones caused a severe impact in 2004, and moderate impacts in 1995, 2006, and 2007. A monsoonal storm caused a severe impact in 2012. C) The mean cover of hard and soft corals changed in response to coral bleaching (1998, 2010, & 2011), cyclones and storms (2004, 2006, 2007, & 2013) and an outbreak of coral disease (2010).

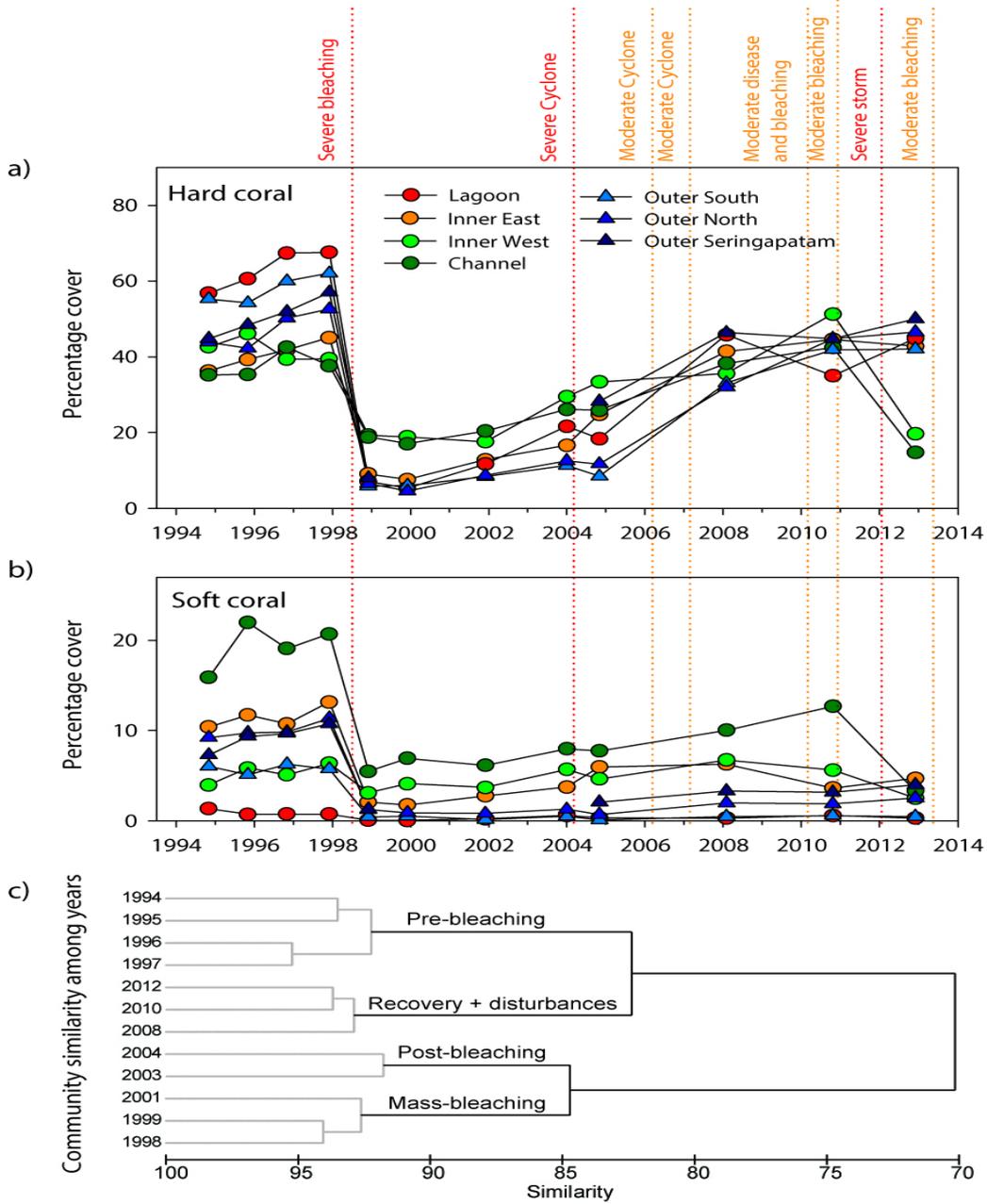


Figure 3.5 Spatial and temporal variation in coral communities at Scott Reef. Changes in the mean cover of a) hard and b) soft corals varied among locations across Scott Reef according to their exposure to disturbances, and c) the resulting changes in community structure grouped according to periods of impact and recovery around major disturbances. At each location were three replicate sites. Community structure was defined by the relative abundance of benthic groups (Table 3.1).

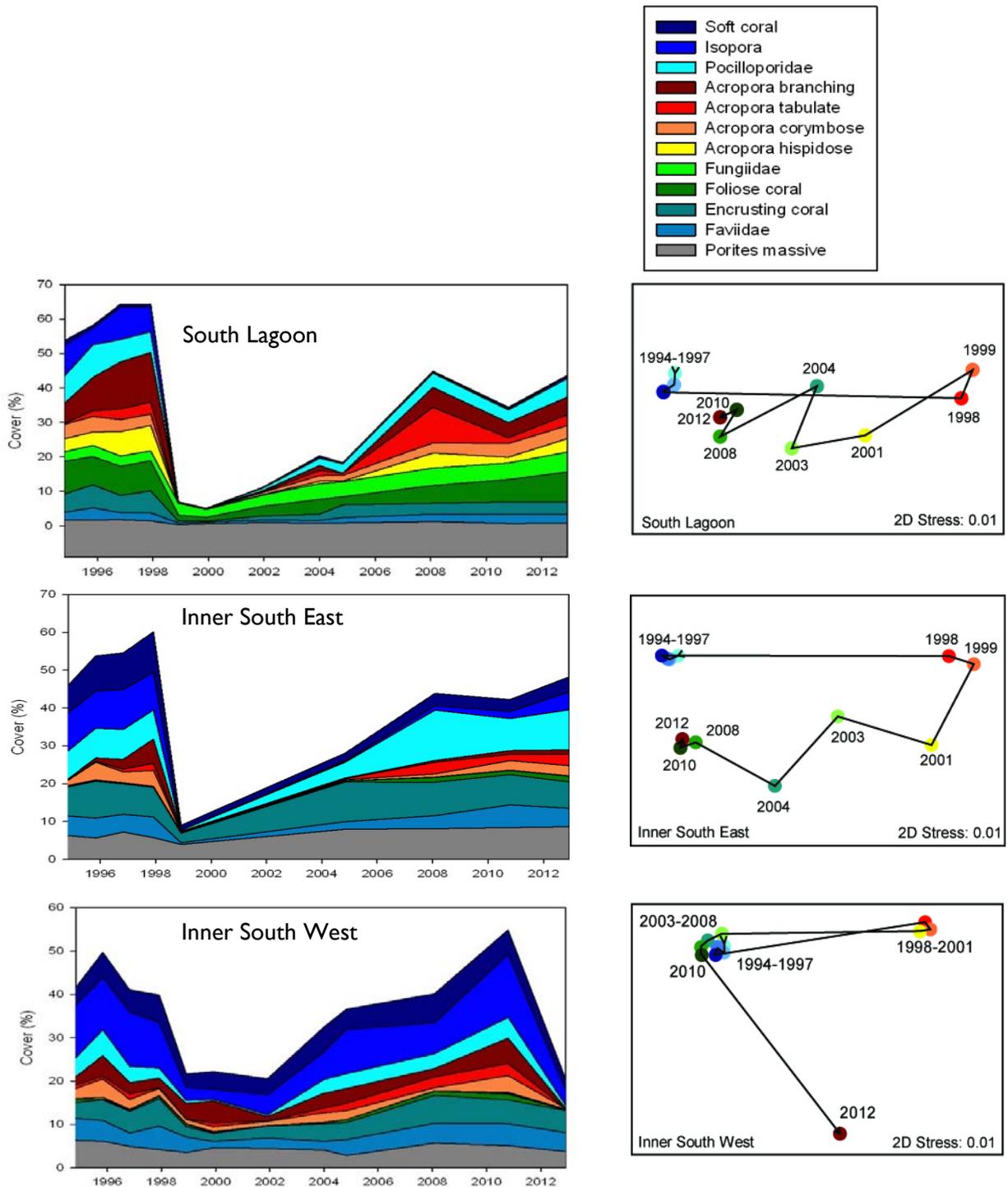
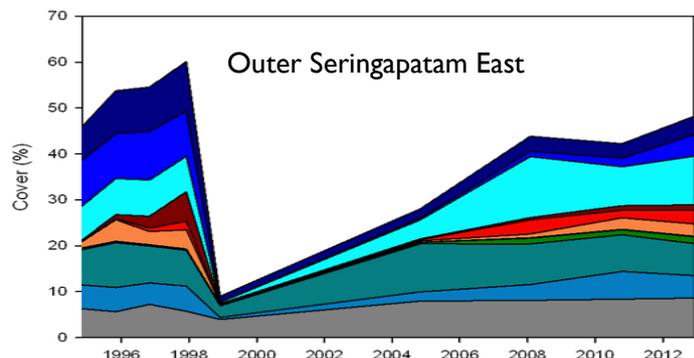
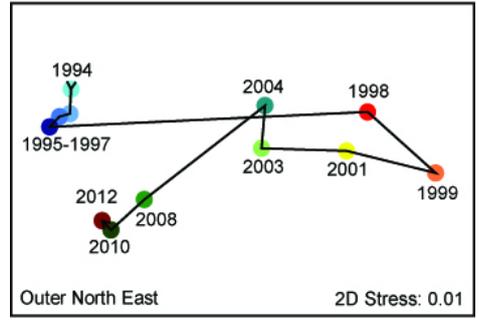
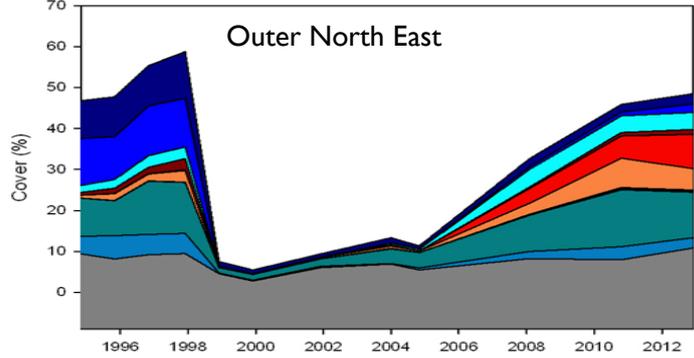
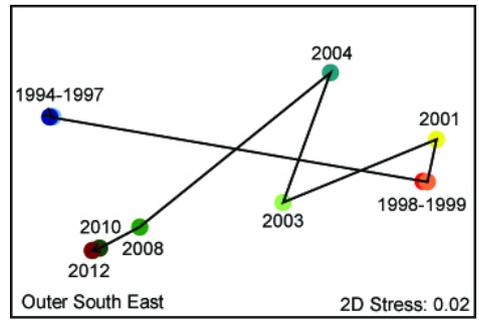
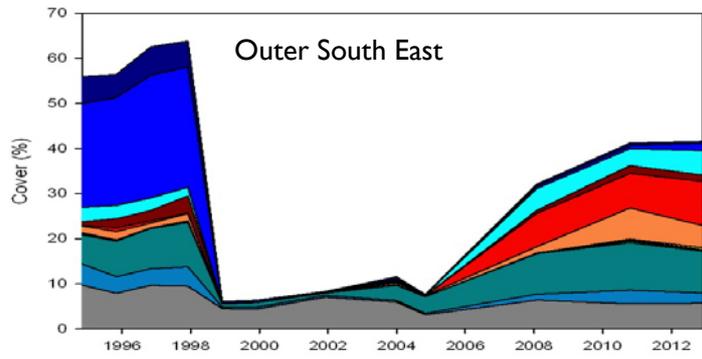
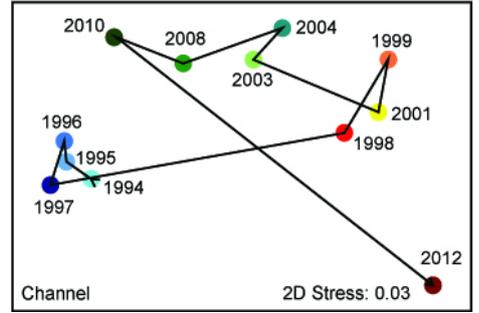
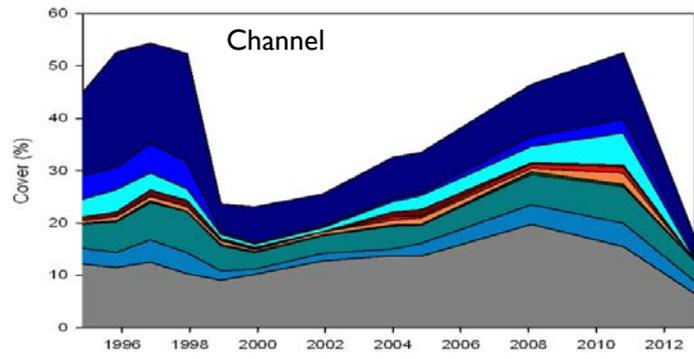
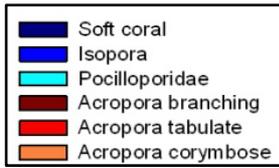


Figure 3.6. Changes in the benthic communities at locations across Scott Reef. Mean percentage cover of coral taxa during each survey at each location (left column) and non-metric multidimensional scaling (nMDS) of temporal changes in assemblage structure (right column), using Bray-Curtis similarities of percentage cover (square root). Locations are the South Lagoon, Inner South East, Inner South West, Channel, Outer South East, Outer North East, and Outer Seringapatam East (Figure 3.1).

Figure 3.6 Continued.



3.4.3 Pre- and post-bleaching (1994 – 2001)

The mean (\pm S.E.) coral cover at Scott Reef increased from 53% (\pm 2) to 61% (\pm 3) through the pre-bleaching years (1994-1997). Coral cover was high (45 – 70%) at all locations, with much of the remaining substrata covered by turfing and coralline algae (30 – 40%). Several coral taxa were common to all assemblages, whereas others clearly distinguished their assemblage structure, reflecting the variation in habitat conditions. Most assemblages had a moderate to high (5 – 15%) cover of massive *Porites*, *Montipora* and encrusting corals, soft corals, *Acropora* and *Isopora*, in addition to a low to moderate (2 – 10%) cover of Pocilloporidae, and Faviidae (Figure 3.5 & Supplementary Table 1). The assemblages at the three outer slope locations and at the Inner South West were most similar; the Inner South East assemblage was a mix of all others, and the Lagoon and Channel assemblages were the most unique (Figure 3.6 & Supplementary Table 1). The Lagoon assemblage was distinguished by the highest cover of branching and hispidose *Acropora*, *Echinopora* and foliaceous corals, and Pocilloporidae, and the lowest cover of massive *Porites* and soft corals. Conversely, the Channel assemblage had the highest cover of massive *Porites* and particularly soft corals, and the lowest cover of *Acropora* and other fragile growth forms.

Elevated water temperatures and mass-bleaching in March 1998 affected all the coral assemblages across Scott Reef (Figure 3.6 & Supplementary Table 1). The relative decreases in coral cover seven months after the mass-bleaching ranged from approximately 50 to 90%, depending on the abundance of susceptible corals and the habitat conditions at each location. Among the coral groups, the relative decreases in cover were highest ($>$ 90%) for the branching *Porites*, *Acropora*, *Millepora*, *Isopora*, and Pocilloporidae (Figure 3.7). For the other coral groups, the decreases ranged between 70-90%, with the exception of massive *Porites* which were least affected (5 – 75% decrease). However, the impact of the mass-bleaching also varied among locations according to their habitat conditions. In particular, the locations closest to the western edge of the deep channel were less exposed to thermal stress due to higher current speeds, tidal mixing, and cool-water intrusions from the deep (Supplementary Figure 1). When considering only the coral groups common ($>$ 1.5% mean cover) to all locations, the relative decreases in total coral cover at the Inner South West and Channel locations were lower ($<$ 60%) than at the other ($>$ 80%) locations, as were the decreases in cover of most coral groups (Figure 3.7). For example, there were relative decreases of 5 to 10% for the massive *Porites*, and 30 to 55% for the Faviidae, at the Inner South West and Channel locations, compared to 25 to 75% for the massive *Porites* and 80 to 97% for the Faviidae at all other locations (Figure 3.7).

Three years after the mass-bleaching (2001), mean coral cover ($+0.05 \pm 0.1\%$) and assemblage structure at Scott Reef had not changed (Figure 3.4). The disturbance had homogenised assemblages among locations, as many of the distinguishing coral taxa were also the most susceptible (e.g. *Isopora*, *Acropora*, Pocilloporidae) (Figure 3.6 & Supplementary Table 1). All of the post-bleaching assemblages were characterised by the taxa that had been most abundant and least susceptible to bleaching, particularly the massive *Porites* and the *Montipora* and encrusting corals (Figure 3.6 & Supplementary Table 1). All other taxa were rare ($<$ 2%) at all locations, with the exception of the soft corals and *Isopora* at the Inner South West and Channel locations where they had been most abundant and were least exposed to thermal stress. Indeed, the small increases in coral cover by 2001 were driven primarily by the regrowth of massive *Porites* at the Inner South West location, whereas the cover of some coral groups at all other locations had continued to decrease.

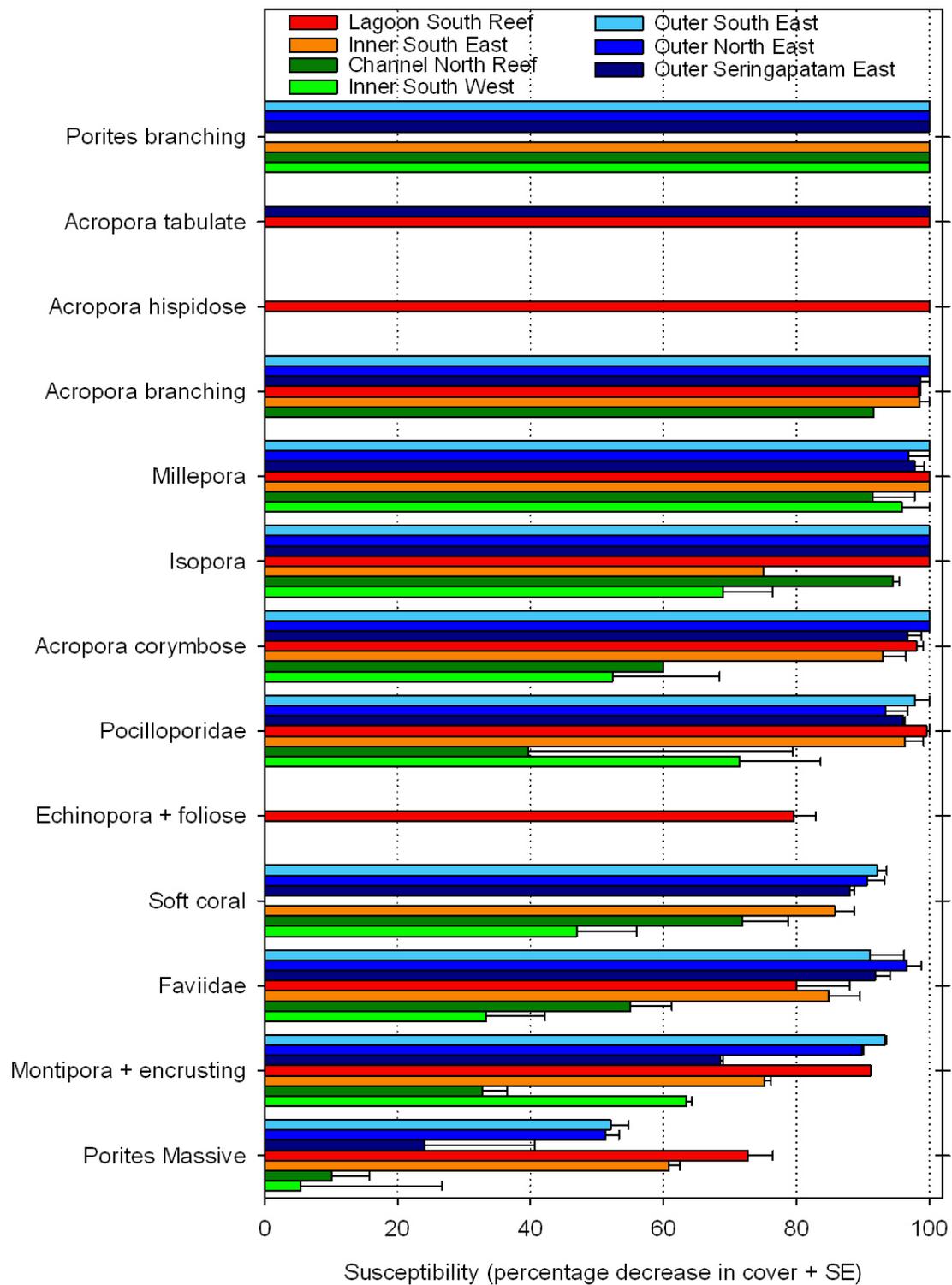


Figure 3.7 The variable impact of mass-bleaching in 1998 among coral groups and locations at Scott Reef. The mean (\pm SE) relative decreases (%) in coral cover before (October 1997) and after (October 1998) mass-bleaching in March 1998. Coral groups and locations were included only if their mean pre-bleaching cover was $>1.5\%$. Coral groups are described in Table 3.1 and locations in Figure 3.1.

3.4.4 Recovery and a severe cyclone (2002 – 2004)

Coral cover had increased more rapidly between 2002 and 2004 than in the previous period and the communities had commenced a trajectory to their pre-bleaching structure, but this recovery was slowed by a severe cyclone (Figure 3.4 & 3.5). The mean cover of turf and coralline algae had decreased to 68% (± 5 s.e.) and coral cover had increased to 23% (± 3 s.e.), driven by the increases of a few percent of several coral groups. There were ongoing increases in cover of *Montipora* and encrusting corals at all locations (but for the Channel) and of massive *Porites* at some locations (Channel, Outer North and Outer Seringapatam) (Figure 3.6, Supplementary Table 1). Additionally, at some locations there were also increases of coral groups that had been more severely impacted by the mass-bleaching, particularly the corymbose *Acropora*, Pocilloporidae and soft corals, and the *Isopora* at the Inner South West location.

Variation in recovery among communities was primarily influenced by their exposure to a severe cyclone and the increased cover of distinguishing coral groups. Although Category 5 Cyclone Fay passed directly over Scott Reef in early 2004, it did not cause large decreases in coral cover because the most fragile groups (e.g. *Acropora*) were still low in abundance following the mass-bleaching. Reductions ($< 3\%$) in coral cover occurred only at the locations with the highest cover of fragile corals (Lagoon) or at the outer-slope locations at South and North Reef that were most exposed to the path of the cyclone (Figure 3.5 & 3.6). The severity of the cyclone at the most exposed locations was evident in the damage to the reef substrata and to all hard and soft corals, including relative decreases in cover of massive *Porites* of 20 – 50%. For the locations least affected by the cyclone, a shift towards their pre-bleaching structure was driven by increases in the coral groups that had previously distinguished their assemblages; in particular, the foliose corals at the Lagoon, the *Isopora* at the Inner South West, and the massive *Porites* and soft corals at the Channel (Figure 3.6).

3.4.5 Recovery and moderate cyclones (2005-2008)

Seven years after the mass-bleaching (2005-2008), there was a rapid increase in coral cover and a return to a pre-bleaching community structure across Scott Reef, but which was slowed by two cyclones (Figure 3.4 & 3.6). The mean cover of turf and coralline algae had decreased to 52% (± 8 s.e.) and coral cover had increased to 44% (± 3 s.e.), driven by variable increases in cover of several coral groups. There were small ($\approx 1\%$) ongoing increases in mean cover of *Montipora* and encrusting corals, soft corals and digitate *Acropora*, and larger (2 – 5%) increases in massive *Porites*, Pocilloporidae and particularly table *Acropora* (Figure 3.6 & Supplementary Table 2).

At all but the Outer South East location, coral cover in 2008 was similar ($>75\%$) to that prior to mass-bleaching, and communities had tracked rapidly towards their pre-bleaching structure (Figure 3.4 & 3.6). The variation in recovery among communities was again influenced by cyclone exposure and coral growth, but during this period (2005-2008) the relative effect of cyclone disturbances was far less than the growth of coral groups. Cyclones Glenda and George passed Scott Reef in 2006 and 2007, respectively, but they caused only moderate impacts to susceptible corals (e.g. branching *Acropora*, *Isopora*) at the Inner West and Channel locations. At these exposed locations, mean coral cover increased from 2004 to 2008 by between 2 and 12%, compared to between 17 and 28% at all other locations. The increases in coral cover were driven by coral groups common across Scott Reef (e.g. table *Acropora*, Pocilloporidae) and by groups that had previously distinguished different assemblages; in particular, foliose corals and branching, hispidose and table *Acropora* at the South Lagoon, Faviidae, soft corals and massive *Porites* at the Channel.

3.4.6 Recovery and moderate bleaching and disease (2009-2010)

More than a decade after the mass-bleaching (2009-2010), communities across Scott Reef had continued to recover, but the rate of recovery and a return to the pre-bleaching structure was again slowed by disturbances. The cover of turf and coralline algae had decreased to 40% (± 3 s.e.), and

coral cover had increased to 48% (± 3 s.e.) (Figure 3.4). Across Scott Reef, there were small (1-2%) mean increases in *Montipora* and encrusting corals, Faviidae and massive corals, *Isopora* and corymbose *Acropora*, but there was also considerable variation among locations due to the selective impacts of coral disease and bleaching.

An outbreak of coral disease in late 2009 caused the largest decreases in cover, primarily affecting the table *Acropora* at the South Lagoon, reducing their cover by 9%. At the South Lagoon, the branching and hispidose *Acropora* were also moderately affected, decreasing in cover by 2-3%. The outbreak of disease also occurred at the Inner South East location, but affected only the table *Acropora* and reduced their cover by 4%. In addition to the spread of disease at two locations, elevated water temperatures caused the bleaching of some corals and assemblages. The incidence of bleaching was highest at the Outer Seringapatam location, particularly for the Pocilloporidae which decreased in cover by 5%. Bleaching was also obvious at the other outer-slope locations at South and North Reef, and in the Fungiidae, but did not cause mean reductions in cover between 2008 and 2010.

The cover of hard corals in 2010 was again higher than during the first survey at all locations, apart from the two worst affected by disease and recent bleaching, but community structure at most locations still differed from that prior to the bleaching (Figure 3.5 & 3.6). The same coral taxa both characterised and distinguished all assemblages as prior to the mass-bleaching, but there remained differences in their relative cover (Figure 3.6 & Supplementary Table 1). Most notably, there was a lower cover of soft corals and *Isopora* in all assemblages, but for those in which they had been most common (or rare). In contrast, the cover of *Montipora* and encrusting corals, Pocilloporidae, and corymbose and table *Acropora*, was generally higher than in the pre-bleaching years. Among the locations, the difference to pre-bleaching structure was most obvious for the outer-slope locations at North and South Reef, which were impacted by many of the disturbances since the mass-bleaching.

3.4.7 Recovery and severe storm (2011-2012)

As with all previous periods, the most recent (2011-2012) changes in coral communities at Scott Reef were punctuated by growth and recovery from mass-bleaching in 1998 and the impacts from disturbances. The impacts from a moderate bleaching in 2011 and a severe storm in early 2012 reduced coral cover to 40% (± 6 s.e.), the first mean decrease in coral cover across Scott Reef since the mass-bleaching, and there was a corresponding increase in the cover of turf and coralline algae to 51% (± 4 s.e.) (Figure 3.4). However, the decrease in coral cover and changes in assemblage structure varied considerably among locations across Scott Reef (Figure 3.5 & 3.6) according to their exposure to the disturbances and the relative abundances of susceptible coral groups.

The largest decreases in coral cover were at the locations with a westerly aspect, which were most exposed to the wind and waves generated by the monsoonal storm. There were relative decreases in the cover of hard and soft corals of between 65 to 75% at the Channel and of between 55 and 65% at the Inner South West locations (Figure 3.5). There were large relative decreases in cover of all coral groups at the Channel, ranging from 40 to 55% for the most robust corals (*Montipora* and encrusting corals, Faviidae, *Porites* and massive corals), 75% for the soft corals, and > 95% for the most fragile corals (*Acropora*, Pocilloporidae) (Figure 3.8 & Supplementary Table 1). The relative decreases were similar (> 90%) for the most fragile corals the Inner South West location, but less for the soft corals (55%) and the most robust corals (5 – 30%). The community at the Inner South East location was also affected by the storm, but the impacts were largely restricted to a relative decrease in cover of 15 to 55% for the various *Acropora* growth forms (Figure 3.6 & 3.8). Among the remaining locations, there was little change in mean coral cover at the outer slope locations at South and North Reef; changes in their assemblages were mostly successional, with the replacement of *Montipora* and encrusting corals, Faviidae, and digitate *Acropora* by table *Acropora* and *Isopora* (Figure 3.6 & Supplementary Table 1). Successional changes in assemblage structure and the abundance of

distinguishing taxa also drove the increases in mean cover of 5 to 10% at the South Lagoon and Outer Seringapatam locations. At the South Lagoon, there were small increases of between 1 and 2% cover of branching *Acropora*, plus the groups that typically distinguished the assemblage from all others (Pocilloporidae, hispidose *Acropora*, *Echinopora* and foliaceous corals, and Fungiidae); at the outer Seringapatam location, there were small increases of 1 to 3% of Pocilloporidae, table *Acropora*, and *Isopora*.

During the most recent survey period (2011-2012), assemblages had moved closer to their pre-bleaching structure, had changed little, or had moved back towards a more degraded state. The South Lagoon and Inner West assemblages were again similar to those prior to the mass-bleaching, with the same coral taxa characterising, or distinguishing, their structure (Figure 3.6 & Supplementary Table 1). There had been little change in the community structure at the outer-slope assemblages at South and North Reef since the large shift towards the pre-bleaching state in 2008. Their exposure to several disturbances had resulted in a higher cover of turf and coralline algae and a lower cover of several coral groups in 2012 than prior to the bleaching, with the exception of a higher cover of corymbose and table *Acropora*. By far the largest shift away from the pre-bleaching structure occurred at the Channel and Inner South West locations following their exposure to the monsoonal storm in early 2012, returning to a similar post-bleaching assemblage as that in 1999.

3.4.8 Disturbances, habitat conditions and coral life histories (1994-2012)

Throughout the study period (1994-2012), the changes in coral assemblages across Scott Reef were influenced by their habitat conditions and exposure to disturbances, plus the life histories of their coral taxa. Reflecting their life histories, coral taxa grouped according to changes in percentage cover among locations and between surveys, with the most variable taxa least likely to characterise coral assemblages (Figure 3.9). Groups such as the massive *Porites*, *Montipora* and encrusting corals, Faviidae, and soft corals, had the smallest changes in cover, and were therefore most likely to characterise the coral assemblages across Scott Reef (spatially) over the course of the study (temporally). Conversely, groups such as the *Isopora*, and the table, hispidose and branching *Acropora*, varied most among the assemblages, and had the largest increases and decreases in cover through time; consequently, these groups were least likely to characterise the coral assemblages across Scott Reef and through time.

Over the 14 years following the mass-bleaching, the life histories of corals and their exposure to disturbances produced successional changes in assemblage structure that were consistent among locations (Figure 3.6, 3.10, & Supplementary Table 1). Following the impact of severe disturbances, such as the mass-bleaching or the monsoonal storm, the most exposed assemblages had a low coral cover ($\approx 10\%$) and were characterised by the least susceptible taxa, such as the massive *Porites*, *Montipora* and encrusting corals, Faviidae and soft corals. Within approximately five years, coral cover had increased to $\approx 20\%$ and assemblages were increasingly characterised by taxa with moderate susceptibility to severe disturbance, such as the Pocilloporidae and the digitate *Acropora*. A decade after the severe disturbance, coral cover had increased to $\approx 40\%$ and assemblages were increasingly characterised by a high cover of table *Acropora*, in addition to a low cover of some of the most susceptible taxa that had been previously rare, such as the branching *Acropora* and the *Isopora*. Finally, in the absence of severe disturbances for a decade or more, coral cover was $\approx 60\%$ and there was a moderate to high cover of several coral groups, including those that had been most severely impacted by disturbance. The increased cover of the most susceptible taxa (e.g. *Isopora*) was at the expense of some taxa (e.g. digitate *Acropora*) that had been most common in the early stages of recovery. However, over almost 20 years, it was the least susceptible taxa that had maintained a moderate level of cover and consistently characterised the assemblages across Scott Reef, through all the successional stages of impact and recovery (Figure 3.10 & Supplementary Table 1).

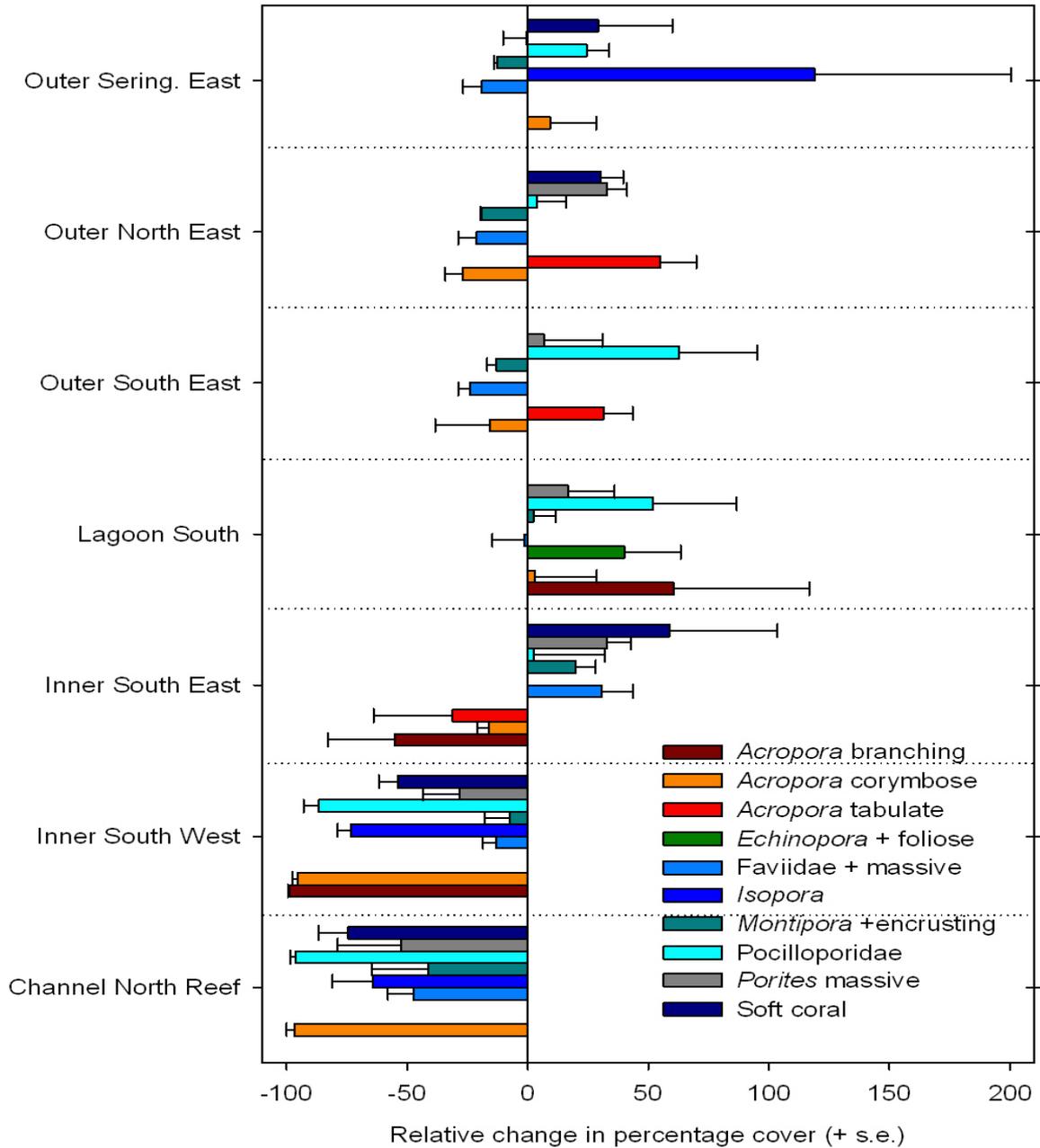


Figure 3.8 The mean (\pm SE) relative change (%) in the cover of coral taxa at locations across Scott Reef between 2010 and 2012. Relative decreases in coral cover were due to the impact of a monsoonal storm in early 2012, primarily at the locations with a westerly exposure (Channel, Inner South West, Inner South East), in addition to successional changes involving the replacement of some coral taxa (e.g. *Montipora* and encrusting) by other taxa (e.g. table *Acropora*). Coral groups and locations were included only if their mean cover in 2010 was >1.5%. Coral groups are described in Table 3.1 and locations in Figure 3.1.

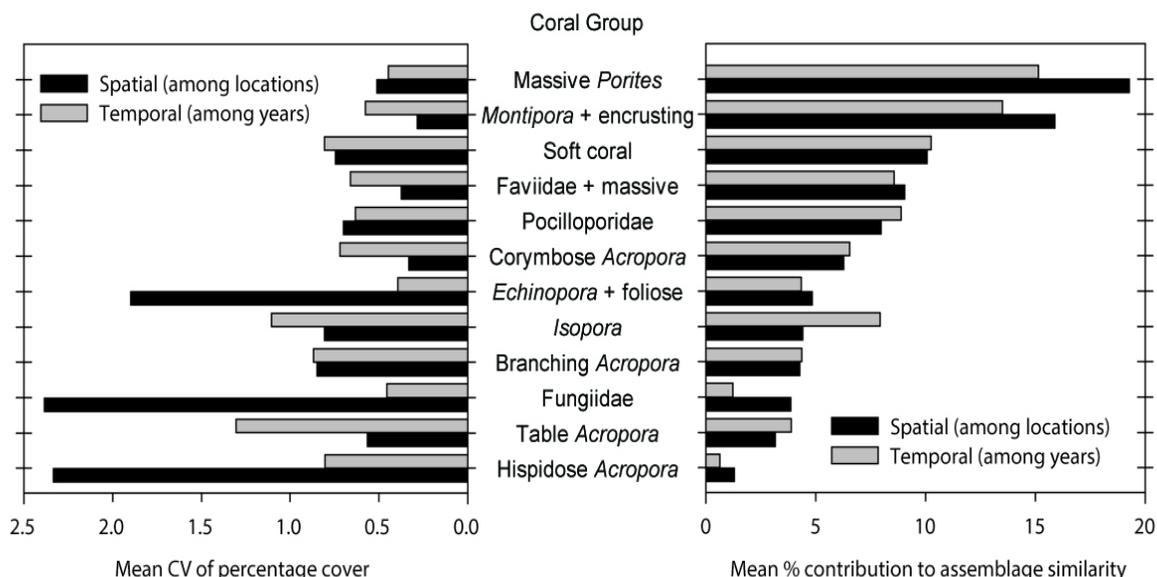


Figure 3.9 Variation in coral taxa and their corresponding contribution to assemblage structures at Scott Reef. Mean coefficient of variation (CV) in percentage cover of coral taxa among locations and between surveys (left plot). Taxa with the largest CV (e.g. table *Acropora*) varied most among locations (spatially) and had the largest increases and decreases in cover between surveys (temporally). The least variable taxa were most likely to characterise the coral assemblages across Scott Reef (spatially) and through time (temporally), based on their mean percentage contribution to Bray Curtis similarities (right plot).

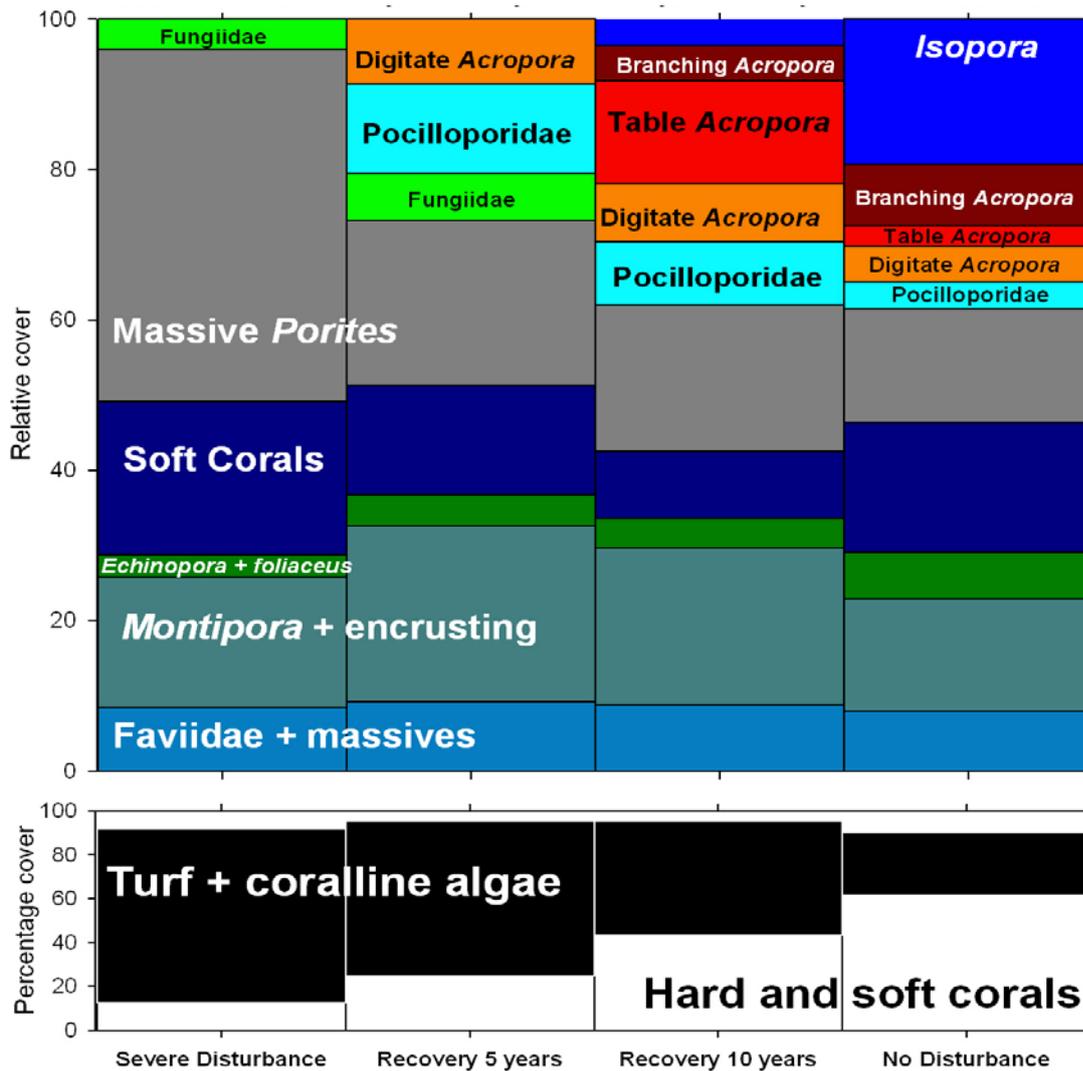


Figure 3.10. Successional changes in coral communities following severe disturbances at Scott Reef. The absolute cover of corals and turf and coralline algae (bottom plot) and the relative abundance of coral taxa (top plot) varied with time since severe disturbance. Assemblages were chosen to define different successional stages based on qualitative assessment of their disturbance regime, which included time since severe disturbance with no subsequent disturbances, and time since severe disturbance and moderate disturbance. Severe Disturbance included all assemblages following mass bleaching in 1999, the outer slope assemblages at South and North Reef following a severe cyclone in 2004, and the Channel assemblage following severe storm in 2012. Recovery 5 years included assemblages approximately 5 years after their exposure to severe disturbance, or between approximate 5 to 10 years after severe disturbance and recent exposure to moderate disturbance; assemblages included all but the outer slope at South and North Reef in 2004, the Lagoon following moderate bleaching and disease in 2010, and the Inner South West following storm exposure in 2012. Recovery 10 years includes assemblages up to 10 years after severe disturbance, or 12 years after severe disturbance and a few years after a moderate disturbance; assemblages were the outer slope at South Reef, North Reef and Seringapatam Reef in 2008 and 2010, the Lagoon and Channel in 2008, and the Inner South East in 2008, 2010, and 2012. No disturbance included assemblages that had not been exposed to severe disturbance for 10 years or more or a moderate disturbance for several years; assemblages included all in 1996 and 1997, but for the Inner South West in 1997, the Inner South West in 2008 and 2010, the Channel in 2010 and the Lagoon in 2012. Rare taxa whose cumulative contribution to total coral cover was < 5% were excluded.

3.5 Discussion

By far the most significant event at Scott Reef in almost two decades of monitoring was the mass-bleaching of corals in 1998, and all subsequent changes in all coral assemblages were interpreted in the context of their recovery from that disturbance. However, the spatial and temporal variation in coral assemblages across Scott Reef were driven by a combination of routine habitat conditions, exposure to disturbances, and the life histories of coral taxa. These drivers had similar consequences for assemblage structure at replicate sites within locations, over distances of less than a few kilometres, but often varied considerably among locations of more than several kilometres.

3.5.1 Routine habitat conditions and assemblage structure

The role of routine habitat conditions in structuring coral reefs is well established, and commonly related to variation in substrata type, water temperature, current speed, wave height, and water quality (turbidity, nutrient concentrations, sedimentation) (Done 1982, van Woerik *et al.* 1999, Ninio and Meekan 2002, Fabricius *et al.* 2005). At Scott Reef, variation in these parameters produced a strong association between the habitat conditions and coral taxa, particularly those that distinguished locations and their assemblages. The environmental gradient at Scott Reef ranged from the outer-slope locations exposed to the open ocean, to inner-slope locations adjacent to the deep channel and in the sheltered south lagoon. Among the outer-slope locations, the most obvious differences were between the western and eastern sides of Scott and Seringapatam reefs.

Coral cover on the western side of the reefs was consistently low (< 5%) because it was exposed to the wind and waves generated by monsoonal storms in austral summer. By comparison, the eastern side of the reefs is sheltered from seasonal storms and has extensive coral communities, with similar habitat conditions and coral assemblages to all but the most unique inner-slope locations. By far the most unique inner-slope location was at the South Reef Lagoon. This sheltered location had relative flat and fragile substrata, low current speeds, high turbidity and chlorophyll concentrations, and sediment deposition characterised by fine particle sizes. Consequently, its coral assemblage was distinguished by taxa with fragile growth forms, such as foliose corals and various *Acropora* growth forms (table, branching, hispidose), in addition to the Fungiidae and Pocilloporidae. Conversely, the Channel location was most exposed to seasonal storms from the west and had a robust and sloping substrata, the highest wave heights and current speeds, low turbidity and chlorophyll concentrations, and the deposition of large particle sizes. Consequently, its coral assemblage was distinguished by the massive Faviidae and *Porites*, encrusting corals and particularly soft corals. The most similar conditions and coral assemblage to that at the Channel was at the Inner South West location, whereas at the Inner South East location, conditions and assemblage structure were a mixture of those at all locations at Scott Reef. The influence of routine habitat conditions was most obvious prior to the mass bleaching (1994-1997), when they structured coral assemblages over several years in the absence of severe disturbance. However, habitat conditions also mediated the effects of acute disturbances and influenced the recovery of coral assemblages.

3.5.2 Acute disturbances and assemblage structure

Over 18 years, the coral assemblages at Scott Reef were exposed to 10 acute disturbances of varying severity and scale. The most severe disturbances reduced the cover of most coral taxa at several locations, and included the mass-bleaching in 1998, a cyclone in 2004 and a monsoonal storm in 2012. The remaining disturbances were more frequent but moderate in their impacts, usually affecting a few coral taxa and locations, and included three cyclones, two bleaching events and the outbreak of disease. As with most coral reefs, the severity of the disturbance and the degree to which patches of corals survived at Scott Reef had important implications for the recovery of assemblages (Connell *et al.* 1997b, Kayanne *et al.* 2002, Graham *et al.* 2011).

The mass-bleaching of corals in 1998 reduced coral cover across Scott Reef by 80% (Gilmour *et al.* 2013). However, the reductions in coral cover varied among assemblages depending on their exposure to thermal stress. Thermal stress during bleaching events can be tempered by current flow and fine-scale variation in temperature regimes (Nakamura and van Woesik 2001, Nakamura *et al.* 2003, Hagan and Spencer 2008, McClanahan *et al.* 2012). At Scott Reef, reductions in cover following the mass-bleaching were lowest at the locations adjacent to the deep channel between South and North Reef, which experienced the highest current speeds and temperature ranges, and cool water intrusions from the deep. In contrast, the coral assemblages within the lagoon at South and North Reef were among the worst affected by the mass-bleaching and experienced the lowest current movements and highest residence times, while the flow of hot water from the lagoon at North Reef over the reef flat also increased the incidence of bleaching at the adjacent outer-slope location.

The reductions in coral cover following the mass-bleaching also varied among assemblages according to the relative abundance of susceptible taxa. Corals have varying tolerances to thermal stress and general patterns of susceptibility have been documented in most studies of coral bleaching (Gleason 1993, Marshall and Baird 2000, McClanahan *et al.* 2004, Baker *et al.* 2008). Similar tolerances were evident at Scott Reef following the mass-bleaching in 1998, with the *Acropora*, *Isopora* and Pocilloporidae among the most susceptible, and the Faviidae, *Montipora* and particularly the massive *Porites*, the least susceptible. Consequently, assemblages with the highest cover of susceptible taxa were worst impacted by the mass-bleaching, and also by the moderate bleaching events that occurred in subsequent years. The Pocilloporidae were among the most susceptible of the coral taxa in all bleaching events, but some variation in the susceptibility of other taxa was apparent; the *Acropora* were severely impacted by the mass-bleaching but not by more recent bleaching, whereas the Fungiidae were not severely impacted by the mass-bleaching but were by more recent bleaching. However, quantitative data were restricted to the changes in percentage cover over one or two years around the bleaching events, and only qualitative observations were recorded during each event, so the apparent variation in susceptibilities was not accurately quantified. Recurrent bleaching events on other reefs have produced consistent, and contrasting, patterns of susceptibility (Marshall and Baird 2000, McClanahan *et al.* 2004), leading to debates about the extent to which the corals and their symbionts may be capable of adapting to predicted increases in water temperatures (Rowan *et al.* 1997, Baird *et al.* 2009, Guest *et al.* 2012).

Following the mass-bleaching, all assemblages were impacted by multiple disturbances. The most severe was a cyclone in 2004 and a monsoonal storm in 2012, which caused large (>50%) relative decreases in cover of all coral taxa. Even the most robust massive and encrusting corals were impacted by the resulting wave energy, but typical patterns of susceptibility were again evident among the taxa, with the *Acropora* and other branching corals being most severely affected (Knowlton *et al.* 1981, van Woesik *et al.* 1995, Adjerdoud *et al.* 2005). However, the impacts from these severe disturbances were limited to the few locations exposed to the prevailing conditions, and within these assemblages many colonies were injured rather than killed. Consequently, recovery was aided by the regrowth of injured colonies and the supply of recruits from other assemblages not affected by the disturbance. Similarly, recovery from the more moderate disturbances was relatively quick, given they mostly impacted a few locations and taxa; the cyclones affected the *Acropora*, the bleaching events the *Acropora*, Pocilloporidae and/or Fungiidae, and the outbreak of disease the *Acropora*. The disease outbreak primarily affected the table *Acropora* at a single location, but did kill the majority of colonies where they had previously been by far the dominant group of corals. The disease was probably white syndrome, and occurred where there was comparatively little water flow, high turbidity and chlorophyll concentrations, and an accumulation of fine sediments on the substrata. The accumulated sediments had been resuspended and deposited through multiple cyclones and the disease outbreak occurred during high summer water temperatures that ended with the moderate bleaching in 2010. This combination of habitat conditions, elevated water temperatures and an abundance of susceptible species can typically promote and sustain outbreaks of coral disease (Bruno *et al.* 2003, Sutherland *et al.* 2004, Heron *et al.* 2010), and was most likely responsible for the outbreak at the Lagoon assemblages where previously there had been a very low incidence of disease.

Coral cover had recovered at most locations across Scott Reef after more than a decade, but there remained some differences to the pre-bleaching structure in several assemblages. The differences in coral cover and structure were greatest at the outer-slope and Lagoon assemblages, which were most severely impacted by the mass-bleaching and by subsequent disturbances, such as the additional bleaching events and a severe cyclone (Outer South Reef) or outbreak of disease (Lagoon). Conversely, the assemblages at the Channel and Inner South West locations were least affected by the mass-bleaching, and despite being exposed to moderate storms and cyclones, had recovered within a decade; following this recovery, the assemblages were then severely impacted by the monsoonal storm in 2012. Among all the assemblages, the most significant difference to pre-bleaching structure was a lower cover of soft corals and/or branching *Acropora* and *Isopora*, and a higher cover of corymbose and table *Acropora*. The differences in relative abundance of these coral taxa reflect their contrasting life histories and the successional changes in assemblage structure following disturbance.

3.5.3 Coral life histories and assemblage structure

The life histories of coral taxa influenced the spatial and temporal variation in assemblage structures at Scott Reef through periods of impact and recovery from disturbances. Among the coral taxa, there were general patterns of susceptibility to all disturbances, with the Pocilloporidae and *Acropora* the most susceptible, and the massive *Porites*, Faviidae and encrusting corals the least susceptible to thermal stress, wave energy and disease. These are among the most common acute disturbances to coral reefs, in addition to outbreaks of coral predators (Moran 1986, Pratchett 2007, De'ath *et al.* 2012), and can all display comparable patterns of selectivity among coral taxa. However, the immediate impacts reflect the resistance of coral taxa to disturbance, but not necessarily their resilience. The most susceptible taxa at Scott Reef were the various *Acropora* growth forms, but more than a decade after the mass-bleaching their cover at most assemblages had recovered. Conversely, the soft corals, massive Faviidae and particularly *Porites* were most resistant to thermal stress, but at several locations they had not recovered from the mass-bleaching. The susceptibility of coral taxa to emerging disturbance regimes is not always obvious, and assessments over many years are required to understand the consequences for population maintenance (Adjeroud *et al.* 2009, van Woesik *et al.* 2011). The apparent disparity between impact and recovery of coral taxa at Scott Reef was clarified by their life history traits. For example, the massive corals and soft corals typically grow slowly and have low fecundity and recruitment (Done 1987, Babcock 1991, Fabricius 1995, Fong and Glynn 1998), so their recovery from comparatively small decreases in cover can take far longer than for more susceptible taxa, such as the *Acropora*, which typically have rapid growth (Ninio *et al.* 2000, Halford *et al.* 2004, Emslie *et al.* 2008), high fecundity and recruitment, and wide larval dispersal (Harrison *et al.* 1990, Graham *et al.* 2008, van Woesik *et al.* 2011). The recovery of *Acropora* was therefore aided by the supply of recruits from the assemblages least affected by the mass-bleaching and subsequent disturbances. The importance of larval supply for the recovery of coral assemblages was evident in the spatial variation in the recruitment and genetic structure of *Acropora* across Scott Reef (Underwood *et al.* 2009, Gilmour *et al.* 2013). Recruitment was consistently high at the Inner South East assemblage where an eddy system traps coral larvae, and the rapid progression of these recruits through increasing colony size classes following the mass-bleaching lead to increased coral cover and recovery. Conversely, other locations had consistently low rates of recruitment because currents carried larvae away, and the recovery of the *Acropora* within these assemblages following the mass-bleaching was far slower, particularly when they were exposed to subsequent disturbances.

Local hydrodynamics had a pronounced influence on the recovery of the *Acropora* corals because they are highly fecund and disperse widely, but far less influence on the recovery of brooding corals whose larvae typically disperse over much shorter distances (Underwood *et al.* 2009, Harrison 2011). The brooding *Isopora* are periodically one of the most abundant taxa at Scott Reef, particularly the branching coral *Isopora bruegemanni* which can form huge mono-specific stands that dominate assemblages. *Isopora bruegemanni* grows rapidly and has high fecundity, but was among the most susceptible taxa to disturbance and its recovery depended strongly on local stock sizes. For

example, the cover of *Isopora* was particularly high (10-25%) at the three outer-slope assemblages until the mass-bleaching reduced cover to 0%, and more than decade later cover remained low (<1.5%). In contrast, the cover of *Isopora* at the Inner South West assemblage was also high (11%), but reduced to 3% following the mass-bleaching and within six years had recovered. For the *Isopora* and other brooding corals at Scott Reef, there was a clear association between the local abundance of adult stocks and their recovery from disturbances, with comparatively little influence of variation in local hydrodynamics and habitat conditions. Indeed, the brooding corals displayed little preference for habitat conditions among the locations, seemingly able to proliferate within all assemblages provided adult stocks were present. The dependence of brooding corals on local stock sizes for their recovery, and their high susceptibility to many disturbances, has important implications for their future persistence should disturbance regimes increase. Their ability to grow and proliferate quickly in a range of habitat conditions means they may be considered among the corals most likely to persist on future coral reefs. However, if the scale and severity of disturbance increase to the point at which most colonies of a brooding species are killed over scales of more than several kilometres, then their recovery may be compromised, depending on whether the few brooded larvae that periodically disperse over longer distances arrive at the site.

The interaction between disturbance regime and coral life histories produced consistent patterns of assemblage structure and succession across Scott Reef. Assemblages following the mass-bleaching were characterised by the least susceptible taxa, particularly the massive *Porites*, Faviidae, *Montipora* and encrusting corals, and the soft corals. Early recovery involved the growth of the dominant survivors, followed by recruitment and increases in cover of Pocilloporidae and corymbose *Acropora*. In the absence of additional disturbances, these taxa became the dominant corals after approximately five years, along with the emergence of more susceptible taxa, such as the table and branching *Acropora* and the *Isopora*; a decade later, the cover of the most susceptible groups increased rapidly, as they grew and outcompeted the corals more typical of the early successional stages. Moderate disturbances had the effect of setting these successional changes back by several years, usually reducing the cover of the most susceptible, but competitively dominant, taxa (e.g. table and branching *Acropora*, *Isopora*). The more susceptible taxa characterised many assemblages prior to the mass-bleaching, and some assemblages in the final successional stages more than a decade later. However, it was the least susceptible taxa that consistently characterised the coral assemblages across Scott Reef, having a moderate to high cover and relative abundance during most years at most locations. Indeed, a low coral cover (<15%) dominated by the least susceptible coral taxa most likely reflects the future of many coral reefs, unless predicted increases in local and global pressures can be curtailed (McClanahan 2002, Hughes *et al.* 2003, Hoegh-Guldberg 2005, Done *et al.* 2007, Thompson and Dolman 2010, De'ath *et al.* 2012). In this scenario, the most obvious consequences for coral reefs ecosystems is the loss of coral taxa that contribute most to structural complexity, particularly the table and branching corals, which are an important source of habitat and food for coral reef fishes (Berumen and Pratchett 2006, Cole *et al.* 2008). The loss of structural complexity and coral and fish diversity are likely to have other, currently unknown, consequences for coral reef ecosystems and the organisms that depend on them.

3.6 Conclusion

Over almost two decades, Scott Reef has displayed a remarkable capacity to absorb multiple disturbances, particularly given the isolation of the reef system and its reliance on surviving corals for recovery through asexual growth and sexual recruitment (Gilmour *et al.* 2009, Underwood 2009, Underwood *et al.* 2009, Gilmour *et al.* 2013). As with other reefs that have recovered from the severe mass-bleaching events, the resilience of Scott Reef is attributed to favourable habitat conditions and the lack of local pressures that are commonly implicated in the degradation of in-shore reef systems, such as overfishing of herbivores and degraded water quality. Consequently, the reductions in coral cover following disturbances at Scott Reef were matched by increases in turf and coralline algae, and then herbivorous fishes (Gilmour *et al.* 2009). The cover of all other benthic organisms remained low, including macroalgae and sponges, which can proliferate following severe

disturbances and prevent the recolonisation by corals. Suitable habitat for coral recruitment, growth and survival therefore remained through disturbance regimes, and promoted high growth and survival of corals between disturbances. However, even in the absence of chronic pressures, sufficient periods of calm between acute disturbances are needed for coral assemblages to recover, particularly for the recovery of more susceptible taxa that contribute significantly to assemblage diversity and structural complexity (McClanahan 2002, Hughes *et al.* 2003, Hoegh-Guldberg 2005, Done *et al.* 2007, Thompson and Dolman 2010, De'ath *et al.* 2012). The influence of climate change on the number and frequency of acute disturbances will be a critical factor determining whether reefs are able to persist in a state of moderate to high coral cover and diversity in the future. In the last two decades at Scott Reef, assemblages were most commonly characterised by a moderate cover of the least susceptible taxa, and the frequency of disturbances in the second decade was far higher than in the first. Although none were as severe as the mass-bleaching in 1998, between 2005 and early 2013 the reef was impacted by two cyclones, a severe storm, an outbreak of disease and three bleaching events. Even, a small increases in the frequency and severity of these disturbances in the next decade is likely to shift community structure to a more degraded state in which the most susceptible taxa (e.g. *Acropora*), and/or brooding corals (e.g. *Isopora*) or corals with slow growth and reproductive output (e.g. soft corals, massive *Porites*) are less common. Should the disturbance regime become so severe that population densities were reduced to a point at which reproduction and recruitment were compromised by allee effects (Knowlton 1992), there would be profound consequences for isolated coral reef systems such as Scott Reef, which receive a negligible supply of larvae from other reefs over ecological time.

The long-term, large-scale data from Scott Reef, and from other coral reefs (Bak and Nieuwland 1995, Connell *et al.* 1997a, Sweatman *et al.* 2011), are invaluable for the global assessment of coral reef ecosystems, which has become so confounded in recent history by the rate of changes and sliding baselines (Jackson 1997). Assessments of reef degradation typically require studies over decadal time-steps (Connell 1997), reflecting the periods over which healthy reefs are likely to recover from severe disturbance regimes. Conversely, the degradation of reefs most commonly occurs over one or more decades (Hughes *et al.* 2012), rather than more abrupt changes. Indeed, even when such abrupt changes have occurred it is usually the consequence of multiple pressures acting over several years, and reversing the consequences at this point is particularly difficult (Mumby *et al.* 2007). Large-scale studies incorporating multiple coral assemblages also provide a balanced assessment of the condition of the entire reef system and valuable insights into the contribution of habitat conditions, disturbance regimes and coral life histories to assemblage dynamics. Understanding the physical and biological drivers of resistance and resilience in coral assemblages is critical for the future design of marine protected areas, as a means of preserving coral reef futures. However, for the assemblages at Scott Reef, multiple factors contributed in contrasting ways to their patterns of impact and recovery. For example, at one location the exposure to cool water intrusions from the deep channel reduced the likelihood of thermal stress, but increased exposure to severe storms and cyclones, and the strong currents carried larvae away and reduced recruitment; another location was sheltered from storms and cyclones, but had low current flow and comparatively high turbidity and nutrients, increasing the likelihood of bleaching or disease outbreaks. Among all the assemblages, only one had comparatively high coral cover and diversity throughout the study, with a low to moderate exposure to all disturbances and consistently high rates of recruitment. Reconciling these drivers of change and applying them to the design of marine protected areas and other conservation initiatives in coming decades represents one of the great challenges to the preservation of coral reefs and the goods and services they provide (Hoegh-Guldberg 2006, Hoegh-Guldberg *et al.* 2008, Hughes *et al.* 2010, McClanahan *et al.* 2012).

3.7 References

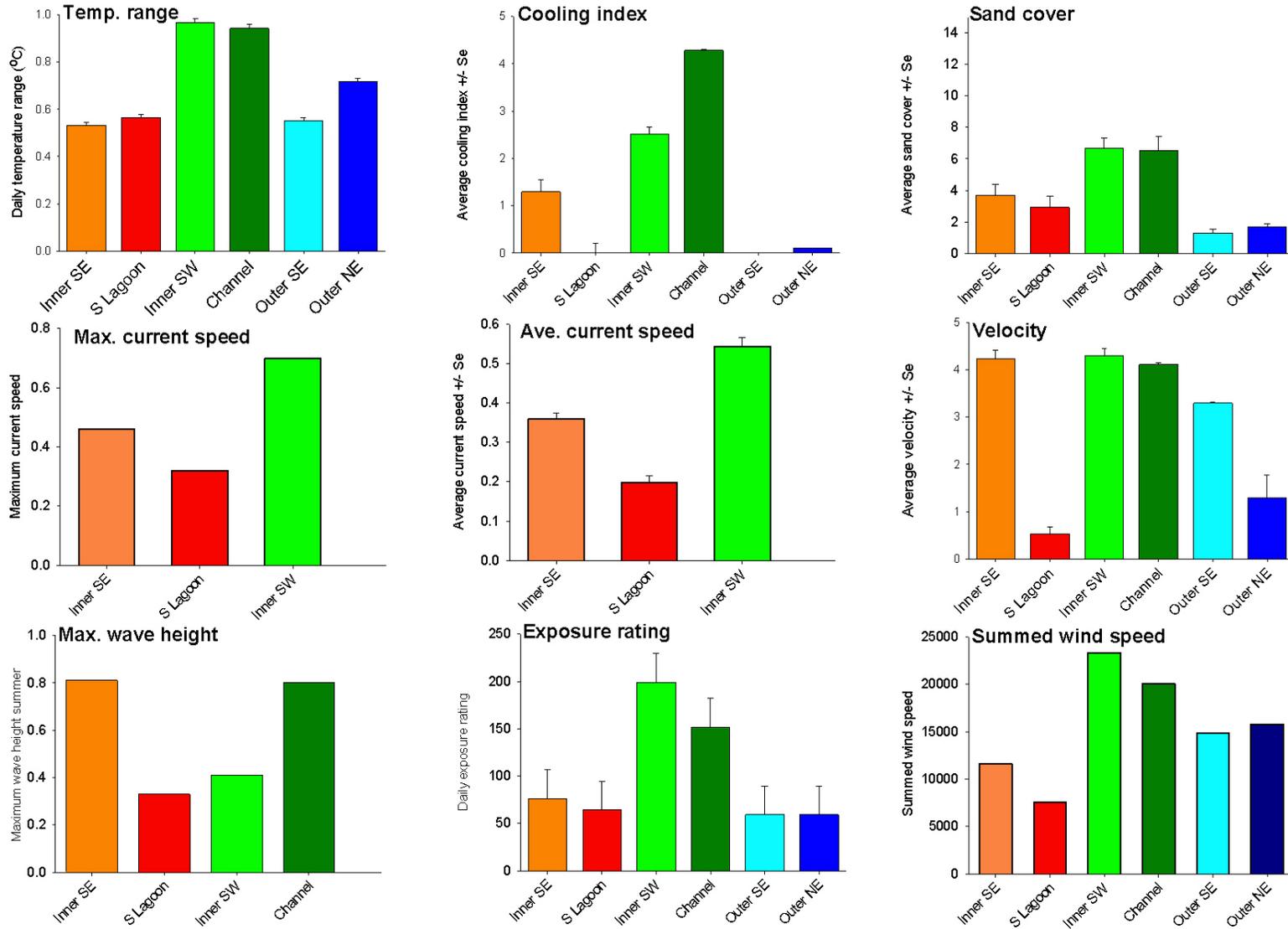
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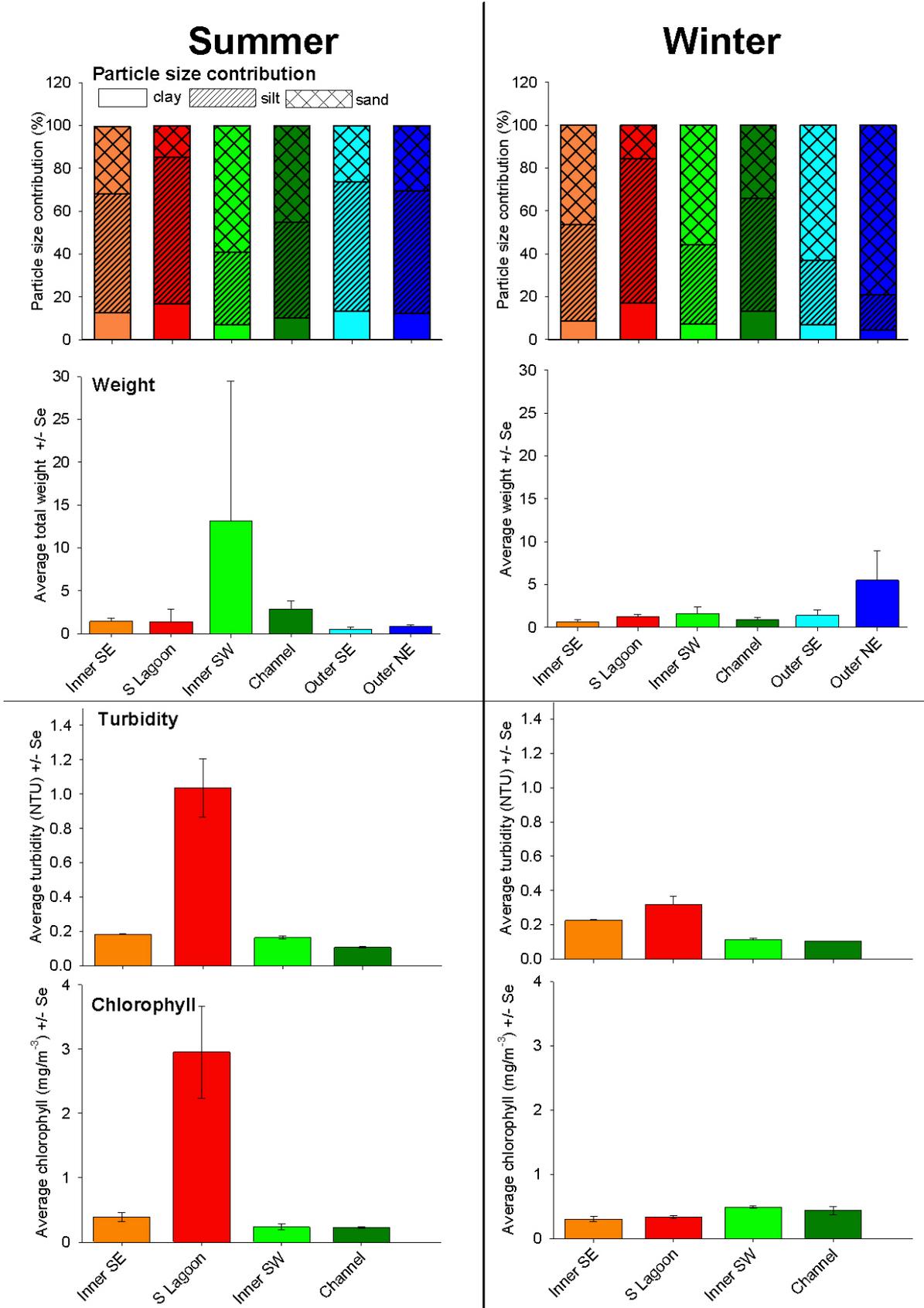
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Supplementary Figure 1



Supplementary Figure 2



Supplementary Table 1

Pre-bleaching (1994-1997)								From Pre-bleaching To Severe bleaching (1994-1997) To (1998-2001)							
	SL2	SL1	SL4	SL3	SS1	SS2	SS3		SL2	SL1	SL4	SL3	SS1	SS2	SS3
Algae turf & coralline	23.717	34.5	31.9	43.0	28.2	33.2	32.3	Algae turf & coralline	64.6	39.5	36.8	28.2	60.4	56.1	53.9
Acropora branching	10.9	2.4	0.8	2.7	2.1	1.3	2.5	Acropora branching	-10.7	-2.4	-0.6	-0.1	-2.1	-1.3	-2.5
Acropora digitate	3.8	3.1	0.8	2.6	1.5	1.7	3.2	Acropora digitate	-3.5	-2.9	-0.2	-1.6	-1.5	-1.5	-3.2
Acropora hispidose	5.6	0.2	0.0	0.1	0.1	0.0	0.0	Acropora hispidose	-5.6	-0.2	0.0	-0.1	-0.1	0.0	0.0
Acropora tabulate	2.1	0.9	0.0	0.6	0.4	0.1	0.7	Acropora tabulate	-2.1	-0.9	0.1	-0.3	-0.4	-0.1	-0.7
Foliose corals	8.6	0.7	0.1	0.4	0.2	0.0	0.3	Foliose corals	-6.9	-0.5	-0.1	-0.2	-0.1	0.0	-0.1
Faviids	2.5	3.5	3.5	4.5	4.0	4.9	5.1	Faviids	-1.9	-2.7	-2.2	-2.0	-3.7	-4.7	-4.7
Fungiids	2.9	0.2	0.0	0.0	0.1			Fungiids	0.0	0.0	0.0	0.1	-0.1		
Isopora	7.7	1.5	4.5	11.5	24.3	10.8	9.9	Isopora	-7.7	-1.5	-4.3	-8.3	-24.3	-10.8	-9.9
Millepora	1.4	1.5	2.2	1.3	2.1	3.2	3.8	Millepora	-1.3	-1.5	-2.1	-1.2	-2.0	-3.2	-3.8
Montipora	5.8	6.9	6.3	5.0	8.2	10.8	8.2	Montipora	-5.1	-4.6	-2.5	-2.6	-7.5	-9.3	-5.7
Pocilloporidae	7.3	3.7	3.1	4.1	2.7	2.3	7.6	Pocilloporidae	-7.0	-3.5	-2.5	-3.6	-2.7	-2.2	-7.3
Porites branching	0.9	3.3	2.8	1.7	0.7	0.7	1.3	Porites branching	-0.8	-3.3	-2.8	-1.7	-0.7	-0.7	-1.3
Porites massive	1.5	9.9	11.6	5.4	9.2	9.0	5.9	Porites massive	-0.9	-4.8	-0.9	-1.2	-4.0	-4.0	-2.1
Soft coral	0.9	11.1	19.3	5.4	5.8	9.7	9.2	Soft coral	-0.8	-9.0	-13.1	-1.8	-5.5	-8.7	-7.9
Severe Bleaching (1998-2001)								Severe Bleaching To Slow recovery and severe cyclone (1998-2001) To (2002-2004)							
	SL2	SL1	SL4	SL3	SS1	SS2	SS3		SL2	SL1	SL4	SL3	SS1	SS2	SS3
Algae turf & coralline	88.4	74.0	68.7	71.2	88.5	89.3	86.1	Algae turf & coralline	-14.6	-5.1	-17.0	-17.9	-3.9	-6.7	-19.4
Acropora branching	0.2	0.0	0.1	2.6				Acropora branching	0.7	0.4	0.8	0.3	0.2	0.1	0.2
Acropora digitate	0.3	0.2	0.6	1.0		0.1	0.1	Acropora digitate	1.4	1.4	0.5	1.1	0.4	0.3	0.2
Acropora hispidose	0.0			0.0				Acropora hispidose	0.5	0.0	0.0	0.0			
Acropora tabulate	0.1	0.0	0.1	0.3				Acropora tabulate	1.1	1.3	0.4	1.0	0.2	0.0	0.2
Foliose corals	1.6	0.2	0.1	0.2	0.1		0.1	Foliose corals	1.3	-0.2	0.1	0.1	0.0	0.0	0.2
Faviids	0.5	0.8	1.4	2.5	0.4	0.3	0.4	Faviids	0.5	0.3	0.2	0.1	-0.1	-0.1	1.6
Fungiids	3.0	0.2		0.1		0.1		Fungiids	1.5	-0.2	0.0	-0.1	0.0	0.0	0.0
Isopora	0.0	0.1	0.2	3.2		0.1	0.0	Isopora	0.0	0.1	0.2	3.4	0.0	0.1	0.3
Millepora	0.1	0.0	0.1	0.1	0.1		2.4	Millepora	0.0	0.0	0.2	0.1	-0.1	0.0	1.0
Montipora	0.7	2.3	3.8	2.3	0.6	1.5		Montipora	1.9	3.3	0.4	1.5	3.0	2.2	8.1
Pocilloporidae	0.3	0.2	0.6	0.4		0.1	0.3	Pocilloporidae	2.1	0.2	1.1	2.3	0.1	0.3	3.8
Porites branching	0.0			0.0				Porites branching	0.0		0.0	0.3	0.0	0.0	0.0
Porites massive	0.6	5.2	10.6	4.2	5.3	5.0	3.8	Porites massive	0.1	0.7	3.4	-0.5	-0.2	1.7	4.0
Soft coral	0.1	2.1	6.2	3.6	0.3	1.0	1.3	Soft coral	0.3	2.4	1.9	1.9	0.0	0.1	0.7
Slow recovery and severe cyclone (2002-2004)								Slow recovery and severe cyclone To Recovery and moderate cyclone (2002-2004) To (2005-2008)							
	SL2	SL1	SL4	SL3	SS1	SS2	SS3		SL2	SL1	SL4	SL3	SS1	SS2	SS3
Algae turf & coralline	73.8	68.9	51.7	53.3	84.6	82.6	66.7	Algae turf & coralline	-23.2	-21.8	-8.1	-1.7	-20.3	-20.2	-20.1
Acropora branching	0.9	0.4	0.9	2.8	0.2	0.1	0.2	Acropora branching	4.8	2.9	-0.7	-0.9	0.5	0.2	0.2
Acropora digitate	1.6	1.6	1.1	2.1	0.4	0.5	0.3	Acropora digitate	1.2	1.1	-0.4	-1.4	1.0	2.2	0.5
Acropora hispidose	0.5	0.0						Acropora hispidose	3.8	0.2	0.0	0.0	0.0	0.0	2.8
Acropora tabulate	1.2	1.3	0.5	1.3	0.2		0.2	Acropora tabulate	8.9	10.3	0.0	1.1	7.1	3.5	1.5
Foliose corals	2.9	0.1	0.2	0.3			0.3	Foliose corals	1.8	0.7	0.3	0.6	0.0	0.1	1.4
Faviids	1.1	1.1	1.5	2.6	0.3	0.2	2.0	Faviids	1.1	1.5	2.2	1.9	1.0	1.6	0.0
Fungiids	4.4	0.0	0.0		0.0	0.0		Fungiids	0.6	0.0	0.0	0.0	0.0	0.0	0.8
Isopora	0.0	0.1	0.4	6.6	0.0	0.1	0.3	Isopora	0.2	0.1	1.3	0.1	0.4	0.5	-0.3
Millepora	0.1	0.0	0.3	0.2		0.1	1.0	Millepora	0.7	0.2	0.3	0.0	0.0	0.1	-1.7
Montipora	2.5	5.6	4.2	3.8	3.6	3.6	10.5	Montipora	0.6	1.8	1.6	2.6	5.3	5.2	-0.2
Pocilloporidae	2.4	0.4	1.7	2.7	0.1	0.4	4.1	Pocilloporidae	1.7	2.2	1.2	0.6	4.6	3.9	0.0
Porites branching		0.0	0.0	0.4				Porites branching	0.1	0.1	0.0	0.2	0.0		
Porites massive	0.8	5.9	14.0	3.7	5.1	6.8	7.8	Porites massive	0.4	1.9	5.7	1.9	1.2	1.4	0.1
Soft coral	0.4	4.6	8.1	5.5	0.3	1.1	2.0	Soft coral	-0.2	1.6	1.9	0.9	0.0	0.8	1.2

Supplementary Table 1 continued

Recovery and moderate cyclone (2005-2008)								Recovery and moderate cyclone to Recovery and moderate disease and bleaching (2005-2008) To (2009-2010)							
	SL2	SL1	SL4	SL3	SS1	SS2	SS3		SL2	SL1	SL4	SL3	SS1	SS2	SS3
Algae turf & coralline	50.6	47.1	43.6	51.6	64.3	62.4	46.6	Algae turf & coralline	-2.0	-8.7	-11.0	-21.7	-13.3	-13.4	-2.7
Acropora branching	5.7	3.3	0.2	1.9	0.6	0.3	0.4	Acropora branching	-1.8	1.2	0.0	4.0	0.9	0.5	0.5
Acropora digitate	2.9	2.8	0.7	0.7	1.4	2.7	0.8	Acropora digitate	1.1	1.9	1.5	3.1	5.2	4.5	1.7
Acropora hispidose	4.3	0.2	0.0	0.0	0.0			Acropora hispidose	-2.8	0.4	0.6	0.1	0.1	0.1	0.0
Acropora tabulate	10.1	11.6	0.5	2.4	7.3	3.5	3.1	Acropora tabulate	-8.5	-4.4		0.2	0.3	1.8	-1.4
Foliose corals	4.7	0.7	0.5	0.9	0.0	0.1	1.0	Foliose corals	1.6	0.4	-0.1	0.4	0.3	0.1	0.0
Faviids	2.2	2.6	3.8	4.5	1.3	1.7	3.4	Faviids	0.5	2.0	0.6	0.6	1.7	1.5	2.6
Fungiids	5.0	0.1	0.0	0.0	0.0			Fungiids	-0.3	0.1	0.0	0.2	0.2	0.1	0.1
Isopora	0.2	0.2	1.8	6.7	0.5			Isopora	0.0	0.2	0.9	7.5	0.0	0.2	0.6
Millepora	0.8	0.2	0.6	0.2	0.0	0.6	1.1	Millepora	-0.7	-0.1	-0.2	0.3	0.3	-0.1	0.1
Montipora	3.1	7.5	5.8	6.4	8.9	0.1	0.8	Montipora	0.4	0.7	1.2	-1.0	1.5	4.9	-0.9
Pocilloporidae	4.0	2.7	2.9	3.3	4.7	8.8	8.8	Pocilloporidae	-0.4	1.3	3.1	1.5	-1.1	-0.2	-4.8
Porites branching		0.1	0.0	0.5	0.0	4.3	13.2	Porites branching	0.2	-0.1	0.1	-0.4	0.0		0.0
Porites massive	1.2	7.8	19.7	5.7	6.3	8.1	7.9	Porites massive	-0.5	-1.6	-4.3	-0.6	-0.7	-0.1	0.5
Soft coral	0.3	6.2	10.0	6.5	0.4	1.9	3.2	Soft coral	0.3	-2.7	2.7	-0.8	0.2	0.0	0.0
Recovery and Moderate Disease and Bleaching (2009-2010)								Recovery and moderate disease and bleaching To Severe storm (2009-2010) To (2011-2012)							
	SL2	SL1	SL4	SL3	SS1	SS2	SS3		SL2	SL1	SL4	SL3	SS1	SS2	SS3
Algae turf & coralline	48.6	38.3	32.6	29.8	51.0	49.0	44.0	Algae turf & coralline	-2.2	5.5	36.6	36.3	-0.7	-5.2	-5.3
Acropora branching	3.9	4.5	0.3	5.9	1.6	0.8	0.9	Acropora branching	1.1	-2.9	-0.3	-5.8	-0.4	0.4	0.2
Acropora digitate	4.0	4.6	2.1	3.8	6.6	7.2	2.5	Acropora digitate	-0.2	-0.8	-2.1	-3.6	-1.7	-2.0	0.2
Acropora hispidose	1.6	0.6	0.0	0.1	0.1	0.1	0.0	Acropora hispidose	2.3	-0.2	0.0	-0.1	0.2	-0.1	0.0
Acropora tabulate	1.6	7.2	1.1	2.6	7.6	5.4	1.6	Acropora tabulate	1.5	-3.2	-1.1	-2.6	2.2	2.9	1.3
Foliose corals	6.3	1.1	0.3	1.3	0.3	0.2	1.1	Foliose corals	2.2	0.0	-0.3	-1.2	-0.2	0.0	0.4
Faviids	2.6	4.6	4.4	5.1	3.1	3.2	6.1	Faviids	-0.1	1.3	-2.1	-0.7	-0.8	-0.7	-1.2
Fungiids	4.7	0.2	0.0	0.2	0.2	0.1	0.1	Fungiids	0.9	0.1	0.0	-0.1	0.0	0.0	0.0
Isopora	0.2	0.4	2.6	14.1	0.4	0.8	1.7	Isopora	0.4	0.6	-1.8	-10.6	1.1	1.2	2.9
Millepora	0.2	0.1	0.4	0.5	0.3	0.0	0.9	Millepora	0.0	0.1	0.0	0.3	-0.3	0.1	0.4
Montipora	3.5	8.1	7.0	5.4	10.4	13.8	8.0	Montipora	0.0	1.7	-3.3	-0.4	-1.3	-2.7	-1.0
Pocilloporidae	3.7	4.0	6.0	4.8	3.6	4.1	8.4	Pocilloporidae	1.6	-0.4	-5.8	-4.2	1.8	0.0	2.1
Porites branching	0.2	0.0	0.1	0.2	0.0	0.0	0.0	Porites branching	0.1	0.2	-0.1	0.0	0.0	0.0	0.2
Porites massive	0.7	6.2	15.4	5.1	5.5	8.0	8.4	Porites massive	0.0	1.9	-9.6	-1.5	0.1	2.7	-0.1
Soft coral	0.6	3.4	12.7	5.6	0.5	1.9	3.2	Soft coral	-0.3	1.3	-9.8	-3.1	-0.1	0.6	0.8
Severe Storm (2011-2012)															
	SL2	SL1	SL4	SL3	SS1	SS2	SS3		SL2	SL1	SL4	SL3	SS1	SS2	SS3
Algae turf & coralline	46.4	43.8	69.2	66.1	50.3	43.8	38.7								
Acropora branching	5.0	1.6	0.0	0.0	1.2	1.2	1.1								
Acropora digitate	3.7	3.8	0.0	0.2	4.9	5.2	2.7								
Acropora hispidose	3.9	0.4	0.0		0.3	0.1	0.0								
Acropora tabulate	3.1	4.0	0.0		9.7	8.3	2.9								
Foliose corals	8.5	1.1	0.0	0.1	0.1	0.2	1.4								
Faviids	2.5	5.9	2.3	4.4	2.3	2.5	4.9								
Fungiids	5.5	0.3	0.0	0.1	0.2	0.1	0.1								
Isopora	0.6	1.0	0.8	3.5	1.6	2.0	4.7								
Millepora	0.2	0.2	0.3	0.8	0.0	0.1	1.3								
Montipora	3.5	9.8	3.6	5.0	9.1	11.1	6.9								
Pocilloporidae	5.3	3.6	0.2	0.6	5.4	4.1	10.5								
Porites branching	0.3	0.2	0.0	0.2	0.0	10.7	0.2								
Porites massive	0.7	8.0	5.9	3.6	5.6	2.5	8.2								
Soft coral	0.3	4.7	2.9	2.5	0.4	0.0	3.9								

4. Long-term monitoring of fish communities

4.1 Introduction

The Scott Reef system is a remote group of shelf-edge atolls in the Indian Ocean between Timor and the north-west coast of Australia. The system is located in a zone of regular cyclonic activity, suggesting that these reefs have evolved over thousands of years to withstand and recover from natural episodes of disturbance (Moberg and Folke 1999). These atolls have a diverse array of flora and fauna (Bryce *et al.* 2009) and currently a relatively low intensity of mostly local human impacts, and are therefore high priorities for conservation. Traditional fishing within Scott and other northern Australian reefs has been taking place for several centuries by Indonesians from as far as Sulawesi and Roti (Flinders 1814, Russell & Vail 1988, Vail & Russell 1989) and is permitted under the 1974 Memorandum of Understanding (MOU74 Box) between the Australian and Indonesian Governments. However, historical evidence has shown that increasing numbers of non-traditional motorised fishing vessels were arriving by the 1980's spurred on by increasing market prices for trochus and shark fin. Since this time, we have strong evidence that shark populations at Scott Reef are chronically low and sit at 20% of those found on comparable non-fished reefs (Meekan & Cappo 2004, Meekan *et al.* 2006) and there is now a sequential trail of historical evidence that fishing targets regularly switch in line with catch availability and market forces, suggesting that traditional subsistence fishing may now be secondary to market sales. Overfishing of trepang (beche-de-mer), trochus and clams has already led to significant declines at nearby Ashmore and Cartier Reefs (Ceccarelli *et al.* 2006, Richards *et al.* 2009), and increasing shark fin prices (Fabinyi 2011) have likely driven fishermen towards concentrated efforts on shark fishing in the past. As yet, there is no evidence that reef fish stocks have been similarly affected at Scott Reef (Meekan *et al.* 2006). However, with dwindling populations of trepang, shark and trochus and an increasingly strong market demand for reef fish in the Asian markets (reviewed in Foale *et al.* 2013), we may see more target-switching towards reef fishes. There is already some evidence showing that other north-west Australian reefs within the MOU74 Box have seen recent declines in the abundance of some reef fish groups (Richards *et al.* 2009).

An absence of human settlement and the reproductive and physical isolation of Scott Reef means that its reef communities are insulated from the damaging interactive disturbances that typically effect more coastal reefs (e.g. nitrification, pollution and freshwater runoff) marking it as an ideal system to document changes in reef biodiversity. To some extent, stability 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 indicate that exchange of propagules with neighbouring systems occurs only sporadically and there may be intervals of years, decades, or even longer between inputs of exogenous larvae into reef populations (Underwood *et al.* 2009, 2012). 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 stable than reefs within an inter-connected, archipelagic system such as the Great Barrier Reef (GBR).

Reef fish groups perform a great variety of different trophic roles on coral reefs and it is the combined activities of all groups that maintain system health and integrity. Herbivores for example, are instrumental in maintaining a healthy balance between coral and algal growth (Lirman 2001, Green & Bellwood 2009) and detritivores provide the most significant trophic pathway for the recycling of primary productivity on coral reefs (Bowen 1983, 1984), making this available to higher trophic levels through predation (Depczynski & Bellwood 2003). The ability of coral reefs to resist change, absorb disturbance and regenerate following disruption (resilience) is to a large part

dependent on the day-to-day activities of reef fishes. A coral reef system with healthy representation of each functional trophic group provides a measure of insurance in the event of any disturbance, a term called the amount of “redundancy” in the system. This highlights the importance of management strategies that not only maintain adequate numbers of coral reef fishes, but also the role that species richness plays and the impact that changes in community composition can have on the on-going health and maintenance of coral reef ecosystems. 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 record that tracks the historical trends in densities, species richness and community composition of an isolated coral reef fish population over an 18-year period. The monitoring program is hierarchical in structure and comprehensively records these metrics along fixed transects and sites at seven locations at Scott Reef. Overall, the value of this dataset is immense, providing an opportunity to examine the resilience, recovery and restructuring of reef fish communities at decadal scales following disturbances (e.g. Halford & Caley 2009). The study provides an exceptional baseline of natural variability within an isolated reef system against which the potential effect of anthropogenic impacts can be determined.

The primary aim of this report was to describe trends in the fish community at Scott Reef in contrast to the 2011 final report (Gilmour *et al.* 2011), which focussed strongly on trends in the fish community relative to the coral bleaching of 1998. Particular emphasis was therefore placed in this report on comparisons between the 2010 and recent 2012 surveys, and background information from the 2011 report was reiterated where appropriate. The 2012 surveys represent a continuation of finfish monitoring that now extends to 18-years and provides a definitive measure of population dynamics of reef fishes at Scott Reef. Our specific aims were to:

- 1) Examine recent and long-term trends in fish diversity, composition and abundance, and
- 2) Investigate whether the community structure in 2012 has stabilized, returned to a pre-bleaching state, or remained distinct.

4.2 Methods

This study was conducted at Scott Reef in October 2012, 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 3.1). The reef system occupies an area of *ca* 800 km² and is biogeographically important as it intersects the Indonesian and north-west Australian faunal provinces (Jones 1973; Wilson and Allen 1987). The system is largely unaffected by many of the anthropogenic stressors of coral reefs close to the coast due to its isolation, distance from shore and the absence of human settlement. However, Scott Reef is close to gas development activities and is an important site for Indonesian fishermen who target a range of reef organisms (mostly shark, trepang and trochus). Stocks of these animals are now chronically over-fished (Cappo *et al.* 2004; Meekan *et al.* 2006). To quantify temporal changes in reef fish communities at Scott Reef, seven locations were surveyed in the same period (October to January) during 13 surveys between 1994 and 2012 as part of the long-term monitoring programme (LTM) at AIMS (Heyward *et al.* 1998).

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 3.1). Within each location, fish were sampled at three sites, separated by a distance of \approx 250 m. At each site, five permanently-marked 50 m long transects were deployed parallel to the reef crest in water depths ranging between 6 - 9 m, each separated by a distance of 10 to 20 m. Each transect was censused by a diver on SCUBA who identified and recorded the number of fishes belonging to 10 non-cryptic families (Acanthuridae, Chaetodontidae, Labridae, Lethrinidae, Lutjanidae, Scaridae, Serranidae, Siganidae, Pomacentridae and Zanclidae). The smaller, more site-attached or territorial species from the family Pomacentridae

were surveyed along a 50 x 1 m corridor within each transect, while the larger, more mobile species from all other families were surveyed along a 50 x 5 m corridor. Fishes were classified into six trophic groups based on their diet and feeding behaviour. Species classified as corallivores included both obligate and facultative coral feeders (Pratchett 2005; Wilson *et al.* 2006). Herbivorous species were identified as by Green & Bellwood (2009) while detritivores (including epilithic algal matrix feeders), planktivores, omnivores and carnivores followed Froese & Pauly (2009) and Wilson *et al.* (2003). Carnivores included both invertivores and piscivores.

For each sampling occasion the counts of fishes were converted to a density per 250m² to account for the difference in transect width. Following this conversion, data for the large and small transects were merged as a single transect, and analyses carried out at the appropriate sampling level (described in more detail below). For each transect the total number of species present, density of each individual fish species, density of functional groups (see above), and the total density of fishes was calculated. For all analyses sampling date was expressed as a decimal year calculated as: decimal year = year + (month/12). When year level averages were desired, these were based on a year code calculated by rounding decimal year to zero decimal places. This effectively summarises data by financial year, rather than calendar year. This year code was used for year level averages because it represents a more meaningful summary for most biological processes on reefs, which tend to follow seasonal trends based on either summer or winter, which are not represented well by the calendar year.

4.2.1 Long-term trends of fish fauna

Temporal trends were examined at the whole of Scott Reef level using generalized additive mixed models (GAMMs) (Pinheiro and Bates 2000; Zuur *et al.* 2009). These models were used to examine the long-term trend in fish abundance, including: Pomacentridae, non-Pomacentridae, functional trophic categories of fishes (corallivores, carnivores, herbivores, detritivores, omnivores and planktivores), influential individual fish species (as determined by simpler, see multivariate analysis below); and species richness. In previous analysis of this data set (Gilmour *et al.* 2011), several models were developed for each measure, including linear regression, linear mixed-effects models and generalized additive models, and compared using various measures of goodness of fit. These analyses indicated that GAMMS were the best model according to most criteria, and therefore only GAMMs were used for analysis here. As temporal trends can take a range of shapes, GAMMs are very useful because of their flexibility in fitting a wide range of patterns, from linear to highly non-linear. GAMMs extend the generalized additive model (GAM) to include random effects to account for correlation among observations on the same sampling unit, necessary to accommodate the hierarchical nature of the Scott Reef dataset (transects, sites and locations).

For all models, a cubic regression spline (smoother) fitted to decimal year was included as a fixed factor (explanatory variables that are not influenced by the hierarchical structure in the data) and used to model temporal trends. The simplest model included a single smoother across all locations, thus making the assumption that the temporal trends are consistent across the whole of Scott Reef. A random effects component was also included to account for spatial variation in fish abundances, and for the simplest model included: location, sites nested within locations, and transects nested within sites. Two more complex models were also examined, one including location as a fixed effect, and the other including the full interaction between location and decimal year. Including location as a fixed effect results in a model that fits a single trend line across all locations, but allows the intercept to differ among them, thereby allowing for different abundances across Scott Reef, but assuming that the pattern of change is similar. A full interaction model allows for a different trend line to be fitted for every location (7 in total), thus allowing for the pattern of change as well as overall abundance of fishes to vary across Scott Reef. These three models were compared using the Bayesian Information Criterion, which is a measure of goodness of fit of the models similar to Akaike's Information

Criterion (AIC, Burnham and Anderson 2002) but is more conservative (will favour simple models) than AIC as sample size gets large, thereby having less tendency to “overfit”. Although all three models were compared, for simplicity of presentation and to allow the overall trend for Scott Reef as a whole to be described clearly, only the estimated trends from the simplest GAMMs fitted using location as random rather than a fixed effect are presented visually. Fits for all variables showing the interaction and decimal year are presented in Table 4.1. Observed means (calculated for each year code, across all locations and site) for each measure were plotted against decimal year to provide a visual interpretation of the temporal patterns. Upper and lower confidence bands were added to the plots at 2 standard errors above and below the estimate of the smooth by setting `se = TRUE` in the plot command, to approximate, 95% confidence bands. The R (version 2.15.2, R Development Core Team 2012) function “`gamm`” from the package “`mgcv`” (Wood 2011) was used for these analyses.

4.2.2 Multivariate analysis

Prior to analysis, the density of each fish species was $\text{Log}_n(x+1)$ transformed, then used to construct Bray-Curtis similarity matrices. The logarithmic transformation of the fish density data ensured that some account was taken of the numerous rare species and to down-weight the contribution of the more dominant species (Clarke and Warwick 2001). The relationship between the log_n of the standard deviations and log_n 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 transformed values (averaged across all transects for each year code) was subjected to hierarchical agglomerative clustering with group average linking (function “`hclust`” from package “`stats`”) and an associated Similarity Profiles test (function “`simprof`” from package “`clustsig`”; Clarke *et al.* 2008) and principle coordinates analysis using the function “`pco`” in the package “`ecodist`” (Goslee & Urban 2007).

Similarity profiles in conjunction with cluster analysis as performed above was used to identify whether samples from particular years grouped together and thus did not differ significantly in their species composition. This analysis was a permutation test that determined whether any significant group structure existed within a set of samples for which there was no a priori grouping hypothesis (Clarke *et al.* 2008). The analysis is achieved by determining for each node of the dendrogram whether the particular group of samples being subdivided contained significant internal differences. This routine provides 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 < 0.05 .

To confirm statistical differences in composition between particular year-group categories identified in the `simprof` procedure and to explore potential differences among locations, a Permutational Multivariate Analysis of Variance test (function “`adonis`” in the package “`vegan`”; Anderson 2001; McArdle and Anderson 2001) was used. This was used in favour of an Analysis of Similarities approach (`anosim`) so that interactions between location and time group category could be included. Similarity percentages (function “`simper`”, from the package “`vegan`”; Oksanen *et al.* 2012) was used to identify the fish species that distinguished the components of those groups identified by the `simprof` analysis and confirmed by `permanova`. We tested for community dispersion (heterogeneity) among years with Permutational analysis of multivariate dispersions (function “`betadisper`” from package “`vegan`”; Anderson 2006) using Bray-Curtis as a distance measure. This function implements Marti Anderson's PERMDISP2 procedure for the analysis of multivariate homogeneity of group dispersions (variances). The above multivariate analyses were implemented using R (version 2.15.2, R Development Core Team 2012).

4.3 Results

4.3.1 Historical trends in fish diversity, composition and abundance

Temporal trends in densities of damselfishes (Pomacentridae), non-damselfish and fish species richness were fitted using GAMMs, with BIC indicating that the model with a single fixed factor (decimal year) was sufficient to explain temporal trends at Scott Reef across all locations (Table 4.1). The trend in the mean densities of the damselfishes was non-linear (Estimated $df=6.6$) with values declining from 1995 through 2000 before returning to higher levels in subsequent years (Figure 4.1a). The most recent survey (2012) indicated a recent decline of 35% in damselfish densities, although additional future surveys would be required to determine the extent to which this trend continues downwards through time. In contrast, the 18-year trends in densities of larger, more mobile fishes (non-damselfishes) and species richness (estimated $df=3.6$ & 4.2 respectively: Figure 4.1b-c) was much smoother, larger fishes increasing slowly for the first decade (1995-2005) and thereafter remaining stable for the remainder of the study period (Figure 4.1b) and species richness remaining relatively stable throughout time, although a recent decline was observed in 2012 (Figure 4.1c).

The composition of the fish community at Scott Reef changed throughout the study and a pronounced shift occurred following the 1998 bleaching (Figure 4.2a). The *simprof* test of significant structure classified the samples into three distinct groups based on time. These included a distinct pre-bleach and early post-bleach group (1994-2000), a period from 2001 through to 2008 that incorporated a period of cyclone activity, and the more recent late stage communities (2010-2013). A PCO ordination of these data showed the trajectory of faunal change through time and indicated that the late stage post-bleach fish community in 2001-2008 was tracking away from earlier pre-bleach communities (Figure 4.2b). The more recent 2010-2011 surveys were suggestive of a return towards pre-bleach communities. Nonetheless, the fish community remains distinct from the pre- and early post-bleach fish community with the most recent 2012 survey reaffirming this conclusion and indicating a similar, but still distinct assemblage to that of the previous surveys (2010-2011).

Unsurprisingly, species composition differed most strongly among locations ($R^2 = 0.41$, $P < 0.001$), but also among the three time periods ($R^2 = 0.03$, $P < 0.001$; Table 4.2). Pair-wise comparisons between the three time periods indicated by the hierarchical clustering showed that species composition at all locations differed significantly (all $P < 0.001$) from each other (Table 4.3). The ten most influential species driving these patterns were highly abundant species from the family Pomacentridae (*Pomacentrus adelus*, *P. moluccensis*, *Chromis weberi*, *C. margarifer*, *C. atripes*, *C. lepidolepsis* & *Amblyglyphidodon curacoa*).

Trends in fish communities at Scott Reef were largely dominated by the response of fishes to the catastrophic bleaching event that removed $\approx 80\%$ of all live coral cover in early 1998 (Smith *et al.* 2008)(Figure 4.3). This response was most striking in species that were either reliant on coral or algae for food (i.e. corallivores & herbivores). A steep initial decline in densities of corallivores from a high of 15 individuals per transect in 1997 was followed rapidly by post-bleaching lows of just 5-7 individuals during 2000-2005. For herbivores, an opposite trend was seen as dead coral skeletons were overgrown by algae. Averages of approximately 40 individuals per transect in 1998 rapidly rose to > 90 by 2002. More recent post-2005 trends in these two groups show a declining and stabilising of herbivore abundance that approximate the 18 year averages (64 / transect) and record numbers of corallivores (>16 / transect) that also show some recent signs of stabilising.

4.3.2 Recent trends in fish diversity, composition and abundance

Comparisons between 2010 and 2012 surveys indicate a relatively stable community of corallivores, herbivores and omnivores (i.e. < 20% variation from 2010); a steep rise (82%) in the numbers of detritivores; and significant declines in both planktivores (39%) and carnivores (33%) (Table 4.4). Historically, densities of both detritivores and planktivores at Scott Reef have been variable and have gone through periods of relative stability, and rapid rises and declines over the last 18 years (Figure 4.3). However, the recent increase in detritivores and decrease in planktivores over the last two consecutive surveys were the largest ever seen in the monitoring record for Scott Reef, surpassing the effects that the 1998 bleaching had on these two groups. In contrast to the variability often seen in these two trophic groups, carnivore densities have traditionally shown a slow steady increase since surveys began in 1994. The most recent 2012 survey is only the second consecutive drop of any consequence in carnivore densities in the historical record and is more significant in scale than the previous 2011 decrease (11% vs 33%). Currently, carnivore densities are similar to those seen in pre-bleach years (1994-1998) and at 7.8 individuals 250m⁻², just below the historical 18 year mean of 9.3.

Relative to 18-year averages, trends in the most recent survey indicate decreases in the carnivores, omnivores and planktivores, increases in the corallivores and detritivores, and the maintenance of herbivores at their approximate 18 year average (Table 4.4). The corallivores in particular show a marked increase of 62% from 18 year averages highlighting the prolonged effects of a severe coral bleaching episode on this community. However, the most striking increase was of detritivores, for which an 82% increase was recorded from the previous 2010 survey. Of the 37 carnivore species recorded at Scott Reef, 25 species were either absent altogether in 2012 or had declined from 18 year averages with 12 species increasing in abundance (Figure 4.4). Declines in this group were represented by all the major carnivore subgroups including coral trout, snappers, emperors and groupers.

The temporal trends for densities of the key fish species identified by the above SIMPER analysis were modelled with GAAMs and highlight contrasting trends among species belonging to the same trophic group (Figure 4.5). Mean densities of carnivore species that were influential in separating out the three time periods indicate that stability through time changes considerably with species in this group. EDF values (see Table 4.1), which describe the overall stability of densities through the time series indicated very stable abundances of *Monotaxis grandoculis* (EDF 1.5) compared to those of *Halichoeres hortulanus* (5.7). Similarly, detritivores and herbivores showed large contrasts between species. Mean densities of corallivores showed highly variable patterns across years in all three species, a result partly driven by declines following the 1998 bleaching event. Both the omnivores and planktivores were wholly represented by damselfishes and exhibited high variability in numbers throughout the 18-year time series.

Table 4.1 Univariate Generalised Additive Model results for abundances of (a) damselfishes, non-damselfishes and total species richness, (b) trophic functional groups, and (c) representative individual species. Standard deviation for the random effects, EDF (estimated degrees of freedom) and R² are only shown for the simplest model (Year) where location, site and transect were entered as random effects. BIC values are shown for all three models, with those in bold indicating the best model.

Response Variable	Random standard deviation				EDF	R ²	BIC			
	location	site	transect	residual			Year	Year + Location	Full Interaction	
a.										
Damselfishes	33.9	35.5	42.3	123.8	6.6	0.08	17499.3	17519.6	17522.7	
Non-Damselfishes	5.4	2.8	5.4	15.0	3.6	0.13	11624.0	11639.0	11623.0	
Species richness	1.6	1.5	1.1	3.9	4.2	0.04	7870.7	7889.1	7896.2	
b.										
Carnivores	1.7	2.7	4.1	7.6	4.7	0.06	9797.7	9821.4	9877.3	
Corallivores	2.3	0.7	0.8	6.5	6.6	0.21	9258.4	9267.9	9162.2	
Detritivores	6.2	0.0	4.2	10.2	6.5	0.06	10592.5	10599.2	10187.4	
Herbivores	16.0	7.4	11.8	25.9	6.5	0.18	13199.0	13211.1	NA	
Omnivores	11.3	5.5	9.6	21.9	6.6	0.08	12730.7	12743.9	12681.1	
Planktivores	44.1	31.9	48.8	115.2	6.5	0.10	17325.5	17345.1	17367.7	
c.										
Carnivores	<i>Lutjanus decussatus</i>	0.6	0.5	1.0	2.0	3.1	0.02	6058.7	6078.7	6055.0
	<i>Halichoeres hortulanus</i>	0.3	0.1	0.2	0.9	5.7	0.04	3872.9	3885.1	3897.9
	<i>Monotaxis grandoculis</i>	0.7	0.4	1.7	3.7	1.5	0.02	7772.8	7793.9	7822.9
Corallivores	<i>Chaetodon trifasciatus</i>	0.6	0.1	0.0	1.8	5.6	0.05	5582.3	5589.2	5597.1
	<i>Chaetodon punctatofasciatus</i>	0.6	0.2	0.2	1.4	6.4	0.09	5001.8	5010.2	5068.6
	<i>Chaetodon ornatissimus</i>	0.3	0.1	0.2	1.2	6.2	0.05	4447.3	4459.2	4465.0
Detritivores	<i>Ctenochaetus spp.</i>	3.0	1.3	1.7	6.6	6.8	0.15	9343.2	9354.6	9082.9
	<i>Stegastes nigricans</i>	6.5	0.0	3.8	6.5	4.6	0.02	9374.4	9378.1	8901.7
	<i>Acanthurus olivaceus</i>	0.2	0.3	0.0	2.4	3.3	0.02	6374.7	6397.4	NA
Herbivores	<i>Chlorurus sordidus</i>	0.0	0.4	0.5	2.7	5.5	0.05	6793.4	6825.4	6899.7
	<i>Chrysiptera rex</i>	20.7	7.2	8.4	22.4	6.7	0.10	12782.4	12796.0	12627.5
	<i>Acanthurus nigricans</i>	1.4	1.5	1.7	2.2	2.5	0.07	6387.7	6407.6	6329.2
Omnivores	<i>Pomacentrus vaiuli</i>	11.7	5.7	6.3	14.4	6.7	0.08	11587.6	11599.0	11568.8
	<i>Plectroglyphidodon lacrymatus</i>	5.6	3.4	6.6	12.5	6.0	0.10	11185.9	11203.0	11159.8
	<i>Pomacentrus ambionensis</i>	6.4	1.2	5.9	7.4	4.8	0.04	9793.4	9802.8	9361.5
Planktivores	<i>Pomacentrus philippinus</i>	19.7	6.8	14.1	26.2	6.0	0.18	13255.9	13266.0	13231.9
	<i>Pomacentrus lepidogenys</i>	22.1	10.8	14.1	36.8	5.1	0.05	14141.0	14153.1	14009.6
	<i>Chromis margaritifer</i>	18.4	7.8	12.6	31.8	6.4	0.05	13747.2	13758.4	13701.7

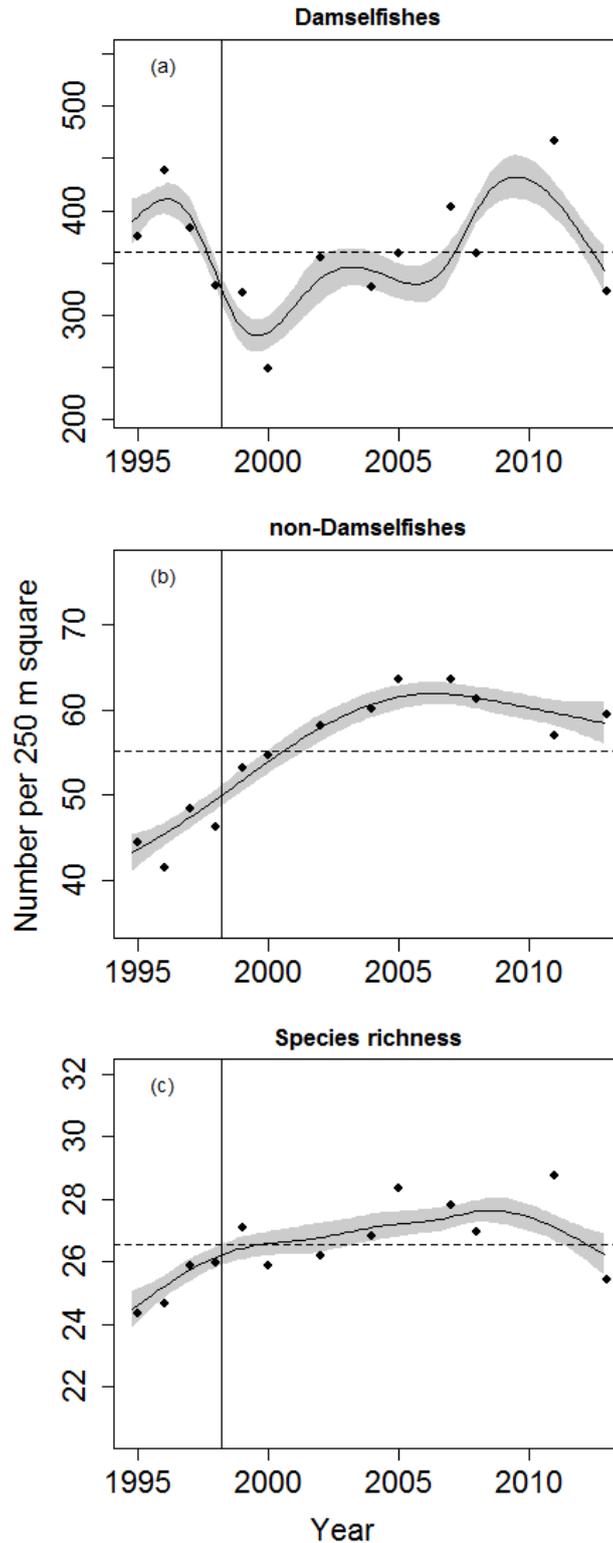


Figure 4.1a-c Mean densities of (a) damselfishes, (b) non-damselfishes, and (c) species richness at Scott Reef between 1994 and 2012. Solid lines are general additive mixed model (GAMM) fits, light grey shading indicates approximate 95% confidence bands and dotted lines are means across the entire 18 year period. Black circles show the observed mean densities for each year code (rounded decimal year) and vertical grey bar indicates period of coral bleaching. All analyses were conducted at the transect level.

Table 4.2 Permutational manova results for the fish communities at Scott Reef between 1994 and 2012., showing the effects of the Simprof cluster group, location, and their interaction.

	Df	SS	MS	F	R ²	Pr(>F)
Time periods	1	0.751	0.751	16.63	0.033	0.001
Location	6	9.240	1.540	34.108	0.411	0.001
Time periods * Location	6	0.593	0.098	2.188	0.026	0.001
Residual	264	11.920	0.045	-	0.527	-
Total	277	22.504	-	-	1	-

Table 4.3 Pairwise R-statistic values from permutational manova of the fish communities at Scott Reef between 1994 and 2012. Bolded values are the partial R² from pairwise tests. Species listed are the top 10 identified by similarity profiles analysis (simper) as distinguishing between the fish assemblages for each pair of periods.

Period	Pre- and early post-bleach (1994-2000)	Cyclonic (2001-2008)
2001-2008	0.057*** <i>Chromis ternatensis</i> <i>Amblyglyphidodon curacao</i> <i>Chromis weberi</i> <i>Pomacentrus moluccensis</i> <i>Chromis margaritifer</i> <i>Chromis lepidolepis</i> <i>Pomacentrus adelus</i> <i>Amblyglyphidodon aureus</i> <i>Pomacentrus amboinensis</i> <i>Chromis atripes</i>	
2009-2012	0.042*** <i>Chromis lepidolepis</i> <i>Amblyglyphidodon curacao</i> <i>Chromis weberi</i> <i>Pomacentrus moluccensis</i> <i>Chromis atripes</i> <i>Pomacentrus adelus</i> <i>Chromis margaritifer</i> <i>Chromis ternatensis</i> <i>Chromis viridis</i> <i>Amblyglyphidodon aureus</i>	0.044*** <i>Chromis ternatensis</i> <i>Chromis weberi</i> <i>Chromis lepidolepis</i> <i>Pomacentrus adelus</i> <i>Chromis viridis</i> <i>Pomacentrus amboinensis</i> <i>Pomacentrus moluccensis</i> <i>Chromis atripes</i> <i>Chromis margaritifer</i> <i>Amblyglyphidodon curacao</i>

*** denotes that P values were significant to less than 0.001 (i.e., $P < 0.001$).

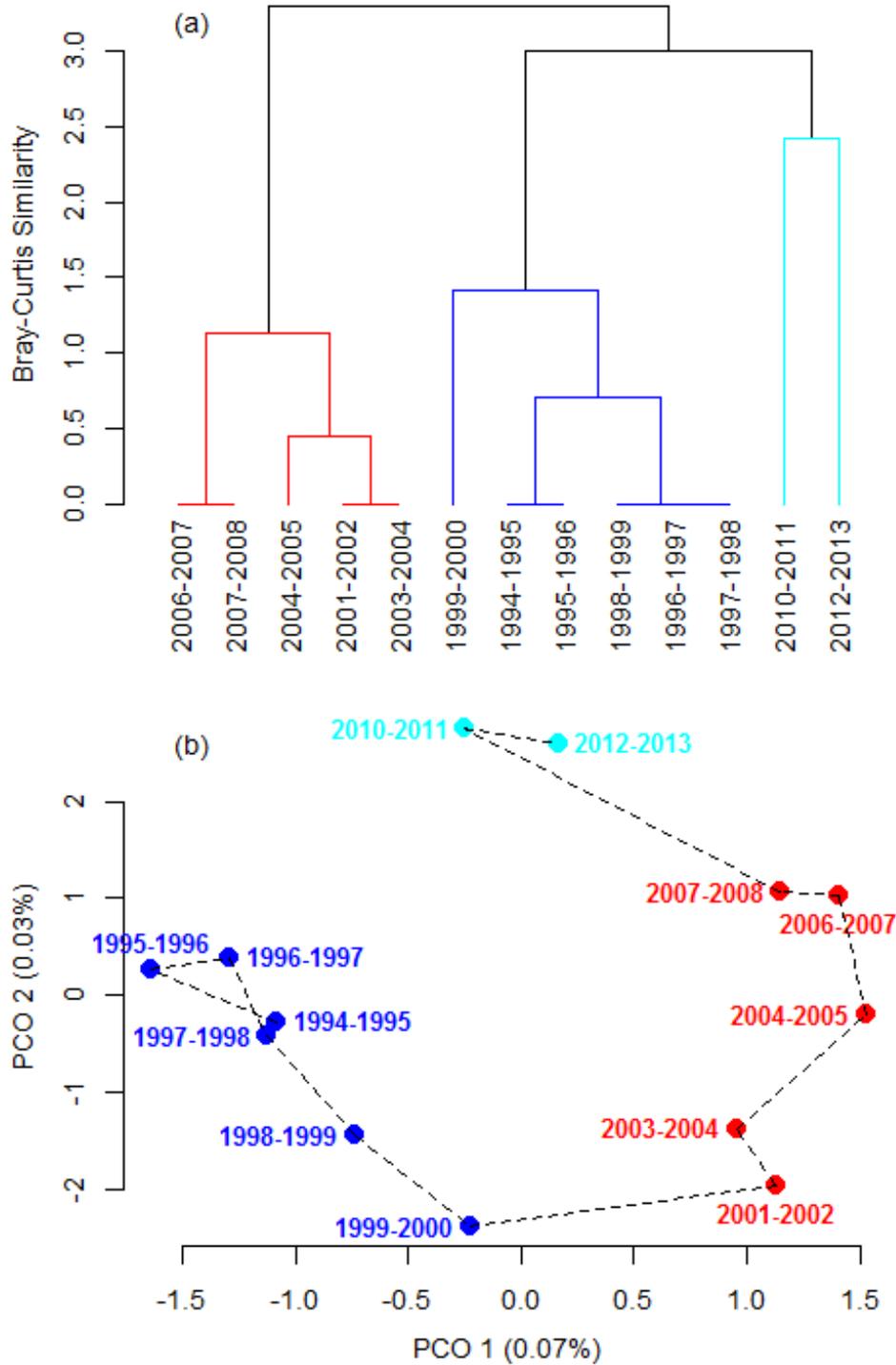


Figure 4.2a-b CLUSTER analysis (a), with SIMPROF of the species compositions of reef fish communities at Scott Reef over 18 years between 1994 and 2012. Different coloured lines indicate groups that SIMPROF determined were significantly different from other groups and (b) Principle coordinates ordination (PCO) showing the trajectory of change in the structure of fish communities at Scott Reef between 1994 and 2012. Points for each year of sampling are coloured according to the significant groups identified in the SIMPROF procedure.

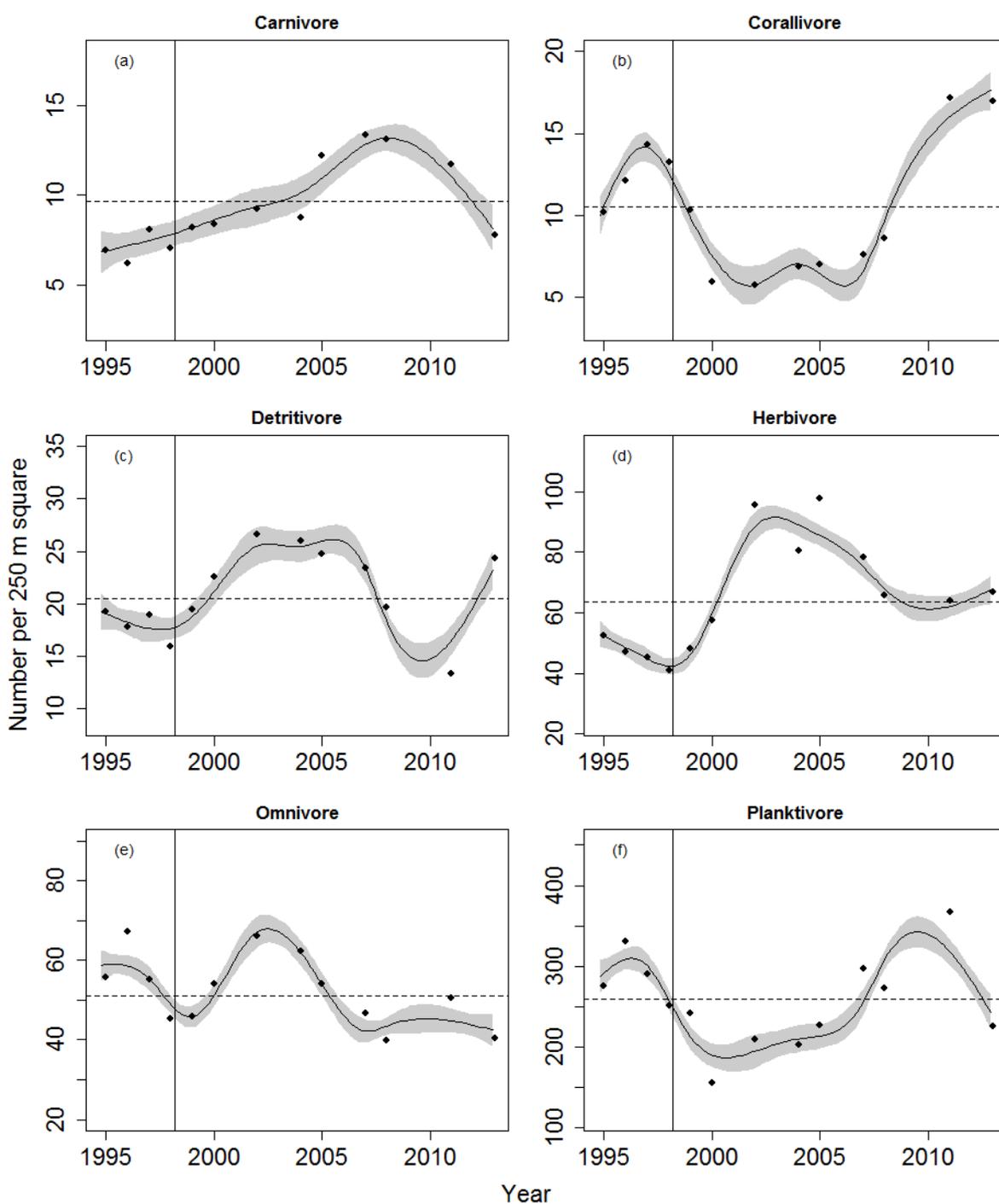


Figure 4.3 Mean (\pm 95% C.I.) densities of functional groups of fishes at Scott Reef between 1994 and 2012. Solid lines are general additive mixed model (GAMM) fits, light grey shading indicates 95% confidence bands, circles are the observed mean densities for each decimal year and the vertical grey bar indicates period of severe coral bleaching. All analyses were conducted at the transect level.

Table 4.4 Summary table comparing trophic group means between the most recent 2012 survey and (a) 18 year means and (b) the preceding 2010 surveys. Deviations in comparisons are bolded if they exceed > 20%.

Trophic group	18yr average	2010	2012	% Deviation from 18yr average	% Deviation 2010-2012
Carnivore	9.3	11.7	7.79	-16.2	-33.4
Corallivore	10.45	17.18	16.93	62.0	-1.5
Detritivore	20.91	13.37	24.35	16.5	82
Herbivore	64.56	63.77	66.83	3.5	4.8
Omnivore	52.52	50.39	40.44	-23.0	-19.7
Planktivore	257.37	367.06	225.66	-12.3	-38.5

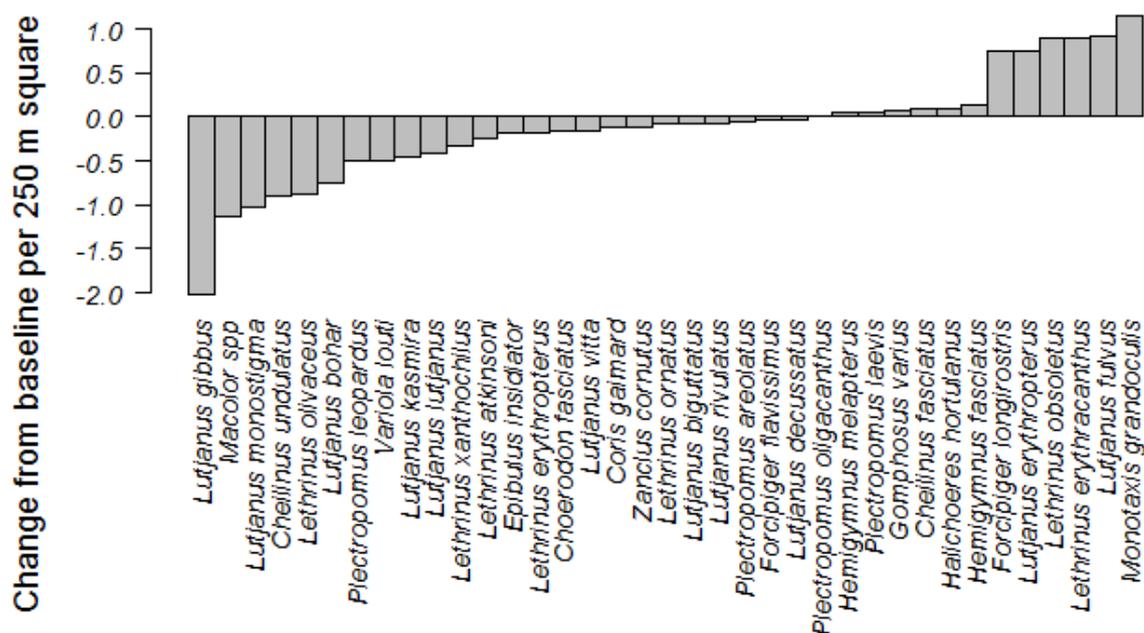


Figure 4.4 Changes in abundance of carnivores between 1994-2010 averages and the recent 2012 surveys. In total, 25 species declined (decreased or absent) and 12 increased in abundance.

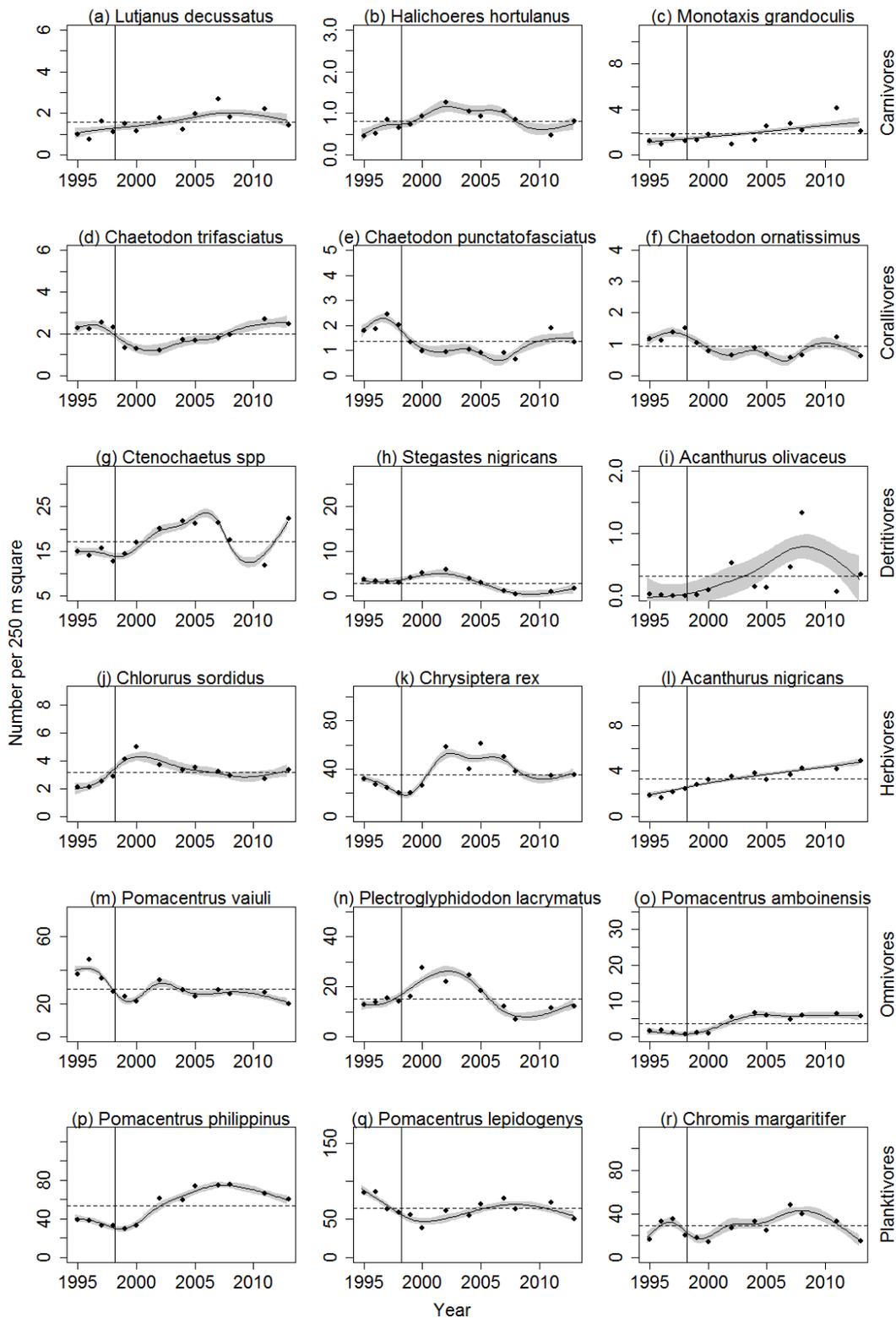


Figure 4.5 Mean (\pm 95 C.I.) densities of fish species identified by SIMPER as distinguishing particular time periods at Scott Reef. Solid lines are general additive mixed model (GAMM) fits, light grey shading indicates 95% confidence bands, circles are the observed mean densities and vertical grey bar indicates year of coral bleaching. All analyses were conducted at the transect level.

4.4 Discussion

The recent addition of the 2012 survey shows a combination of new trends in densities of some trophic groups and a stabilisation of a distinct fish assemblage that continues to differ widely from that of pre-bleach surveys. Comparisons between 2012 and the previous 2010 survey indicate sharp recent declines in the site-attached damselfishes as well as in the carnivore and planktivore (the bulk of which are damselfishes) trophic groups in conjunction with a drop in mean species richness at Scott Reef. Alongside these recent declines, steep increases in detritivores and stable numbers of corallivores, herbivores and omnivores were observed that drove the continued maintenance of densities of large mobile species. Patterns in group densities against 18-year historical averages indicated an overall decline in omnivores alongside the highest densities of corallivores recorded to date at Scott Reef (62% above 18-year averages) with all other groups exhibiting changes in abundance of < 20%.

There were large declines in numbers of planktivores (38%) and damselfishes (31%), a pattern that should be monitored in the future to determine the extent to which this trend continues downwards. However, these fishes have the ecological and life history characteristics that are likely to amplify the potential for abundances to vary widely and rapidly. These include high recruitment variability (Sale *et al.* 1984, Doherty 1987), high mortality rates from predation (Beukers-Stewart & Jones 2004; Kingsford 1992), early maturation and relatively short life spans (5-15 years – Depczynski & Bellwood 2006), characteristics likely to promote instability in abundances over decadal time scales. It is also noteworthy that recent declines in this group have also been observed at nearby Cartier Reef (Richards *et al.* 2009). In contrast, species within the carnivore group were mobile predators with the tendency to mature later and live significantly longer lives (15-60 years – reviewed in Depczynski & Bellwood 2006), attributes that promote stability in abundances through time in undisturbed systems (Pears *et al.* 2006). In agreement with their life history traits, 18-year trends for this carnivore group at Scott Reef have shown a gradual increase in abundance since surveys began in 1994 and it is the recent abrupt and successive declines in this ecologically important group (2010 decline-11%, 2012-33% & 16% compared with 18-year averages) that warrant the attention. Within the 37 species that made up this group, 25 were either completely absent in 2012 or had reduced in numbers with 12 species making marginal gains. Within these 25 declining species, all the major predatory taxonomic groups were represented including members of the snapper, coral trout, emperor and grouper groups. Considering evidence suggesting that Scott Reef fishes may rely strongly on self-replenishment (Underwood *et al.* 2012), a lack of reproductive adults threatens the integrity of stocks within the Scott Reef ecosystem.

There are two main hypotheses that might explain this recent drop in carnivore numbers. Firstly, the corresponding decline in associated prey species (i.e. planktivorous damselfishes) may have caused a migration of some large carnivore species to another nearby reef system (e.g. Seringapatam, Cartier reefs). This seems unlikely given that even these larger species maintain spatially restricted home ranges (Samoily 1997, Hutchinson & Rhodes 2010). Secondly, it is interesting to note that of the 37 species, the 12 that have increased tended to be the smaller species (e.g. *Monotaxis grandoculis* & *Forcipiger longirostris*) and many of the larger species (e.g. *Plectropomus leopardus*, *Macolor* spp.) that declined are well-known fishing targets, presumably because they readily take baits. This suggests that increased selective fishing pressure on larger species may be resulting in their loss to the system. Previous research at AIMS has identified that sharks are actively targeted by Indonesian fishermen and that their abundances are approximately 20% of those found in similar nearby reefs such as the Rowley Shoals (Meekan & Cappo 2004, Meekan *et al.* 2006). If this is the case, then Indonesian fisherman may be placing demand on the next tier of species by deliberately switching to smaller species effectively fishing down the food chain as numbers at upper trophic levels diminish (Pauly *et al.* 1998). Anecdotal evidence of changes in fishing techniques and reports from Indonesian fishing villages suggest that within the last 3-4 years there has been a major switch from shark fishing to the targeting of reef fishes. Furthermore, reductions in catches of trepang (holothurians) and

trochus, historically a traditional target of Indonesian fishermen (Vail & Russell 1989) might have also resulted in a heavier fishing effort on reef fishes. Irrespective of the drivers for this reduction in abundances of carnivores, future surveys should focus on this group and record size-structures. Overfishing provides a plausible explanation for the dramatic and sudden decline in this trophic group.

Fish communities at Scott Reef have undergone a significant change in composition through an 18-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 80% (Smith *et al.* 2008). The 2012 community continues to be distinct from pre-bleach communities, although with some possible evidence of stabilisation in community composition. 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 shelter such as many planktivorous damselfishes (Wilson *et al.* 2008). Densities of corallivores seem to have recently stabilised and are currently at the highest level ever seen in the monitoring record, in line with the near full recovery of corals (Gilmour *et al.* 2013). Planktivorous damselfishes in contrast, recovered relatively quickly from the bleaching but have now declined after reaching their peak in 2010.

The Scott Reef fish data-set is very likely one of the longest running coral reef fish datasets in the world and is unique because the remote location of the study site escapes most of the chronic anthropogenic impacts seen on reefs near population centres. The 2011 Scott Reef Report (Gilmour *et al.* 2011) posed the question of whether the fish community of 2010 was a transitional rather than a stable state community. This report adds weight to other findings that fish communities are never fully at a stable or climatic state (see Bellwood *et al.* 2006, 2012, Halford & Caley 2009). Rather, there are periods of relatively minor change and periods of more radical change driven by significant events such as coral bleaching episodes, acute and chronic pollution events, major storms and cyclones. The impact from these on different fish groups varies enormously across all metrics (i.e. abundance, biomass, species richness & composition). From this viewpoint, the value of the long-term fish data at Scott Reef cannot be understated. Although the response of fish communities to these events may be challenging to predict, the preservation of all functional groups is our best insurance policy to ensure the future integrity of Scott Reef.

4.5 References

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Supplementary Table 2: Table comparing overall and site-specific means in 2012 with those of all other years combined for all fish species at Scott Reef. The COV defines the average deviation among all sampling years as a percentage of the mean. For example, *A auranticavus* has a COV of 26% so any variation > 26% might be cause for concern.

Family	Species	Functional groups	1994-2010 Mean	SE's	COV	2012	SL1	SL2	SL3	SL4	SS1	SS2	SS3
Acanthuridae	<i>Acanthurus albipectoralis</i>	planktivore	0.08	0.08	100.0	0	0	0	0	1	0	0	0
	<i>Acanthurus auranticavus</i>	herbivore	4.93	1.29	26.1	3.3	7.5	2.3	5.3	12.5	6.2	3.8	6.6
	<i>Acanthurus bariene</i>	herbivore	0.17	0.11	67.4	0	0	0	0	1	0	0	0
	<i>Acanthurus blochii</i>	detritivore	2.78	0.41	14.7	1	5	3	2.9	1.7	3	2.4	3.6
	<i>Acanthurus dussumieri</i>	detritivore	1.48	0.19	13.0	0	2.5	0	1	1.7	0	0	1.4
	<i>Acanthurus fowleri</i>	herbivore	1.04	0.17	16.8	1.2	1.4	1.1	1	0	1.5	1	1
	<i>Acanthurus grammoptilus</i>	detritivore	1.58	0.48	30.2	0	1.3	4.8	1	3.6	1	0	2.5
	<i>Acanthurus leucocheilus</i>	detritivore	0.58	0.18	30.9	0	1.5	1	0	1.1	4	1.2	1.3
	<i>Acanthurus lineatus</i>	herbivore	3.28	0.29	8.7	5.6	4.2	1.5	4.5	1	1	2	1.8
	<i>Acanthurus maculiceps</i>	detritivore	0.42	0.23	54.9	0	0	0	1	1	0	0	2
	<i>Acanthurus mata</i>	planktivore	0.58	0.42	71.4	0	0	0	5	1	1	0	0
	<i>Acanthurus nigricans</i>	herbivore	4.18	0.26	6.2	5.9	3.3	1.4	3.8	5.6	6.4	4.6	3.4
	<i>Acanthurus nigricauda</i>	herbivore	1.64	0.15	9.0	1.7	1.7	1.4	2.3	2.1	1.4	1.5	1.6
	<i>Acanthurus nigrofuscus</i>	herbivore	3.33	0.19	5.8	3	2.8	1.3	2.7	2.4	3.6	5.7	2.1
	<i>Acanthurus olivaceus</i>	detritivore	2.25	0.66	29.5	7.2	11.1	2.2	6.2	1.6	2.5	4.1	1.3
	<i>Acanthurus pyroferus</i>	herbivore	1.18	0.04	3.1	1.4	1	1.2	1.2	1	1.3	1.1	1.5
	<i>Acanthurus spp</i>	herbivore	0.25	0.18	71.8	0	0	0	0	0	0	0	1.5
	<i>Acanthurus thompsoni</i>	planktivore	3.26	0.35	10.7	2.5	1	1.4	1.2	0	3.2	3.1	3.4
	<i>Acanthurus xanthopterus</i>	detritivore	0.93	0.30	31.9	0	3	1	0	1	1	1	1.8
	<i>Ctenochaetus spp</i>	detritivore	16.88	1.01	6.0	22.3	18.8	15.2	16.2	21.4	17.1	20.2	11.3
<i>Naso lituratus</i>	herbivore	1.45	0.06	4.4	1.5	1.6	1.5	1.6	1.4	1.9	1.4	1.2	
<i>Naso tuberosus</i>	herbivore	0.39	0.18	44.7	0	0	0	0	1	1.4	0	0	

Family	Species	Functional groups	1994-2010 Mean	SE's	COV	2012	SL1	SL2	SL3	SL4	SS1	SS2	SS3
	<i>Naso unicornus</i>	herbivore	2.88	0.84	29.0	0	3.5	1.9	2	1.2	2.4	4	6.3
	<i>Zebrasoma scopas</i>	herbivore	4.28	0.21	5.0	4.6	4.5	6.1	4	3	3.5	3.2	4.1
	<i>Zebrasoma veliferum</i>	herbivore	2.11	0.14	6.8	1.7	2.8	1.3	1.8	1.9	1.5	1.9	1.9
Chaetodontidae	<i>Chaetodon adiergastos</i>	corallivore	2.17	0.08	3.9	2.8	3	1.6	2.1	2	1.8	2.3	2.2
	<i>Chaetodon auriga</i>	corallivore	1.33	0.06	4.7	1.4	1.4	1.3	1.4	1.6	1.2	1.1	1.2
	<i>Chaetodon baronessa</i>	corallivore	1.45	0.09	6.0	2	2	1.4	1.4	1.3	1.6	2.2	1.5
	<i>Chaetodon bennetti</i>	corallivore	1.14	0.05	4.8	1	1.2	1	1.1	1.1	1	1	1
	<i>Chaetodon citrinellus</i>	corallivore	0.83	0.24	28.9	0	0	0	0	0	0	1.5	0
	<i>Chaetodon ephippium</i>	corallivore	1.53	0.06	3.8	2.1	1.7	1.4	1.5	1.5	1.8	1.6	1.6
	<i>Chaetodon kleinii</i>	corallivore	1.80	0.12	6.9	1	0	0	0	0	1	1.8	1.7
	<i>Chaetodon lineolatus</i>	corallivore	0.58	0.15	25.5	1	1	1	1	1	1	1	0
	<i>Chaetodon lunula</i>	corallivore	1.52	0.08	5.0	1.2	1.4	1.6	1.2	1.9	1.2	1.5	1.3
	<i>Chaetodon melannotus</i>	corallivore	1.58	0.15	9.5	1.4	0	0	1	1.6	1	1.5	1.4
	<i>Chaetodon meyeri</i>	corallivore	1.34	0.05	3.9	1.2	1.4	1.2	1.3	1.3	1.2	1.4	1.6
	<i>Chaetodon octofasciatus</i>	corallivore	0.17	0.11	67.4	0	0	1	0	0	0	0	0
	<i>Chaetodon ornatissimus</i>	corallivore	1.91	0.06	3.1	1.5	1.9	1.5	2.2	1.8	2.2	1.7	1.8
	<i>Chaetodon oxycephalus</i>	corallivore	0.08	0.08	100.0	0	0	1	0	0	0	0	0
	<i>Chaetodon punctatofasciatus</i>	corallivore	2.37	0.12	5.1	2.4	2.3	1.5	2.2	2.6	2.4	2.8	2.5
	<i>Chaetodon rafflesii</i>	corallivore	1.46	0.25	17.2	2	1.3	2	0	1.3	1	1.8	0
	<i>Chaetodon reticulatus</i>	corallivore	0.08	0.08	100.0	0	0	1	0	0	0	0	0
	<i>Chaetodon semeion</i>	omnivore	1.32	0.05	3.7	1.4	1.2	1.2	1.3	1.4	1.4	1.3	1.4
	<i>Chaetodon speculum</i>	corallivore	0.42	0.15	35.7	1	1	0	0	1	1	0	1
	<i>Chaetodon trifascialis</i>	corallivore	1.03	0.20	19.4	1.8	1.5	1.9	1.3	1.4	2.6	1.9	1.5
	<i>Chaetodon trifasciatus</i>	corallivore	2.81	0.13	4.6	3.5	2.6	4.1	2.4	3	2.4	2.6	2.9
	<i>Chaetodon ulietensis</i>	corallivore	2.02	0.06	2.9	1.6	2	1.9	1.8	2.1	1.9	2.3	1.8
	<i>Chaetodon unimaculatus</i>	corallivore	1.30	0.20	15.7	2	0	1	1	1.7	1.2	1.7	1
	<i>Chaetodon vagabundus</i>	corallivore	1.38	0.05	3.5	1.2	1.2	1.2	1.6	1.4	1.3	1.4	1.3
	<i>Forcipiger flavissimus</i>	carnivore	1.83	0.07	3.9	1.8	1.7	1	1.5	1.6	1.8	1.8	2

Family	Species	Functional groups	1994-2010 Mean	SE's	COV	2012	SL1	SL2	SL3	SL4	SS1	SS2	SS3
Labridae	<i>Forcipiger longirostris</i>	carnivore	0.75	0.24	31.4	1.5	0	0	0	1	1.7	1	1.5
	<i>Cheilinus fasciatus</i>	carnivore	1.32	0.04	2.8	1.4	1.2	1.6	1.1	1.1	1.1	1	1.2
	<i>Cheilinus undulatus</i>	carnivore	0.91	0.25	27.3	0	1	1	1	1.6	1	1.3	2.5
	<i>Choerodon fasciatus</i>	carnivore	0.17	0.17	100.0	0	0	2	0	0	0	0	0
	<i>Coris gaimard</i>	carnivore	1.13	0.15	13.4	1	1	1.2	1.2	1	1.4	1.1	1
	<i>Epibulus insidiator</i>	carnivore	1.38	0.04	3.2	1.2	1.4	1	1.1	1.4	1.5	1.4	1.5
	<i>Gomphosus varius</i>	carnivore	1.23	0.05	3.8	1.3	1.4	1.4	1.3	1.1	1.3	1.2	1.5
Lethrinidae	<i>Halichoeres hortulanus</i>	carnivore	1.60	0.06	3.8	1.7	1.6	1.2	1.4	1.9	1.5	1.9	1.5
	<i>Lethrinus atkinsoni</i>	carnivore	0.25	0.18	71.8	0	0	0	1	2	0	0	0
	<i>Lethrinus erythracanthus</i>	carnivore	0.50	0.15	30.2	1.4	1	1.3	1	1	1	1	1
	<i>Lethrinus erythropterus</i>	carnivore	1.18	0.04	3.6	1	1.1	1.3	1.1	1.1	1.2	1.2	1.1
	<i>Lethrinus obsoletus</i>	carnivore	1.11	0.19	17.2	2	1.2	1.7	1.9	1.4	1	0	0
	<i>Lethrinus olivaceus</i>	carnivore	0.88	0.28	31.5	0	1	1	0	1.4	1.3	3	1.3
	<i>Lethrinus ornatus</i>	carnivore	0.08	0.08	100.0	0	0	0	1	0	0	0	0
	<i>Lethrinus xanthochilus</i>	carnivore	0.33	0.19	56.4	0	0	0	1	2	1	0	0
	<i>Monotaxis grandoculis</i>	carnivore	3.96	0.39	9.8	5.1	2.7	5.2	2.9	3.5	3.1	5.8	6.4
	Lutjanidae	<i>Lutjanus biguttatus</i>	carnivore	0.08	0.08	100.0	0	0	1	0	0	0	0
<i>Lutjanus bohar</i>		carnivore	1.76	0.13	7.3	1	1.5	2.4	1.5	1.3	1.9	1.4	2.1
<i>Lutjanus decussatus</i>		carnivore	2.43	0.18	7.6	2.4	2.6	1.8	1.9	3.8	2	2.8	1.7
<i>Lutjanus erythropterus</i>		carnivore	0.25	0.13	52.2	1	0	1	1	0	1	0	1
<i>Lutjanus fulvus</i>		carnivore	5.08	2.08	41.0	6	0	0	0	0	0	0	7.4
<i>Lutjanus gibbus</i>		carnivore	5.42	0.93	17.2	3.4	5.4	6.1	5.3	9.9	3	12.5	5.1
<i>Lutjanus kasmira</i>		carnivore	3.77	0.47	12.5	3.3	1	0	0	2.1	0	1.5	5.5
<i>Lutjanus lutjanus</i>		carnivore	0.42	0.19	46.3	0	0	1.2	0	0	0	0	0
<i>Lutjanus monostigma</i>		carnivore	1.03	0.44	42.9	0	1	0	0	1	0	1	2.3
<i>Lutjanus rivulatus</i>		carnivore	0.08	0.08	100.0	0	1	0	0	0	0	0	0
	<i>Lutjanus vitta</i>	carnivore	0.17	0.17	100.0	0	0	2	0	0	0	0	0
	<i>Macolor spp</i>	carnivore	2.63	0.35	13.4	1.5	2.5	1.3	3.3	3.4	3.1	2.4	2.9

Family	Species	Functional groups	1994-2010 Mean	SE's	COV	2012	SL1	SL2	SL3	SL4	SS1	SS2	SS3
Pomacentridae	<i>Abudefduf vaigiensis</i>	omnivore	7.71	7.71	100.0	0	0	0	0	0	100	0	85
	<i>Amblyglyphidodon aureus</i>	planktivore	11.80	0.63	5.4	14.6	11.2	0	8.1	14.3	11.2	9.6	13.7
	<i>Amblyglyphidodon curacao</i>	planktivore	26.51	2.30	8.7	49.1	16.1	50.3	12.2	11.4	8.8	7.5	6.2
	<i>Amblyglyphidodon leucogaster</i>	planktivore	6.58	0.37	5.6	15	5	8.9	5	7.5	7.8	0	5
	<i>Amphiprion chrysopterus</i>	planktivore	0.42	0.42	100.0	0	0	5	0	0	0	0	0
	<i>Amphiprion clarkii</i>	planktivore	6.94	1.44	20.7	13.8	0	6.2	0	16.2	7.5	8.5	10.8
	<i>Amphiprion ocellaris</i>	planktivore	2.08	2.08	100.0	0	0	0	0	25	0	0	0
	<i>Amphiprion percula</i>	planktivore	0.42	0.42	100.0	0	0	0	0	0	0	0	5
	<i>Amphiprion perideraion</i>	planktivore	1.25	0.90	71.8	0	0	5	0	10	5	0	0
	<i>Amphiprion sandaracinos</i>	planktivore	3.33	1.42	42.6	0	0	0	0	8.8	11.7	0	0
	<i>Amphiprion spp</i>	planktivore	0.42	0.42	100.0	0	0	0	0	0	5	0	0
	<i>Chromis amboinensis</i>	planktivore	13.41	1.23	9.2	10	16.2	0	5	6	13.4	0	12.6
	<i>Chromis atripectoralis</i>	planktivore	18.47	4.51	24.4	24.5	21	39.3	25.5	0	11.9	11.2	31.2
	<i>Chromis atripes</i>	planktivore	17.94	1.68	9.4	15	20.4	0	24	15	13.4	10	14.6
	<i>Chromis lepidolepis</i>	planktivore	24.70	3.52	14.3	20	21.4	10	28.4	19.9	26.7	30.7	28
	<i>Chromis lineata</i>	planktivore	3.56	1.65	46.3	0	0	0	5	0	13	10	16.4
	<i>Chromis margaritifer</i>	planktivore	41.16	3.27	8.0	25.6	17.8	5	56.3	28.8	33.5	42.7	60.4
	<i>Chromis ternatensis</i>	planktivore	77.55	10.16	13.1	52	74.3	21.7	100.8	45.2	94.5	108.2	117.2
	<i>Chromis vanderbilti</i>	planktivore	2.42	2.01	83.0	0	0	0	5	0	20	26.7	0
	<i>Chromis viridis</i>	planktivore	40.84	8.56	21.0	35.8	41.7	43.5	56.3	45	59.4	25	15
	<i>Chromis weberi</i>	planktivore	30.43	3.75	12.3	51.6	37.5	20	50.5	24.8	34.3	47	24.8
	<i>Chromis xanthochira</i>	planktivore	2.18	1.17	53.7	0	0	0	5	0	0	10	8
	<i>Chromis xanthura</i>	planktivore	21.64	1.58	7.3	22.3	17.8	11.7	26.1	15.2	21.3	27.7	25.2
	<i>Chrysiptera hemicyanea</i>	planktivore	7.41	1.67	22.5	18.2	5	12.3	0	0	0	0	0
	<i>Chrysiptera rex</i>	herbivore	42.13	3.34	7.9	36.8	36.1	14.4	21.3	66	40.1	67.5	27.2
	<i>Chrysiptera talboti</i>	planktivore	1.25	0.65	52.2	0	0	0	0	5	0	0	5
	<i>Dascyllus aruanus</i>	planktivore	18.42	3.01	16.3	54.7	11.7	30.2	10.9	0	0	0	0
	<i>Dascyllus reticulatus</i>	planktivore	8.23	1.75	21.2	9	15.2	10	11.2	14.3	10	10.3	9.6

Family	Species	Functional groups	1994-2010										
			Mean	SE's	COV	2012	SL1	SL2	SL3	SL4	SS1	SS2	SS3
	<i>Dascyllus trimaculatus</i>	planktivore	9.92	0.94	9.4	17	5	5	6.8	15	8.6	9.4	14.3
	<i>Dischistodus perspicillatus</i>	herbivore	0.83	0.56	67.4	0	0	5	0	0	0	0	0
	<i>Hemiglyphidodon plagiometopon</i>	detritivore	0.42	0.42	100.0	0	0	5	0	0	0	0	0
	<i>Hemigymnus fasciatus</i>	carnivore	1.16	0.03	2.9	1.3	1.2	1.2	1.1	1.1	1.4	1.2	1.3
	<i>Hemigymnus melapterus</i>	carnivore	1.35	0.06	4.4	1.4	1.2	1.4	1.1	1.3	1.3	1	1.2
	<i>Neoglyphidodon melas</i>	corallivore	5.35	0.64	12.0	10	5.8	6.5	6.1	5	0	5	0
	<i>Neoglyphidodon nigroris</i>	omnivore	21.09	1.34	6.3	25	6.1	22.2	5	0	0	0	0
	<i>Plectroglyphidodon dickii</i>	corallivore	6.73	0.81	12.0	12.2	6.7	5	6.2	9.6	9.5	10.6	8.6
	<i>Plectroglyphidodon johnstonianus</i>	corallivore	6.94	0.44	6.4	7.7	5.3	0	6.2	5.7	7.5	9.1	7.7
	<i>Plectroglyphidodon lacrymatus</i>	omnivore	20.78	1.40	6.7	17	13.7	26	21.1	14.6	17.8	22.3	22.1
	<i>Pomacentrus adelus</i>	herbivore	27.63	2.80	10.1	52.5	7.4	46.9	15.8	5.8	0	0	0
	<i>Pomacentrus amboinensis</i>	omnivore	17.49	1.53	8.7	30.5	10.8	29.8	13.1	5.9	5	0	5
	<i>Pomacentrus bankanensis</i>	omnivore	4.92	0.71	14.4	15	5	5	8.2	9.2	5	5.3	5
	<i>Pomacentrus coelestis</i>	planktivore	6.43	3.25	50.5	0	0	0	0	0	33.3	5	5
	<i>Pomacentrus grammorhynchus</i>	herbivore	2.63	1.41	53.6	0	0	10	0	0	0	0	0
	<i>Pomacentrus lepidogenys</i>	planktivore	68.44	4.03	5.9	52.2	60.5	34.1	74.9	101.6	85.9	58.8	46.1
	<i>Pomacentrus moluccensis</i>	planktivore	22.07	1.65	7.5	22.5	17.5	34.6	18.4	7.9	10	5	5
	<i>Pomacentrus nigromarginatus</i>	planktivore	1.67	0.71	42.6	0	5	0	0	0	5	0	5
	<i>Pomacentrus philippinus</i>	planktivore	52.74	5.02	9.5	60.8	71.2	26	55.3	87.9	62.1	45.2	34.5
	<i>Pomacentrus vaiuli</i>	omnivore	31.89	1.80	5.6	22.3	45.4	11.7	43.7	35.3	26.6	21.4	25.8
	<i>Pomachromis richardsoni</i>	planktivore	4.38	2.89	66.0	33.3	0	0	10	5	0	20	26.2
	<i>Premnas biaculeatus</i>	planktivore	2.71	1.04	38.5	0	5	5	5	10	0	0	7.5
	<i>Stegastes fasciolatus</i>	herbivore	0.00	0.00	0.0	5	5	0	0	0	0	0	0
	<i>Stegastes lividus</i>	herbivore	0.42	0.42	100.0	0	0	5	0	0	0	0	0
	<i>Stegastes nigricans</i>	detritivore	23.48	2.71	11.5	13.1	0	24.3	5	10	0	0	0
Scaridae	<i>Bolbometapon muricatum</i>	corallivore	4.21	2.13	50.5	0	1	0	0	3	0	15.5	8.4
	<i>Cetoscarus bicolor</i>	herbivore	1.28	0.04	3.3	1.2	1.4	1.1	1.1	1.3	1.6	1.4	1.5
	<i>Chlorurus bleekeri</i>	herbivore	1.74	0.11	6.3	1.7	1.9	1.9	1.4	1.6	1.6	1.3	1.5

Family	Species	Functional groups	1994-2010 Mean	SE's	COV	2012	SL1	SL2	SL3	SL4	SS1	SS2	SS3
	<i>Chlorurus microrhinos</i>	corallivore	1.95	0.11	5.7	2	1.8	1.3	1.5	2.3	1.8	2.2	3.2
	<i>Chlorurus sordidus</i>	herbivore	3.73	0.19	5.1	4	3.9	3.7	3.5	3.4	4.2	4.1	3.3
	<i>Hipposcarus longiceps</i>	herbivore	1.95	0.37	18.8	1.5	3.2	1	1.1	1.8	1.4	1.5	1.2
	<i>Scarus altipinnis</i>	herbivore	0.13	0.13	100.0	0	0	0	0	0	1.5	0	0
	<i>Scarus chameleon</i>	herbivore	0.25	0.13	52.2	0	1	1	0	1	0	1	0
	<i>Scarus dimidiatus</i>	herbivore	1.70	0.07	4.3	1.2	1.6	1.5	1.6	1.9	1.6	1.8	1.3
	<i>Scarus flavipectoralis</i>	herbivore	1.79	0.14	7.8	1.3	1.4	2.1	1	1	1	1	1
	<i>Scarus forsteni</i>	herbivore	1.27	0.08	6.6	1.5	1.1	1	1.1	1.3	1.2	1.4	1.1
	<i>Scarus frenatus</i>	herbivore	1.13	0.12	11.0	1	1.2	1	1	1	1.2	1.2	1.7
	<i>Scarus ghobban</i>	herbivore	0.08	0.08	100.0	0	0	0	0	1	0	0	0
	<i>Scarus globiceps</i>	herbivore	1.39	0.17	12.2	0	1.3	1	1.9	1	1.2	1.3	2
	<i>Scarus longipinnis</i>	herbivore	0.25	0.18	71.8	0	1.5	0	0	0	0	0	0
	<i>Scarus niger</i>	herbivore	2.22	0.05	2.3	2.7	2.2	2.2	2.2	2.2	2	2.2	2.7
	<i>Scarus oviceps</i>	herbivore	1.08	0.18	16.7	1	0	1	1	1	0	1.4	1.5
	<i>Scarus prasiognathos</i>	herbivore	1.88	0.27	14.3	1.3	2.1	1.3	1.3	3.4	1	1.2	1.1
	<i>Scarus psittacus</i>	herbivore	1.90	0.14	7.2	1.8	1.8	2.2	1.7	1.4	2.5	2.3	2.3
	<i>Scarus rubroviolaceus</i>	herbivore	1.09	0.04	3.3	1.2	1.2	0	1.2	1	1.1	1.1	1.2
	<i>Scarus schlegeli</i>	herbivore	1.71	0.09	5.1	2.2	1.9	2	1.5	1.8	1.5	2.2	1.4
	<i>Scarus spinus</i>	herbivore	1.20	0.04	3.6	1	1.3	1	1.4	1.1	1.2	1	1.3
Serranidae	<i>Plectropomus areolatus</i>	carnivore	1.06	0.03	2.7	1	1.1	1	1	1.1	1	1.1	1.1
	<i>Plectropomus laevis</i>	carnivore	0.94	0.09	9.5	1	1.5	1	1	1	1	1	1
	<i>Plectropomus leopardus</i>	carnivore	1.51	0.16	10.5	1	1	1.7	1	1	0	1	1
	<i>Plectropomus oligacanthus</i>	carnivore	1.19	0.03	2.4	1.2	1.3	1	1.2	1.2	1.3	1.1	1
	<i>Variola louti</i>	carnivore	0.50	0.15	30.2	0	0	1	0	0	1	1	1
Siganidae	<i>Siganus argenteus</i>	herbivore	2.29	1.23	53.7	0	0	22.5	0	1	1	3.7	0
	<i>Siganus corallinus</i>	herbivore	1.78	0.07	4.1	2	1.6	1.7	1.7	1.9	1.8	1.7	1.5
	<i>Siganus doliatus</i>	herbivore	0.25	0.25	100.0	0	3.3	2	0	0	0	0	0
	<i>Siganus puellus</i>	herbivore	1.85	0.05	2.4	1.7	1.9	1.5	2	1.8	1.8	1.9	2

Family	Species	Functional groups	1994-2010 Mean	SE's	COV	2012	SL1	SL2	SL3	SL4	SS1	SS2	SS3
	<i>Siganus punctatissimus</i>	herbivore	2.21	0.69	31.3	1.7	1.5	5.3	1.4	1.6	1.5	1.5	1.5
	<i>Siganus punctatus</i>	herbivore	0.58	0.22	37.3	1.8	2	1.4	1.5	1.5	1.5	1.3	1.2
	<i>Siganus vulpinus</i>	herbivore	1.89	0.03	1.7	2	1.8	2	1.9	1.8	1.9	1.8	2
Zanclidae	<i>Zanclus cornutus</i>	carnivore	1.92	0.06	3.3	1.8	2.1	1.5	1.8	1.9	1.9	1.8	2.3