## Chapter 10 D.2 AIMS Scott Reef and Rowley Shoals LTM 2017 report

Australian Government

Australian Institute of Marine Science

# Long-term monitoring at Scott Reef and Rowley Shoals 2017: Summary Report

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# Executive Summary

Coral communities at Scott Reef and the Rowley Shoals have experienced substantial change over the history of monitoring (1994–2017). Various disturbances – mass bleaching, cyclones and moderate bleaching – and their effects on coral communities are described, with differences in impact and recovery linked to local disturbance regimes, routine environmental conditions, variation in community composition and coral life history traits.

In 2016, heat stress and coral bleaching affected reefs worldwide, including those in north-western Australia. Heat stress in the region was the highest on record, but far higher at Scott Reef (16.5° C-weeks) than at the Rowley Shoals (5.8° C-weeks). The heat stress caused mass bleaching (> 70%) across Scott Reef, but only minor (< 10%) bleaching at most locations at the Rowley Shoals.

The 2016 mass bleaching devastated coral communities at Scott Reef, which had only recently recovered from mass bleaching in 1998. Both mass bleaching events had similar impacts, reducing coral cover in shallow water habitats (< 20 m) by approximately 75% and affecting all coral taxa; there was a similar pattern of susceptibility among taxa in both events, including those that had not yet recovered from the 1998 mass bleaching. In contrast, mass bleaching has not impacted the Rowley Shoals and the 2016 bleaching did not reduce mean cover at any of its three reefs.

Over more than two decades of impact and recovery, the coral communities at Scott Reef transitioned through four states indicative of their condition. The pre-bleaching and recovery states had a higher cover (> 45%) of hard and soft corals and an abundance of different coral taxa. The mass bleaching and post-bleaching states were the more degraded, with much lower coral cover (< 22%) and the absence of vulnerable taxa (e.g. soft corals, *Acropora*, *Isopora*, Pocilloporidae), including those providing food and shelter to fishes and other reef organisms. Smaller changes in community structure at the Rowley Shoals grouped into three periods, around local impacts and rapid recovery (< 5 years) from cyclones, all of which reflected a healthy reef system.

The recovery of Scott Reef following the 1998 mass bleaching was facilitated by its healthy fish stocks, high water quality and a decade (1999–2009) with few disturbances. Given comparable impacts in 1998 and 2016, a similar timeline for recovery (10–15 years) might be expected if the future water quality, fish stocks and disturbances regime were also similar. However, from 2010 impacts from bleaching and cyclones increased, and ongoing climate change is expected to cause further increases in heat stress and cyclone intensity. Recovery of Scott Reef will not follow a similar trajectory as after the 1998 mass bleaching if severe disturbances occur more frequently (< 10 years) – meaning communities will remain in more degraded states. Global increases in the severity of heat stress and cyclones are also likely to affect the Rowley Shoals. However, since 2010 there was a consistently high (> 40%) coral cover at the Rowley Shoals and its low level of degradation makes the reef system an important benchmark for assessing the condition of other coral reefs, locally and globally.

# 1. Introduction

Western Australia's coral reefs span more than 12,000 km of coastline and 20 degrees of latitude, ranging from tropical to temperate climates (Veron and Marsh 1988). The most diverse reefs are in the Kimberley region of north-western Australia (McKinney 2009; Richards et al. 2014), where the oceanic reef systems of Ashmore, Scott and the Rowley Shoals sit near the edge of the continental shelf, hundreds of kilometres from the mainland and from each other. The Scott (South Reef, North Reef, Seringapatam) and Rowley Shoals (Imperieuse, Clerke, Mermaid) reef systems have high water quality and relatively low fishing pressures (Halpern et al. 2015; Zinke et al. 2018; Gilmour et al. 2019). However, traditional fishing of shark fin, *Trochus* and sea cucumber still occurs at Scott Reef (Stacey 2007), and these targeted species are all overfished (Meekan et al. 2006; Bryce 2007).

Damaging waves generated by storms and cyclones have historically been the most common acute disturbance to coral reefs in the Kimberley region. Scott Reef and the Rowley Shoals are buffeted by waves from a westerly and south-westerly direction, particularly between November and April when monsoonal storms and cyclones are common (Berry and Marsh 1986; Bowman et al. 2010; Drost et al. 2017). However, heat stress during El Niño conditions is increasingly affecting these reefs (Hughes et al. 2017; Benthuysen et al. 2018; Gilmour et al. 2019). Heat stress has caused repeated bleaching of varying severity at Ashmore Reef, Scott Reef and the Rowleys Shoals. The Rowley Shoals has so far escaped mass bleaching (Gilmour et al. 2019) and Scott Reef has been worst affected, particularly during the global bleaching events in 1998 and 2016 (Gilmour et al. 2013b; Eakin et al. 2018; Gilmour et al. 2019).

Despite the isolation of Scott Reef and the loss of 80% of its corals, communities had largely recovered from the 1998 mass bleaching within 10–15 years (McKinney 2009; Gilmour et al. 2013b). The resilience of the system was attributed to high rates of growth and survival of corals over several generations, due to high water quality and healthy fish stocks. However, not all coral taxa had recovered and there was associated variation in impacts and recovery among communities across the reef system. Changes in coral communities at both Scott Reef and the Rowley Shoals were structured by a complex regime of disturbances over more than two decades, whose effects were mediated by local environmental conditions and expressed through the life history traits of dominant coral taxa. The complexity of these processes and the degradation of the world's reefs (Hughes 1994; Knowlton 2001; Jones et al. 2004) highlight the importance of large-scale, long-term, studies that provide insights into the processes underlying their maintenance or degradation. Long-term studies are particularly important at reef systems that have escaped chronic local pressures but experienced varying levels of heat stress and coral bleaching, as climate change emerges as the most immediate threat to the future of coral reef ecosystems.

Here, we describe the changes in coral communities at Scott Reef and the Rowley Shoals over 23 years, from 1994 to 2017. We document the impacts of mass bleaching, cyclones and moderate bleaching on coral communities and attribute differences in impact and recovery to local disturbance regimes, routine environmental conditions, variation in community composition and coral life history traits. We divide changes in community structure into states of increasing disturbance and degradation, describing the corresponding reductions in coral cover and taxa that contribute most to reef structure and the maintenance of associated organisms. These processes are considered in the context of the most recent heat stress (2016) and ongoing climate change.

# 2. Methods

## 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 and 400 km from the Rowley Shoals (**Figure 1a**). The system consists of South Reef, North Reef and Seringapatam Reef. Benthic communities and habitat conditions were studied at seven locations (**Figure 1b**) in the reef-slope habitat (6 m depth at Lowest Astronomical Tide [LAT]). 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). At each location, three replicate sites were surveyed during each year up to 2016. From 2016, only the first site at each location was surveyed and additional sites established in the adjacent reef crest habitat (3 m LAT), and within the lagoon at North Reef and Seringapatam Reef (SRLGA, SRLGB, NL_M23A), in response to predicted mass bleaching.

The Rowley Shoals is a group of three isolated reef atolls, 260 km from the mainland of north-western Australia (**Figure 1a**). The system consists of Imperieuse Reef, Clerke Reef and Mermaid Reef; each separated by 30–40 km. Benthic communities were surveyed at long-term monitoring locations in the outer reef-slope habitat (6 m LAT) at each reef (RS1, RS2, S3; **Figure 1c**). At each location, three replicate sites were surveyed during each year up to 2016. From 2016, only the first site at each location was surveyed. In 2013, 2016 and 2017, additional sites were established in the adjacent reef crest habitat (3 m LAT) at each reef, and in the lagoon at Mermaid (M11, M12) and Clerke (C13, C20) reefs, for comparison among habitats and in response to predicted mass bleaching in 2016. These additional lagoon sites were located at the top (edge) and base (7 to 12 m) of isolated coral outcrops (bommies). Data collection at all sites followed the standard AIMS LTM methods (Jonker et al. 2008).

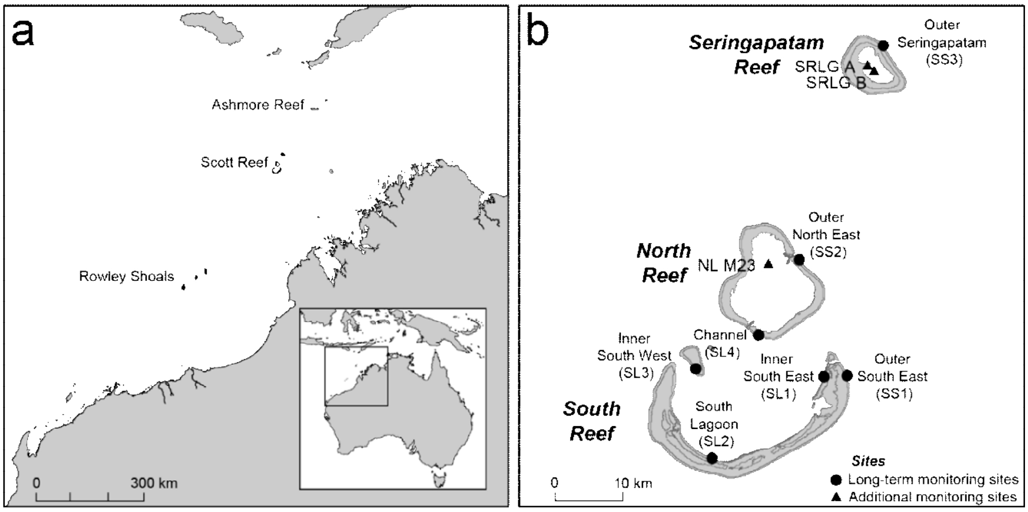
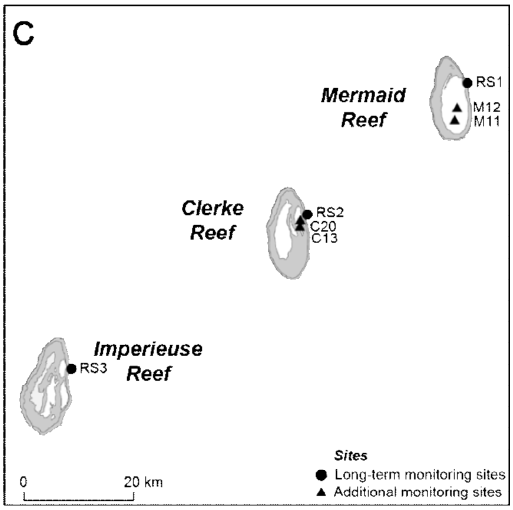



**Figure 1: (a) Position of Scott Reef and the Rowley Shoals off north-western Australia; location of monitoring sites at (b) Scott Reef and (c) the Rowley Shoals. Long-term monitoring sites (black circles) have been surveyed since 1994 and additional monitoring sites (black triangles) since 2013 at the Rowley Shoals and 2016 at Scott Reef.**




## 2.2 Benthic communities

### 2.2.1 Survey Methods

At each of the long-term monitoring locations (**Figure 1**), three replicate sites were separated by approximately 300 m, each consisting of 250 m of permanent transects marked at 10 m intervals. At Scott Reef, surveys were conducted annually between 1994 and 1999, and then in 2003, 2004, 2005, 2008, 2010, 2012, 2014, 2016 and 2017. In 2016, additional surveys were conducted in January, April and October 2016; before, during and after the mass bleaching. At the Rowley Shoals, surveys were conducted annually between 1995 and 1998, then in 2001, 2005, 2008, 2010, 2013, 2016 and 2017.

During each survey, a tape was laid along the permanent transect and images of the benthic community captured from a distance 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). These data were then divided among benthic groups according to taxa (i.e. family, genus) and growth form (encrusting, foliose, massive, branching) (**Table 1**). At Scott Reef, the six most abundant genera accounted for 80% of total hard coral cover. At the Rowley Shoals, the seven most abundant hard coral genera accounted for more than 75% percent of total hard coral cover. In instances where genera were rare (< 3% in all surveys) or difficult to distinguish, they were grouped to family or growth forms that distinguished their response to disturbances.

### 2.2.2 Statistical Analyses

Benthic communities were compared by multivariate analyses using the software PRIMER (Clarke and Warwick 2001). Percentage cover of each benthic group, at each site, location and year were transformed (Square root or Log + 1) to reduce the influence of dominant groups (e.g. crustose coralline algae) but to retain the major differences in community structure. 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 scale at which community structure varied spatially (sites) and temporally (years) was investigated using a cluster analysis and dendrograms, tested using the SIMPROF (5%) procedure in PRIMER. Over the entire survey period, there was considerable variation in community structure among the seven locations across the reef system, but little variation among the replicate sites within each location (**Appendix 1**). Consequently, data are presented at the location level throughout the Results, with associated variances derived from site replication.

## 2.3 Spatial and temporal variation in habitat conditions

### 2.3.1 Local variation in local environmental conditions at Scott Reef

Study sites within the reef slope habitat across the Scott Reef system experience different local environmental conditions. To explore the influence of local conditions on the community recovery following the 1998 mass bleaching, physical parameters predicted to have the greatest influence on community structure were quantified (**Table 2**). At the Rowley Shoals, these physical parameters have not been quantified, so equivalent comparisons cannot be made. The mean percentage cover of sand at each location was quantified along the permanent transects (250 m) during the study period (1994 to 2017) according to the AIMS LTM methods (Jonker et al. 2008). Comparative sedimentation rates were quantified using replicate (*n* = 5) sediment traps spaced at 10 m intervals along a permanent transect at each of the long-term study locations at South Reef and North Reef between July 2008 and February 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 and transported to the Particle Analysis Service Laboratory of CSIRO where samples were processed to determine particle size distributions (PSD) and the total dry weight of sediment. Mean rates of sediment accumulation (mg $cm^{-2}$ $d^{-1}$) 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) were measured using up to replicate samples taken from each location. Initially, mean sediment size was grouped into nine size classes ranging from clay to coarse sand, however for our analysis these size classes are grouped into three broad categories (clay, silt and sand).

To assess variation in temperature regimes among communities (3–6 m depth) i*n situ* temperature readings were collected every 2–15 minutes using VEMCO Minilog-II-T data loggers from 2003-2017. In addition, satellite SST data and local currents were modelled to produce tidal cooling indices for communities (see Bird 2005 for details). Tidal mixing is the interaction of currents with the substratum through friction that creates bottom-up mixing, while solar heating acts to stabilise the water column (Bird 2005). Tidal cooling provides an indication of locations that are well mixed and deep enough to generate considerable surface cooling. Maps of these modelled variables were created, from which mean values were derived for each of the seven monitoring locations (1 $km^2$) for modelled current speed and mixing.

Adjacent to (20–40m depth) all inner-slope communities, current speed, wave height, 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 wave heights were 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 at four locations and acoustically recorded vertical current velocities through the water column as five-minute averages, every 30 minutes.

All environmental data were explored and summarised as either mean or maximum averages per location per day, in addition to mean maximum current speeds and wave heights. Sediment particle size and weight, turbidity and chlorophyll were averaged at each location $d^{-1}$ + S.E. for summer and winter seasons (**Appendix 2c**). For all environmental parameters, data were summarised in ways that best explained the spatial variation among study 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 (Clarke and Warwick 2001). 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 2**). Of the many parameters that were initially investigated, nine remained after excluding those which explained a low proportion of variation and those highly correlated ($r > 0.9$) with another (**Appendix 2b**). The final parameters were: percentage cover of sand, cumulative wind speeds, range in water temperature, rate and composition of sedimentation, turbidity and chlorophyll concentration (fluorescence), and maximum current speed and wave height, in summer and/or winter months.

**Table 1: Benthic groups used to describe coral communities at locations across Scott Reef and the Rowley Shoals. Most groups were common at most communities during one or more periods, except for groups that were most common at the South Lagoon (South Reef); and groups that characterised the Mermaid Reef community.**

| Benthic group | Description | |
|---|---|---|
| **Non-coral** | | |
| Crustose coralline algae | Crustose coralline algae and fine turf algae, suitable for colonisation by coral recruits. | |
| Macroalgae + sponge | Large fleshy algae and sponges, which are rare across the reef systems, and which can exclude and outcompete coral recruits. | |
| *Millepora* | Hydrozoa within the Family Milleporidae. | |
| | **Scott Reef** | **Rowley Shoals** |
| **Soft coral** | Mostly *Sinularia* and *Lobophytum* (≈ 40%), *Sarcophyton* (≈10%), found in all communities but most common at the Channel and Inner South West. | Mostly *Lobophytum* and *Sinularia* (> 75%) found in all communities but most common at Mermaid Reef. |
| **Hard coral** | | |
| *Acropora* | Including tabulate, corymbose, digitate growth forms common across Scott Reef, and arborescent and hispidose growth forms most common at the South Lagoon. | Including tabulate, corymbose, digitate and branching growth forms common across the Rowley Shoals. |
| *Diploastrea* | N/A (rare at Scott Reef). | Characteristic of Mermaid Reef. |
| Foliose corals | *Echinopora* (≈55%) and other foliose corals, most common at the South Lagoon community. | *Echinopora* (≈ 40%) and other foliose corals. |
| *Isopora* | *I. brueggemanni* (≈ 80%) and *I. palifera* (≈ 20%). | *I. brueggemanni* (≈ 25%) and *I. palifera* (≈ 75%). |
| Merulinidae | *Goniastrea, Coelastrea, Dipsastrea, Favites* and other Merulinidae species, with mostly a massive growth form. Corals from the Family Diploastreidae and the genus *Leptastrea* (Insertae Sedis) are also included in this group. | *Goniastrea, Coelastrea, Dipsastrea, Favites* and other Merulinidae species, with mostly a massive growth form. Corals from the genus *Leptastrea* (Insertae Sedis) are also included in this group. |
| *Montipora* | Mostly *Montipora* (≈75%), and other encrusting corals. | Mostly *Montipora* (> 60%), and other encrusting corals. |
| *Pavona* | N/A (rare at Scott Reef) | Including encrusting and submassive growth forms. |
| Pocilloporidae | *Pocillopora, Seriatopora, Stylophora.* | *Pocillopora, Seriatopora, Stylophora.* |
| *Porites* branching | Most common at the South Lagoon. | N/A (rare at Rowley Shoals). |
| *Porites* massive | Common across Scott Reef, but dominant at the Channel and Inner South West. | Common across the Rowley Shoals. |

**Table 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 9 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 Oct 14) | 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 (mg cm$^{-2}$ day$^{-1}$) | Divided between summer and winter months | Mean daily weight of sedimentation in summer and in winter (mg cm$^{-2}$ day$^{-1}$) |
| | | Mean sediment particle size (µm) | Excluded | |
| | | Percentage composition of sediment particle sizes, for nine size classes ranging from clay to course sand (µm) | Divided between summer and winter months and size classes combined | Mean percentage of silt and clay (<63µm), sand (63-500µm) and coarse sand (>500µm), 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-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-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 |

### 2.3.2 Temporal variation in acute disturbances

Throughout the monitoring period, coral communities at one or more locations at Scott Reef and the Rowley Shoals experienced heat stress and coral bleaching, damaging waves generated by cyclones and storms, and an outbreak of coral disease. Heat stress was quantified by Degree Heating Weeks (DHW), extracted from NOAA Coral Reef Watch's 5km global dataset v3.1 (NOAA 2018). DHW values were extracted for pixels overlying study sites using MATLAB R2017b (http://www.mathworks.com/) and averaged for each reef. The duration of heat stress was defined as the period when DHW exceeded 4 °C-weeks. Damaging waves (both cyclonic and non-cyclonic) were identified for each monitoring site, then averaged to reef level. Hourly cyclone-generated wind speeds were reconstructed along cyclone tracks from 1985 to 2015 (McConochie et al. 2004). To account for the contribution of non-cyclonic winds to sea state, at each time step cyclone-generated winds were blended with synoptic winds (https://climatedataguide.ucar.edu/climate-data/climate-forecast-system-reanalysis-cfsr). Cyclonic winds were weighted by proximity to cyclone centres, and synoptic winds weighted by increasing distance beyond 3 radii of the cyclone eye. Following Puotinen et al. (2016), data and fetch were used to estimate whether the resulting waves were capable of damaging coral colonies, with damaging waves defined as having the top one-third of wave heights ≥ 4 m (significant wave height [$H_s$] ≥ 4 m). A lack of high-resolution bathymetry and reef/island mapping prevented any adjustment of localised fetch effects using custom-fit numerical wave models. However, for each cyclone from November 2010 – May 2018, wave height and direction were extracted from the nearest WaveWatch III global hindcast dataset at ~ 50 km resolution (http://polar.ncep.noaa.gov/waves/index2.shtml) (Tolman 2009) and maps of the study sites used to assess the exposure of each long-term monitoring location to damaging waves. For cyclones from January 1998 – December 2013, a finer-resolution assessment was possible using data extracted from an Australia-wide hindcast wave dataset produced by CSIRO and BOM at 11 km resolution using the WaveWatch III model.

# 3. Results

## 3.1 Scott Reef

### 3.1.1 Periods of impact and recovery across Scott Reef

Over 23 years, acute disturbances of varying severity impacted Scott Reef (**Figure 2**), but the system's resilience was facilitated by the lack of chronic disturbances, high water quality and abundant fish stocks. The most severe disturbances caused mean reductions in coral cover across the entire reef system and affected all coral groups, with recovery taking several years to over a decade. Moderate disturbances reduced coral cover at one or more communities, usually for a subset of coral groups, and recovery took less than a few years.

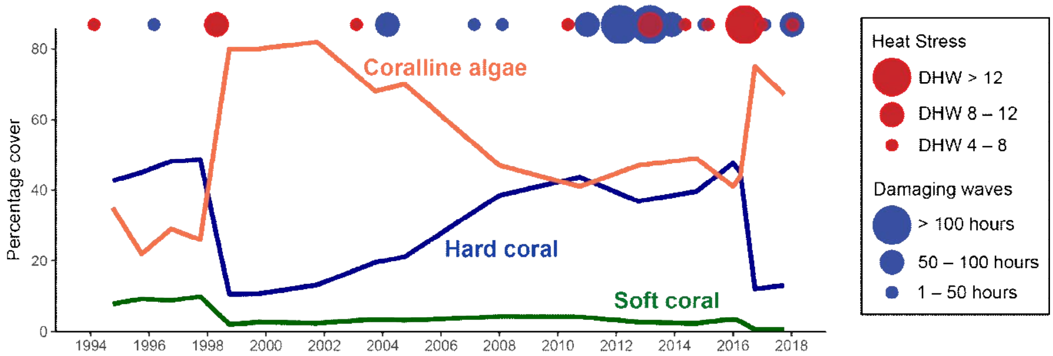



**Figure 2: Over 23 years multiple acute disturbances altered community structure across Scott Reef. Disturbances were heat stress (DHW > 4 °C-weeks) and damaging waves from storms and cyclones (significant wave heights ≥ 4 m).**

From 1994 to 2017, total coral cover (hard corals, soft corals, *Millepora*) across the reef system was 37%, and ranged from 12% to 61%. Reductions in cover were caused by damaging waves generated by cyclones and tropical lows, heat stress causing coral bleaching and a single outbreak of coral disease. Damaging waves (significant wave heights ≥ 4 m) impacted the reef system 13 times (**Table 3**) but affected only a few exposed communities. Heat stress (DHW > 4 °C-weeks) occurred 9 times, including three periods predicted to cause wide-spread bleaching and mortality (DHW ≥ 8 °C-weeks; **Table 3**). Mass bleaching in 1998 reduced coral cover to the lowest on record (**Figure 2**). Subsequent recovery was slowed by the local effects of cyclones and coral bleaching, but by 2010 the mean cover of hard corals had reached pre-bleaching levels; although cover of soft corals was still approximately half that prior to the 1998 mass bleaching (**Figure 2**). From 2010, heat stress and damaging waves were more frequent, but cover had increased to 51% by January 2016. Heat stress in April 2016 was the most severe on record and mass bleaching caused another large reduction in coral cover, which in 2017 was similar (14%) to that following the 1998 mass bleaching (**Figure 2**). Through the cycles of impact and recovery, benthic communities were dominated (86%) by hard corals, soft corals and coralline algae (**Figure 2**). Following the loss of corals, the available substrata were colonised by coralline algae, whereas the cover of other benthic groups (e.g. sponges, macroalgae) remained low (< 7%).

The changes in community structure across Scott Reef were driven by their exposure to two mass bleaching events and many less-severe disturbances. However, community dynamics were also mediated by the routine environmental conditions at each location and the life histories of the dominant coral taxa. The temporal dynamics grouped into five periods of impact and recovery (**Appendix 3**), which were also indicative of the condition of the reef system:

1) Pre-bleaching (1994–1997): Start of monitoring and before mass bleaching;
2) Mass bleaching (1998–2001): Up to three years after mass bleaching;
3) Post-bleaching (2002–2004): Up to six years after mass bleaching;
4) Recovery and multiple disturbances (2005–2015): Seven to fifteen years after mass bleaching;
5) Mass bleaching (2016–2017): Up to two years after mass bleaching.

### 3.1.2 Pre-bleaching and local environmental conditions (1994–1997)

In the absence of severe disturbances, the structure of coral communities reflected local environmental variation. Communities were distinguished by water temperatures, current speeds, exposure to winds and waves, and water quality (sedimentation, chlorophyll and turbidity) (**Appendix 2, 4, 5**). These conditions varied with proximity to the sheltered lagoon at South Reef, the deep channel between North and South Reef, and the outer eastern slope at each of the three reefs (**Figure 1, Appendix 4, 5**). Consequently, environmental conditions and community structures were most similar at the outer eastern slope locations (Outer South East, Outer North East, Outer Seringapatam), followed by the Inner South East. Communities at the Inner South West, Channel and South Lagoon locations were most unique. The South Lagoon was the most sheltered and its community distinguished by the highest cover of fragile corals, such as the foliose corals (usually *Echinopora*) and *Acropora* (particularly arborescent and hispidose forms). The Inner South West and Channel had the highest current speeds and wave heights, including those generated by seasonal storms and cyclones; they also had the highest daily temperature ranges, due to internal tides and cool water intrusions. The Inner South West and Channel communities had the highest cover of massive *Porites* and soft corals, and the lowest cover of *Acropora* and other fragile growth forms. These fundamental differences in local conditions and community structure influenced the severity of impacts from disturbances and the rates of recovery over the next two decades.

In 1996, damaging waves were generated by Cyclone Kirsty (37 hours $H_s \geq 4$ m, **Table 3**). However, from October 1994 to 1997 mean coral cover (hard corals, soft corals, *Millepora*) across the reef system increased from 53% (± 2) to 61% (± 3). There were comparable increases (7–11%) in cover at most communities, but for smaller increases at those exposed to the damaging waves (3–5% at Channel and Inner South West). Coral cover was high (45–70%) at all communities, with massive *Porites, Montipora*, soft corals, *Acropora* and *Isopora* the most common taxa (5–15%), followed by Pocilloporidae and Merulinidae (2–10%) (**Figure 3**).

**Table 3: Disturbance history at Scott Reef (Oct 1994–Dec 2017). Heat stress is defined as DHW > 4 °C-weeks (yellow rows) for pixels overlying Scott Reef monitoring locations (NOAA Coral Reef Watch 2018); widespread bleaching and mortality is likely when DHW > 8 °C-weeks (orange rows). Double lines between rows indicate timing of coral monitoring surveys. Where DHW remained at its maximum ("peak date") over more than one day, the peak date given is the first day of the maximum value. Cyclone and storm events (blue rows) are defined by hours of damaging seas ($H_s$ > 4 m). A higher number of hours at $H_s$ > 4 m indicates greater potential for wave damage at the coral monitoring sites, assuming vulnerable colonies are present. For pre-2010 cyclones, directions of exposure are unknown and peak dates are approximate (details in Methods).**

| Event | Year | Peak date/s | Peak DHW | Duration | Bleaching observations; wave direction |
|---|---|---|---|---|---|
| Cyclone Kirsty | 1996 | 9-10th Mar | | 37 hrs | Directions unknown |
| Heat stress | 1998 | 27th Apr | 9.6 | 90 days | Widespread bleaching and mortality |
| Heat stress | 2003[1] | 11th Feb | 7.6 | 83 days | No known surveys, coral cover increased |
| Cyclone Fay | 2004 | 19th-23rd Mar | | 54 hrs | E, NE |
| Cyclone George | 2007 | 4-6th Mar | | 19 hrs | W, WNW |
| Cyclone Nicholas | 2008 | 15-16th Feb | | 23 hrs | W, WNW |
| Heat stress | 2010 | 27th Apr | 7.4 | 82 days | Bleaching observed at some locations |
| Cyclone Vince | 2011 | 11-14th Jan | | 87 hrs | WNW, W |
| Cyclone Iggy | 2012 | 24-29th Jan | | 95 hrs | W, WNW |
| Cyclone Lua | 2012 | 14-18th Mar | | 168 hrs | W, WNW |
| Cyclone Narelle | 2013 | 7-11th Jan | | 62 hrs | W, ENE, NW, WNW |
| Heat stress | 2013[1] | 11th Feb | 10.4 | 145 days | Bleaching observed but not quantified |
| Cyclone Rusty | 2013 | 23rd-28th Feb | | 135 hrs | W, WNW |
| Cyclone Christine | 2013 | 28-29th Dec | | 73 hrs | WNW |
| Low 05U | 2014 | 19-20th Jan | | 40 hrs | WSW, W |
| Heat stress | 2014 | 17th Apr | 5.4 | 68 days | No signs of bleaching in surveys later that year |
| Low 05U I | 2015 | 7-9th Jan | | 48 hrs | W |
| Heat stress | 2015[1] | 10th Feb | 4.5 | 47 days | No signs of bleaching in surveys the following year |
| Heat stress | 2016 | 5th May | 16.5 | 170 days | Widespread bleaching and mortality |
| Heat stress | 2016[1] | 21st Dec | 5.9 | 73 days | No known surveys |
| Cyclone Yvette | 2016 | 22nd-23rd Dec | | 61 hours | WNW, W |
| Low 15U | 2017 | 6-8th Feb | | 39 hours | W, WNW |
| Heat stress | 2017[2] | 27th Dec | 5.5 | 13 days | No known surveys |
| Low 11U | 2018 | 29th-31st Jan | | 87 hours | W, WNW |

[1]Heat stress conditions started in December of the previous year but are listed by the year when heat stress peaked. [2] Heat stress extended past the end of downloaded data (31st December 2017).

### 3.1.3 Mass bleaching (1998–2001)

In 1998, heat stress (DHW > 4 ° C-weeks) affected the reef system for 90 days, peaking at 9.6° C-weeks in late April (**Table 3**). Mass bleaching was observed in April at all shallow water habitats at all reefs to 20 m depth. Six months later, mean (± SE) hard coral cover decreased from 48% (± 7) to 10% (± 3), a relative decrease of ≈ 80% (**Figure 2**). Among the communities, the relative decreases ranged from 50 to 90% and depended on the abundance of susceptible coral groups. The relative decreases in cover were highest (> 90%) for the branching *Porites*, *Acropora*, *Millepora, Isopora,* and Pocilloporidae, ranged from 70 to 90% in the other coral groups, and were lowest (12–75%) in the massive *Porites* (**Figure 3**). The impact of the bleaching also varied among communities according to their environmental conditions. The Inner South West and Channel communities experience less heat stress (**Appendix 2**) and had smaller (< 60%) relative decreases in common taxa than others (> 80%) (**Figure 3, Appendix 6**). For example, the relative decreases in massive *Porites* (5–10%) and Merulinidae (30–55%) at the Inner South West and Channel were lower than at all other communities (massive *Porites* 25–75%, Merulinidae 80–97%).

The mass bleaching had homogenised the reefs, as coral taxa that had previously distinguished communities were also the most susceptible (e.g. *Isopora, Acropora,* Pocilloporidae). Three years later, there were only small increases (< 3%) in cover, due mostly to the regrowth of surviving corals (massive *Porites, Isopora,* soft corals) at communities least affected. The reefs were still characterised by taxa that had been most abundant and most resistant to heat stress, particularly the massive *Porites* and the *Montipora* and encrusting corals (**Figure 3, Appendix 6**).

### 3.1.4 Post-bleaching (2002–2004)

In 2003, heat stress (DHW > 4 ° C-weeks) affected the reef system for 83 days and peaked at 7.6 °C-weeks in February, followed in 2004 by damaging waves generated by Cyclone Fay (54 hours $H_s \geq 4$ m, **Table 3**). These disturbances had little obvious effect on the coral communities because the most susceptible coral taxa were still rare following the mass bleaching. The reef system had commenced a trajectory back to pre-bleaching structure, and by 2004 mean (± SE) hard coral cover had increased to 19% (± 4) (**Figure 2**). Cover ranged from 9–26% among the communities, depending on the severity of mass bleaching and exposure to Cyclone Fay. However, increases in cover were still driven by the regrowth of corals (*Isopora,* massive *Porites*, soft corals) at the communities least affected by mass bleaching, and by massive *Porites* at most communities.

### 3.1.5 Recovery and multiple disturbances (2005–2015)

From 2005 to 2010, damaging waves were generated by cyclones George (19 hours $H_s \geq 4$ m) in 2007 and Nicholas (23 hours $H_s \geq 4$ m) in 2008 (**Table 3**). Impacts were largely restricted to susceptible corals (e.g. *Acropora*, Pocilloporidae) at the Channel and Inner South West communities, where cover had increased by 2–12% by 2008, compared to 17–28% at the other locations (**Figure 3**). Heat stress then affected the reef system for 82 days, peaking at 7.4° C-weeks in April 2010. The resulting outbreak of disease and coral bleaching was most severe at South Lagoon, where there was a large decrease (12%) of predominantly *Acropora*. Bleaching in 2010 was also observed at the Inner South East and outer-slope communities, but caused only a small reduction in cover (5%) of Pocilloporidae at Outer Seringapatam.

More than five years after the 1998 mass bleaching, a more rapid return to pre-bleaching structure had commenced across the reef system. By 2010, mean (± SE) hard coral cover was similar (44% ± 3) to that before the mass bleaching and ranged from 35–51% among the communities. Despite the variable susceptibility and reductions in cover among taxa, most had also returned to a similar pre-bleaching cover. The exceptions were a much higher cover of *Acropora* and a much lower cover of *Millepora*, branching *Porites, Isopora* and soft corals (**Figure 3, Figure 4**). *Acropora* had returned to a similar or higher cover at all communities except for South Lagoon, where they were impacted by the recent bleaching. Branching *Porites* and *Millepora* were the most susceptible of all taxa and were previously rare at most communities, so their cover in 2010 had returned to < 20% of that before the mass bleaching (**Figure 4, Figure 5**). *Isopora* were common (10–30%) at most communities before the 1998 mass bleaching but were also among the most susceptible taxa (**Figure 5**) and returned to only 30% of pre-bleaching cover (**Figure 4**). However, local recovery of *Isopora* depended on the post-bleaching cover; where some (0.5–3%) remained, they had returned to between 50% and 130% of their pre-bleaching cover, whereas communities where no (0%) *Isopora* remained had returned to < 20% of their pre-bleaching cover (**Figure 3**). Soft corals were also common (5–20%) at most communities, were moderately susceptible, and had returned to 42% of their pre-bleaching cover (Figure 4). As with *Isopora,* the remaining cover of soft corals influenced their recovery, but in 2010 was lower than before the mass bleaching all at but one community (**Figure 3**).

Between 2010 and 2012, damaging waves were generated by cyclones Vince (87 hours $H_s \geq 4$ m), Iggy (95 hours $H_s \geq 4$ m) and Lua (168 hours $H_s \geq 4$ m), reducing mean cover across the reef system from 44% (± 3) to 36% (± 8) (**Figure 2, Table 3**). Despite causing the first reduction in mean cover since the 1998 mass bleaching, cyclone impacts were restricted to the few communities with a westerly aspect. There were large relative decreases (≈ 65%) in cover at the Channel and Inner South West, where even the most robust corals were impacted (**Figure 3**). For example, the relative decreases in cover at the Channel were 40–55% for the most robust corals (*Montipora* and encrusting corals, Merulinidae, *Porites* and massive corals), 75% for the soft corals, and > 95% for the more fragile corals (*Acropora,* Pocilloporidae). The impacts were greater than those caused by the mass bleaching in 1998 at these communities, and over the next two years small reductions (≈ 1%) in cover had continued for some groups (soft corals, Merulinidae, massive *Porites*). Although the Inner South East was less exposed to the damaging waves, the relative decreases were similar (> 90%) for the most fragile corals, but less for the soft corals (55%) and the most robust corals (5–30%); over the next two years there was a rapid increase (8%) in cover of predominantly *Acropora* and *Isopora*.

Between 2012 and 2016, damaging waves were generated by cyclones Rusty (135 hours $H_s \geq 4$ m) and Christine (73 hours $H_s \geq 4$ m) in 2013, and by tropical lows in 2014 (40 hours $H_s \geq 4$ m) and 2015 (48 hours $H_s \geq 4$ m) (**Table 3**). The Inner South West and Channel were again most exposed to the cyclone impacts. The increases in cover at these communities were largely restricted to the regrowth of massive *Porites* and soft corals following cyclone damage, and in 2015 they had the lowest cover (≈ 28%) of all communities (**Figure 3**). In 2013, the reef system was also affected by heat stress for 145 days, which peaked at 10.4° C-weeks in February (**Table 3**). The associated bleaching was largely restricted to some Pocilloporidae at the outer-slope communities, which had been sheltered from the recent cyclones. By January 2016, mean (± SE) cover across the reef system had increased to 47% (± 7) and was high (50–56%) at all communities but those worst affected by recent cyclones (**Figure 2, Figure 3**). At all communities, *Acropora* (8–15%) and *Isopora* (2–5%) had the largest increases since 2010, but cover of *Millepora*, branching *Porites*, *Isopora* and soft corals was still much lower than before the mass bleaching in 1998.

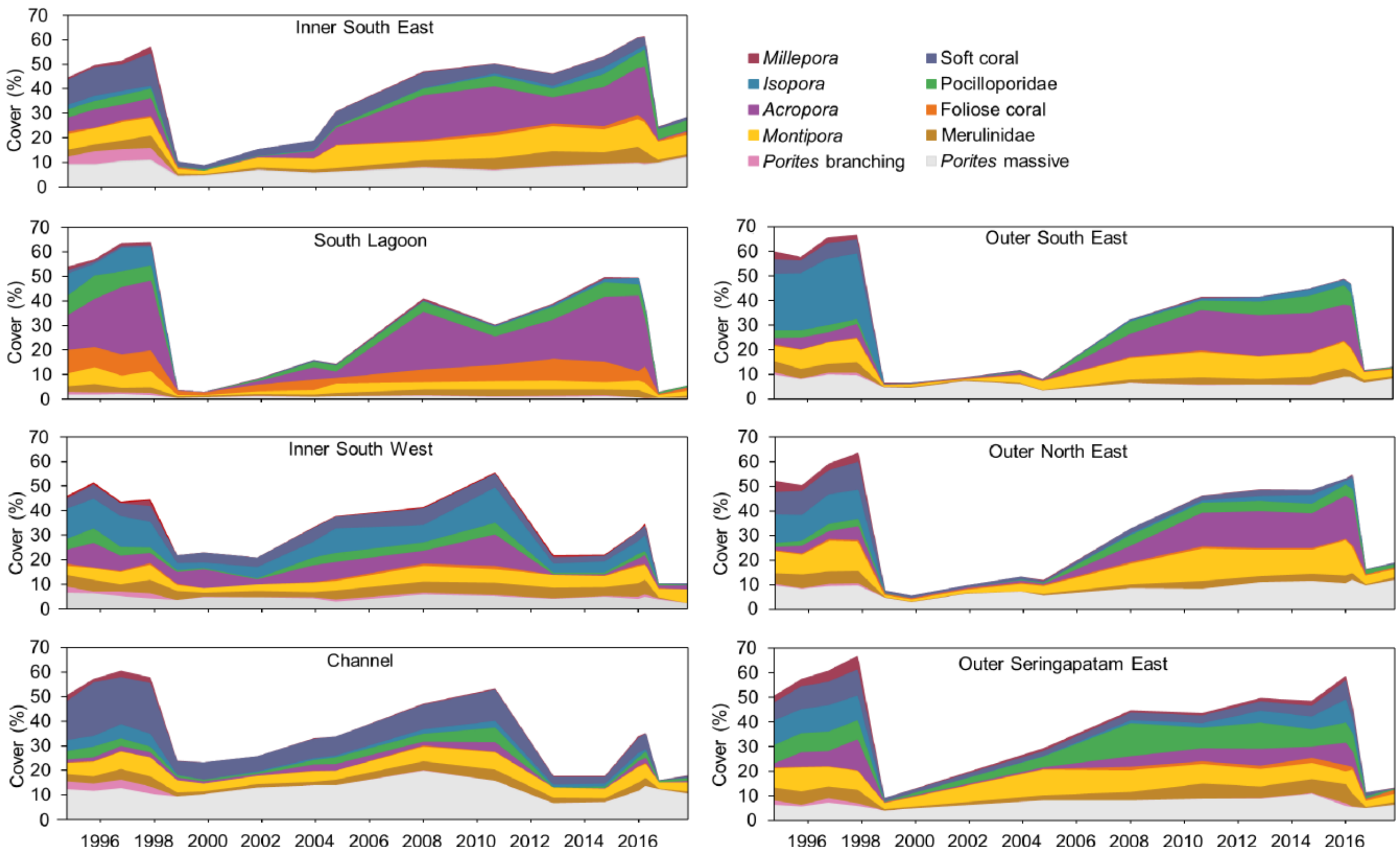



**Figure 3: Temporal variation in community structure across the reef system from 1994 to 2017.**

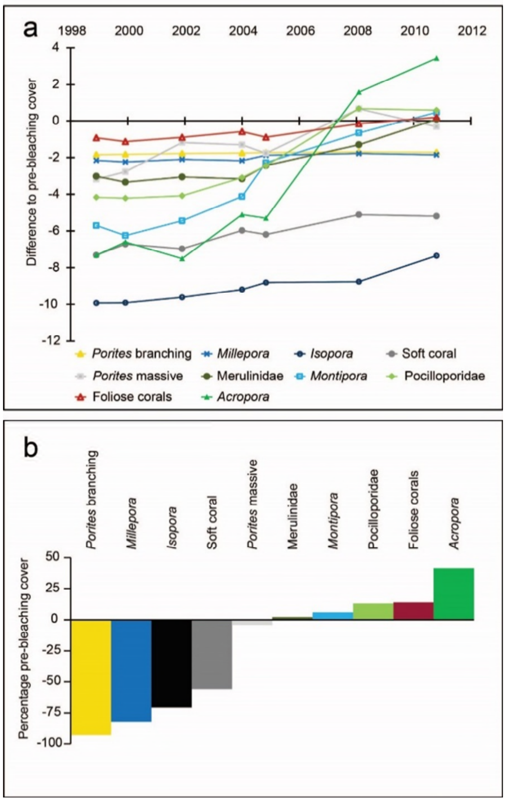



**Figure 4: Recovery of coral groups following the 1998 mass bleaching. (a) Difference between mean pre-bleaching (1995 to 1997) cover at each location and in consecutive surveys to October 2010. (b) Mean percentage difference in cover between pre-bleaching years and in 2010.**

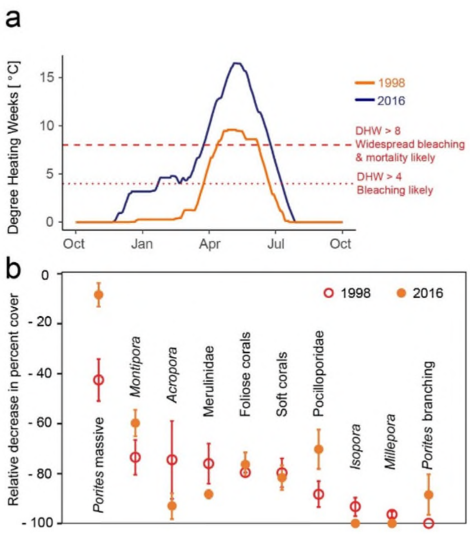



**Figure 5: (a) Heat stress at Scott Reef in 1998 and 2016. Duration and maximum Degree Heating Weeks (NOAA Coral Reef Watch 2018); and (b) Susceptibility of coral groups to heat stress and mass bleaching in 1998 and 2016. Mean relative (%) decrease in cover at communities across the reef system, between approximately one year before and after each mass bleaching.**

### 3.1.6 Mass bleaching (2016–2017)

In 2016 and 2017, three periods of heat stress (DHW > 4 °C-weeks) affected the reef system (**Table 3**). The heat stress in early 2016 was the highest on record, persisting for 170 days and peaking at 16.5° C-weeks in May (**Figure 5**). An additional 73 days of heat stress peaked at 5.9° C-weeks in December 2016, and 13 days peaked at 5.5° C-weeks in December 2017 (**Table 3**). Damaging waves were also caused by Cyclone Yvette in 2016 (61 hours $H_s \geq 4$ m) and a tropical low in 2017 (39 hours $H_s \geq 4$ m) (**Table 3**), but the heat stress in early 2016 and the resulting mass bleaching was by far the most severe disturbance.

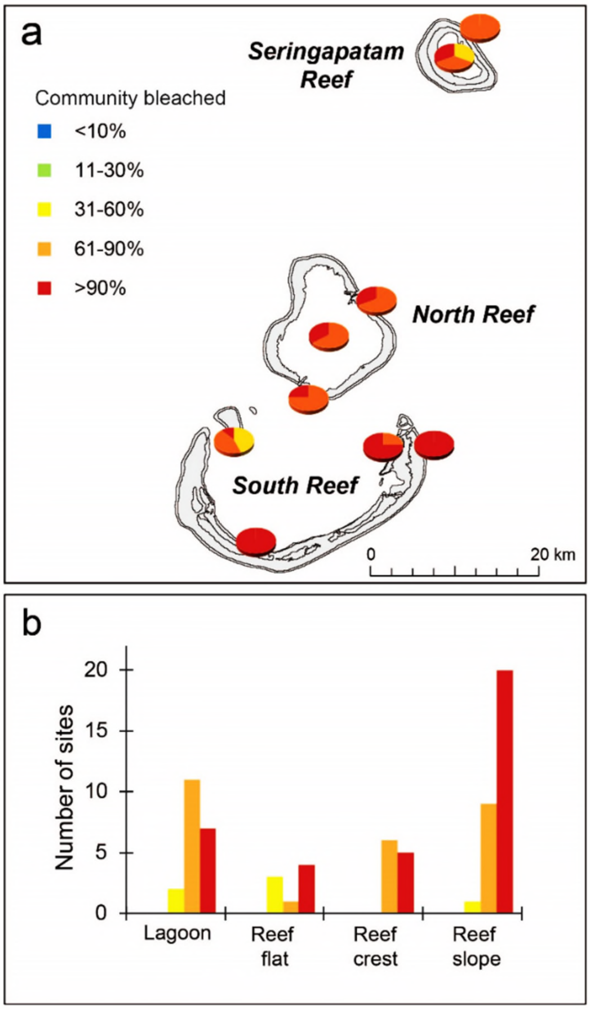



**Figure 6: Percentage of bleached corals in April 2016 in communities (a) across the reef system and (b) in each habitat. Habitats are the lagoon (coral bommies and lagoon floor; 0–17m), reef flat (0–3m), reef crest (3–6m) and reef slope (6–9m). Colonies included were fully bleached or recently dead.**

Mass bleaching in April 2016 was recorded at all shallow water (< 20 m depth) habitats across Scott Reef, with little variation in bleaching among locations or habitats (lagoon, reef flat, reef crest and reef slope (**Figure 6**). All 69 communities surveyed had > 30% of colonies bleached, and many (30–70%) had > 90% of corals bleached. The sites least affected were on the reef flat or in the deepest (15–20 m depth) parts of the lagoon at North Reef and Seringapatam Reef. Bleaching was observed to 30 m at the deep lagoon at South Reef, but rare at 50 m.

The bleaching estimates and the reduction in coral cover six months later (**Figure 7**) were comparable, with little variation in mortality among reefs, habitats and communities. The mean (± SE) cover of hard corals at the reef crest and reef slope had decreased from 47% (± 8) to 14% (± 5), and the soft coral from 3% (± 2) to 0.6% (± 0.3). The relative reductions in cover were similar (> 70%) at most (9 of 14) communities across the reef system, but lower (40–60%) at those worst affected by recent cyclones and exposed to the lowest heat stress. For example, at the Channel, Inner South West and Inner South East communities, there were smaller relative decreases in cover of massive *Porites* (5%) and *Montipora* (30–60%) than at the other communities (10–33% and 50–80% respectively) (**Figure 3, Appendix 6**). Among the coral groups, the relative decreases in cover were highest (> 90%) for the *Millepora*, branching *Porites, Isopora* and *Acropora*, followed by Merulinidae and soft corals (80–90%), foliose corals (mostly *Echinopora*) and Pocilloporidae (70%–80%), *Montipora* (60%) and massive *Porites* (9%) (**Figure 5; Appendix 6**).

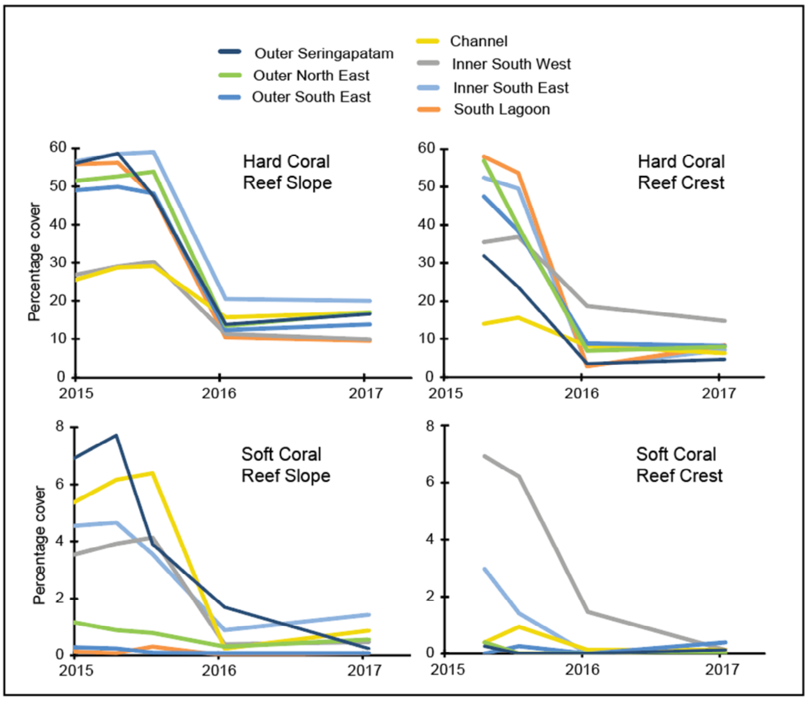



**Figure 7: Changes in mean cover of hard and soft corals at reef slope (6 m) and reef crest (3 m) habitats following the 2016 mass bleaching.**

### 3.1.7 1998 versus 2016 mass bleaching

Heat stress in 2016 lasted longer and was more severe (170 days; 16.5° C-weeks) than in 1998 (90 days; 9.6° C-weeks) (**Figure 5, Table 3**). However, the mass bleaching and mortality in 1998 and 2016 were similar in scale and severity, with mean cover across the reef system decreasing from the highest (≈ 50%) to the lowest on record (10–15%). All habitats, locations and coral groups were affected, and the loss of corals was matched by comparable increases in crustose coralline algae (**Figure 2, Figure 3, Figure 5**).

Following the mass bleaching in 1998 and 2016, the coral communities were more similar than at any other time in 23 years, and were distinguished by the loss of *Isopora*, *Acropora*, Pocilloporidae, Merulinidae, and soft corals (**Figure 5, Appendix 6**). However, the relative decreases in mean cover of some taxa were smaller following the 2016 mass bleaching than 1998. Where massive *Porites* were common (> 5% cover), their relative decreases in 2016 were smaller (10–30%) than in 1998 (30–60%), even after excluding communities recently impacted by cyclones. Similarly, in 2016 there were smaller relative decreases in *Montipora* (66%) and Pocilloporidae (62%) than in 1998 (78% and 80% respectively; **Figure 5**). However, the smaller mean reductions in cover for these taxa were mostly at the Inner South East community (**Appendix 6**), where the relative reduction in total hard coral cover was also lower (56%) in 2016 than in 1998 (79%). Among the communities, the Inner South West and Channel consistently had the lowest relative reductions (45–60%) in hard corals following both mass bleaching events, because they experienced more variable temperatures (**Appendix 2**) and had fewer susceptible taxa. For other communities, relative reductions were similar following both mass bleaching events, despite some having a much lower cover of susceptible taxa in 2016 (e.g. *Isopora*, *Millepora*).

### 3.1.8 Disturbance regimes, community structure and degradation

Over 23 years, Scott Reef transitioned through four general periods of impact and recovery that were indicative of the health of the reef system: healthy (pre-bleaching years, 1994 to 1997), mass bleaching (up to four years after mass bleaching in 1998 and 2016); post-bleaching (five and six years after mass bleaching) and recovery (10 to 15 years after mass bleaching). The most obvious difference between communities among the four states was the reduction in cover of hard and soft corals with increasing degradation, and the corresponding increases in crustose coralline algae (**Figure 8**).

Among the taxa, the massive *Porites*, *Montipora* and Merulinidae consistently characterised communities in all four of the states, because they were common and underwent the smallest changes in cover. However, their relative contribution to the community changed as the system transitioned from the degraded to the healthy states, indicative of the changes in communities when the return times for severe disturbances are less than a decade (**Figure 8**). As the condition of communities improved, the cover of all coral groups increased, but the most significant increases were in the *Isopora*, Pocilloporidae and particularly *Acropora*. Nonetheless, there remained some important differences between the recovery and pre-bleaching states, because the taxa most susceptible and least resilient to the mass bleaching required well over a decade to recover. This included *Millepora* and branching *Porites* that were most susceptible and were previously rare at most communities, and *Isopora* and soft corals that failed to recover at communities where they were worst affected (**Figure 3, Figure 8**).

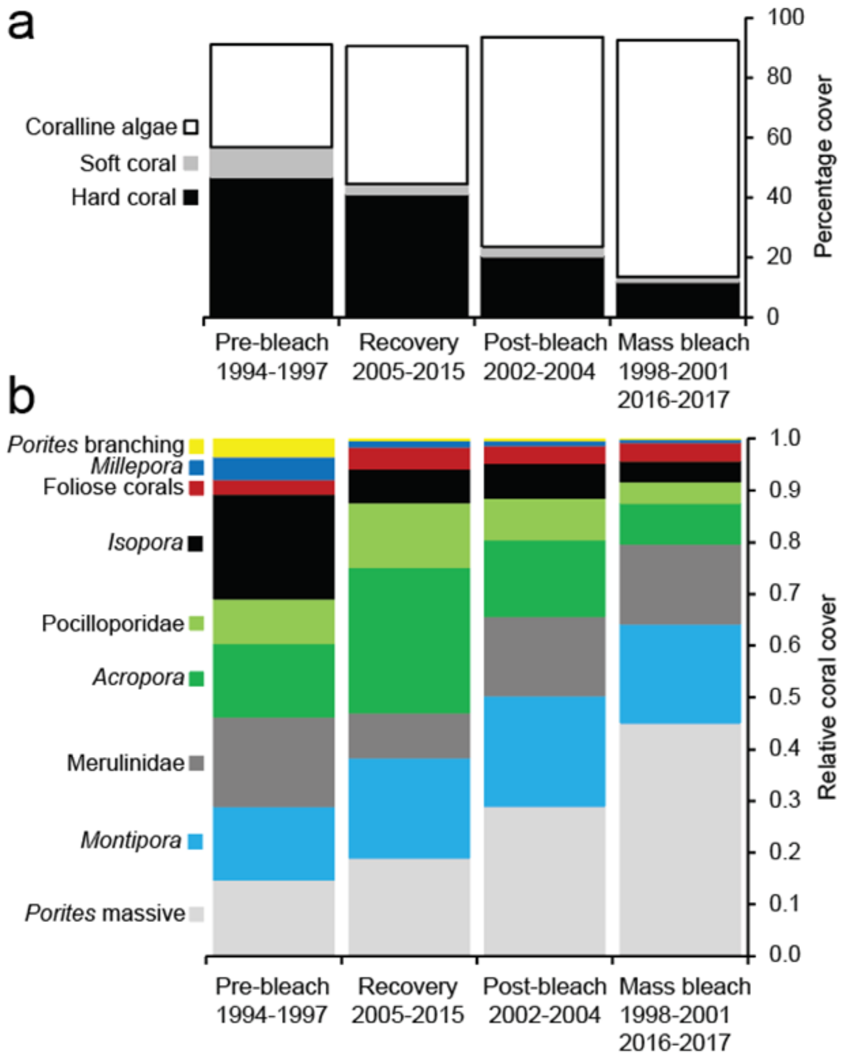



**Figure 8: Community structure at Scott Reef in four states of impact and recovery, indicative of the condition of the reef system. States are: Pre-bleaching (1994-1997), Mass bleaching (1998–2001, 2016–2017), Post-bleaching (2002–2004), and recovery from mass bleaching (with local disturbances, 2005–2015); (a) percentage cover of hard corals, soft corals and coralline algae; and (b) relative cover of different coral groups, in each community stage.**

## 3.2 Rowley Shoals

### 3.2.1 Periods of impact and recovery across the Rowley Shoals

Over 22 years, acute disturbances of moderate severity impacted the Rowley Shoals (**Figure 9**). Although frequent, disturbances usually reduced coral cover in only a few communities and coral taxa, and a rapid recovery was aided by the lack of chronic disturbances, high water quality and abundant fish stocks.

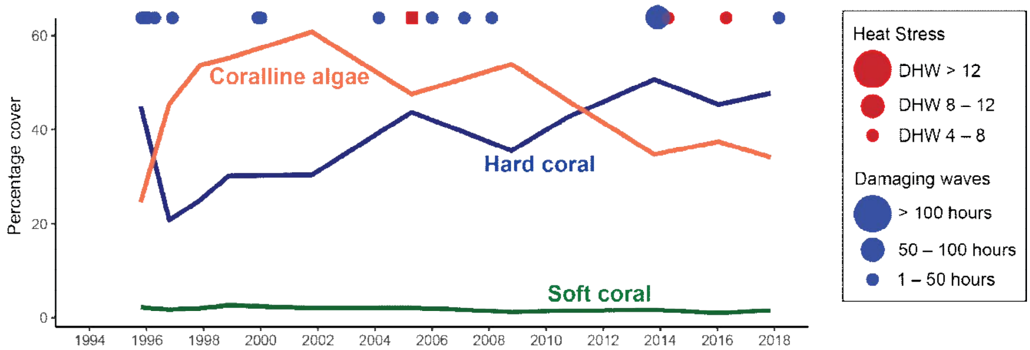



**Figure 9: Over 22 years, multiple acute disturbances altered community structure across the Rowley Shoals. Disturbances were damaging waves from storms and cyclones (significant wave heights ≥ 4 m) and heat stress (DHW > 4 °C-weeks). Red square indicates observed moderate bleaching where heat stress did not exceed 4 °C-weeks.**

From 1995 to 2017, mean coral cover (hard corals, soft corals, *Millepora*) across the Rowley Shoals was 45% and ranged between 28% and 58%. At least 13 cyclones produce damaging waves (**Table 4**), and eight coincided with mean reductions (up to 22%) in coral cover across the reef system (**Figure 9**). Multiple cyclones caused the largest reduction in mean coral cover, from 50% in 1995 to 28% in 1996. Between 2005 and 2008, another mean reduction in cover (from 52% to 41%) followed three cyclones and a moderate bleaching event (**Table 4**). Heat stress (DHW > 4° C-weeks) occurred three times since 1995, but not in 2005 when moderate bleaching was observed. The highest heat stress on record (5.8 °C-weeks) occurred in 2016, but caused only moderate bleaching at a few sites (**Table 4**). Severe heat stress (DHW > 8° C-weeks) and mass bleaching has not occurred at the Rowley Shoals (**Table 4**). Through cycles of impact and recovery, benthic communities were dominated (> 70%) by hard corals, soft corals and coralline algae (**Figure 9**). Following the loss of corals, available substrata were colonised by coralline algae, while the cover of other benthic groups (e.g. sponges, macroalgae) remained low. Since 1997, mean coral cover has increased through rapid cycles of impact and recovery, and has been consistently high (> 40%) since 2010 (**Figure 9**).

Changes in community structure across the reef system were driven by their local exposure to cyclones and moderate heat stress and mediated by the life histories of their dominant taxa. The temporal dynamics grouped into three periods of impact and recovery (**Appendix 7**), all of which were indicative of a healthy reef system:

1) Cyclone disturbance and decreased coral cover (1996–1997)
2) Recovery, cyclones and coral bleaching (1995, 2001, 2005)
3) Cyclones, recovery and coral bleaching (2008–2017)

**Table 4: Disturbance history at the Rowley Shoals (Oct 1995–Dec 2017). Cyclone and storm events causing damaging seas (hours Hs > 4 m) are shown in blue cells. Heat stress is defined as DHW > 4 °C-weeks (yellow cells) for pixels overlying Rowley Shoals monitoring locations (NOAA Coral Reef Watch 2018). Double lines between rows indicate timing of coral monitoring surveys. Where DHW remained at its maximum ("peak date") over more than one day, the peak date given is the first day of the maximum value. A higher number of hours at $H_s$ > 4 m indicates greater potential for wave damage at the coral monitoring sites, assuming vulnerable colonies are present. For pre-2010 cyclones, directions of exposure are unknown and peak dates are approximate (details in Methods).**

| Event | Year | Peak date/s | Peak DHW | Duration (days; hours) | Disturbance observations; wave direction |
|---|---|---|---|---|---|
| Cyclone Frank | 1995 | Dec | | 3–6 hrs | Directions unknown |
| Cyclone Gertie | 1995 | Dec | | 11 hrs | Directions unknown |
| Cyclone Jacob | 1996 | Feb | | 7 hrs | Directions unknown |
| Cyclone Olivia[1] | 1996 | Apr | | 9 hrs | Directions unknown |
| Cyclone Phil[1] | 1996 | Dec | | 10 hrs | Directions unknown |
| Cyclone Isla | 1999 | Dec | | 21 hrs | Directions unknown |
| Cyclone John | 1999 | Dec | | 30 hrs | Directions unknown |
| Cyclone Fay | 2004 | Mar | | 40 hrs | Directions unknown |
| Heat stress[2] | 2005 | 27th Apr | 2.1 | – | Moderate bleaching observed |
| Cyclone Daryl | 2006 | Jan | | 11 hrs | Directions unknown |
| Cyclone George | 2007 | Mar | | 26 hrs | Directions unknown |
| Cyclone Nicholas | 2008 | Feb | | 47 hrs | E |
| Cyclone Christine | 2013 | Dec | | 62 hrs | WNW, E to SE, W |
| Heat stress | 2014 | 12th Apr | 5.6 | 71 days | No signs of recent bleaching in surveys later that year |
| Heat stress | 2016 | 28th Apr | 5.8 | 71 days | Minor bleaching |
| Cyclone Marcus | 2018 | Mar | | 20 hrs | NE to ENE to NNE |

[1]Wave zones for cyclones Phil and Olivia did not intersect the long-term monitoring sites, but may have caused impacts given the positional uncertainty of these cyclone tracks. [2]Heat stress in 2005 did not exceed 4° C-weeks but moderate bleaching was observed.

### 3.2.2 Cyclone disturbances and decreased coral cover (1995–1997)

Damaging waves were generated by cyclones Frank (3–6 hours $H_s \geq 4$ m) and Gertie (11 hours $H_s \geq 4$ m) in 1995, and Jacob (7 hours $H_s \geq 4$ m) Olivia (9 hours $H_s \geq 4$ m) in 1996 (**Table 4**). The mean (± SE) cover of hard corals at Rowley Shoals decreased from 45% (± 8) in 1995 to 21% (± 4) in October 1996 (**Table 4**). However, decreases were limited to Clerke (13%) and particularly Imperieuse Reef (46%), mainly due to the loss of *Acropora* (**Figure 10**). In contrast, at Mermaid Reef hard corals had increased (7%), mainly due to *Millepora* (**Figure 10**).

Cyclone Phil generated damaging waves (10 hours $H_s \geq 4$ m) in December 1996. By 1997, cover had changed little at Clerke and Imperieuse reefs and had increased (13%) at Mermaid Reef, due mainly to encrusting corals (10%). Following the recent cyclones, *Acropora* were rare (< 2%) at all three reefs in 1997 and Merulinidae, *Millepora* and encrusting corals were most common (3–16%) (**Figure 10**).

### 3.2.3 Recovery, cyclones and coral bleaching (1998–2005)

Damaging waves were generated by cyclones Isla (21 hours $H_s \geq 4$ m) and John (30 hours $H_s \geq 4$ m) in December 1999 (**Table 4**). Between 1997 and 2001, the cover of hard corals had decreased (13%) at Mermaid Reef, due to the loss of Merulinidae (2%), *Diploastrea* (3%) and particularly encrusting corals (8%). In contrast, cover increased at Clerke (13%) and Imperieuse reefs (16%), due to large increases of *Acropora* (9–10%) and smaller (< 4%) increases of Pocilloporidae and massive *Porites* (≈ 4%) (**Figure 10**).

Damaging waves were generated by Cyclone Fay (40 hours $H_s \geq 4$ m) in 2004 (**Table 4**). Between 2001 and 2005, hard coral cover changed little at Mermaid Reef, but increased at Clerke (17%) and Imperieuse (24%) reefs, due to large increases (13–22%) in *Acropora* and smaller increases (< 5%) in *Isopora* and other coral groups (**Figure 10**). Coral communities in 2005 were similar at Clerke and Imperieuse reefs, with a relatively high cover of and *Acropora* (24–32%) and *Isopora* (4–5%; **Figure 10**), whereas *Acropora* were rare (< 3%) at Mermaid Reef and cover of *Diploastrea*, *Millepora*, and soft corals was higher (6–8%).

Coral bleaching was observed at all three reefs during the survey in March 2005, despite DHW not exceeding 4° C-weeks (maximum 2.1° C-weeks, **Table 4**). Moderate bleaching has been recorded on other reefs at levels of 2° C-weeks, showing that other factors influencing bleaching, such as fine-scale variability in temperatures, may not be captured by satellite sea-surface temperatures (SST) and the derived DHW metric. 10–50% of *Acropora*, Pocilloporidae, Merulinidae and *Diploastrea* colonies had bleached, but the incidence of bleaching varied among reefs. Most of the bleached corals were alive when surveys were conducted and there was little evidence of recent mortality.

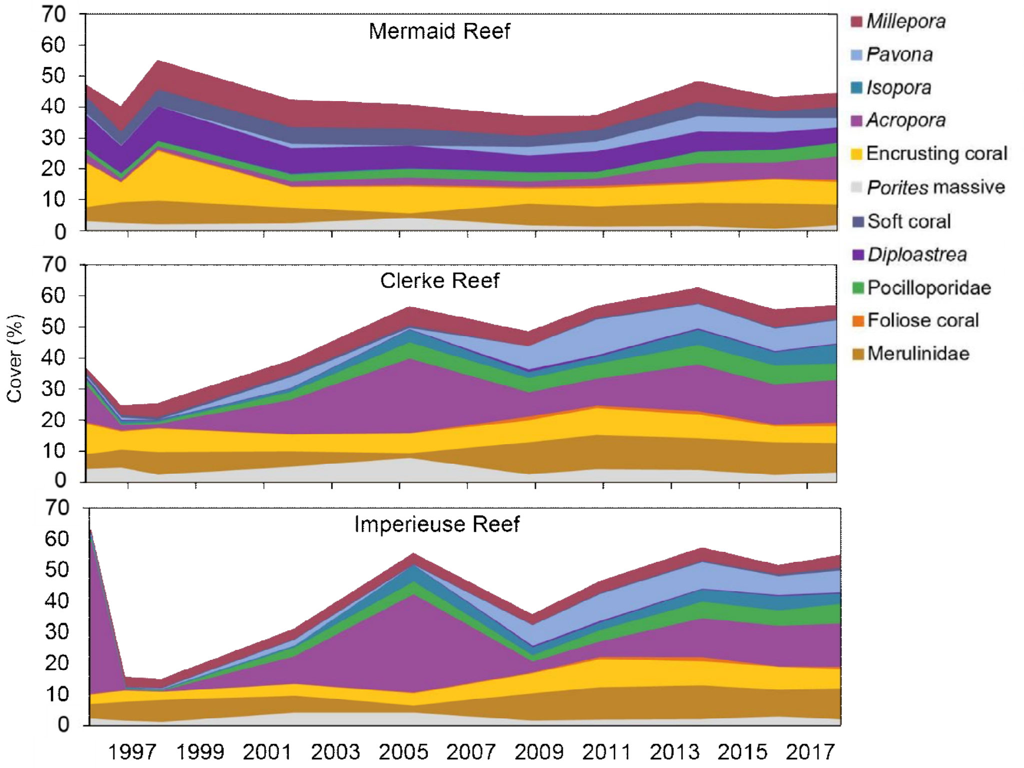



**Figure 10: Temporal variation in community structure at reef slope locations at the Rowley Shoals from 1995 to 2017.**

### 3.2.4 Cyclones, recovery and coral bleaching (2006–2017)

Damaging waves were generated by cyclones Daryl (11 hours $H_s \geq 4$ m) in 2006, George (26 hours $H_s \geq 4$ m) in 2007, and Nicholas (47 hours $H_s \geq 4$ m) in 2008 (**Table 4**). The combined effects of these cyclones and coral bleaching in 2005 (**Table 4**) caused a mean reduction in cover across the Rowley Shoals from 2005–2008. Decreases in cover of hard corals were larger at Imperieuse (20%) than at Clerke (7%) or Mermaid (3%) reefs (**Figure 10**), due to the higher abundance of susceptible corals. In particular, there were large (16–28%) decreases in *Acropora* at Imperieuse and Clerke, and small (< 5%) changes in other coral taxa at all three reefs (**Figure 10**).

Between 2008 and 2013, no cyclones affected the Rowley Shoals and hard corals increased at Mermaid (11%), Clerke (16%) and Imperieuse (22%) (**Figure 10**). *Acropora* had the largest increases in cover at all reefs (4–9%), and there were smaller increases (< 4%) in *Isopora*, Pocilloporidae and encrusting corals. (**Figure 10**). By 2013, most coral taxa had recovered from previous cyclones and coral bleaching, but for *Acropora* at Imperieuse Reef (**Appendix 7**).

Damaging waves were generated by Cyclone Christine (62 hours $H_s \geq 4$ m) in December 2013, and heat stress (DHW > 4 ° C-weeks) affected the reef system for 71 days in 2014, peaking at 5.6° C-weeks in April (**Table 4**). Between 2013 and January 2016, mean hard coral cover had decreased at Clerke (11%) and Imperieuse (5%), with the largest decreases in *Acropora* and *Montipora*. There was little change in hard coral cover at Mermaid Reef, but there were small decreases in *Millepora* and soft corals and increases in other taxa.

In 2016, heat stress affected the Rowley Shoals for 71 days, peaking at 5.8° C-weeks in late April (**Table 4**). Little (≤ 10%) or no bleaching was recorded at most reef slope and lagoon sites. However, 30% of the community had bleached at some sites in the Mermaid lagoon (**Figure 11**), particularly *Acropora*, *Montipora* and Fungiids. Despite the bleaching, mean (± SE) hard coral cover across habitats and reefs increased from 45% (± 4) in January 2016 to 48% (± 6) in 2017 (**Figure 9**). The increases in cover were largest (3–4%) at the reef slope at Clerke and Imperieuse reefs, due mainly to increases in *Acropora* (**Figure 10**). The largest decreases (4%) in cover occurred at the few sites in the Mermaid lagoon that experienced the worst bleaching (**Figure 12**), mainly due to the loss of *Acropora*. However, mean cover at the other lagoon sites, and across Mermaid Reef, had changed little by 2017 (**Figure 12**).

In 2017, the differences in reef slope communities across the Rowley Shoals were consistent with those throughout the monitoring period (**Figure 10; Appendix 7**). Reef slope communities at Imperieuse and Clerke were most similar, characterised by a higher cover of Pocilloporidae, *Isopora*, massive *Porites* and particularly *Acropora.* Hard coral cover was generally higher and more variable at Imperieuse and Clerke reefs, due mainly to changes in *Acropora*. In contrast, Mermaid Reef was distinguished by a higher cover of *Diploastrea*, *Millepora* and soft corals. Hard coral cover was usually lower and less variable at Mermaid Reef, due to the low cover of *Acropora.* Merulinidae, *Montipora* and other encrusting corals were common at all three reefs and remained relatively stable through time (**Figure 10**).

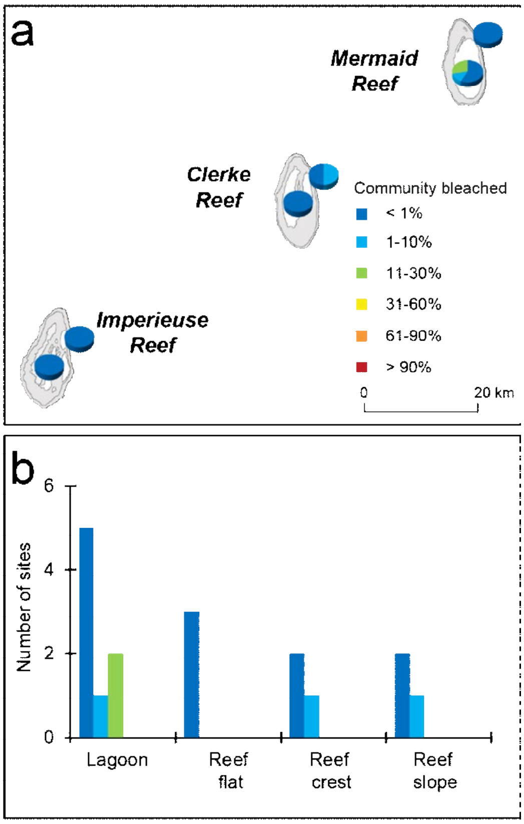



**Figure 11: (a) Percentage of bleached corals in communities across the reef system in April 2016, and (b) number of sites in each habitat, using the same categories. Habitats are the lagoon (including coral bommies and lagoon floor), reef flat (0–3m), reef crest (3–6m) and reef slope (6–9m). Colonies included were fully bleached or recently dead.**

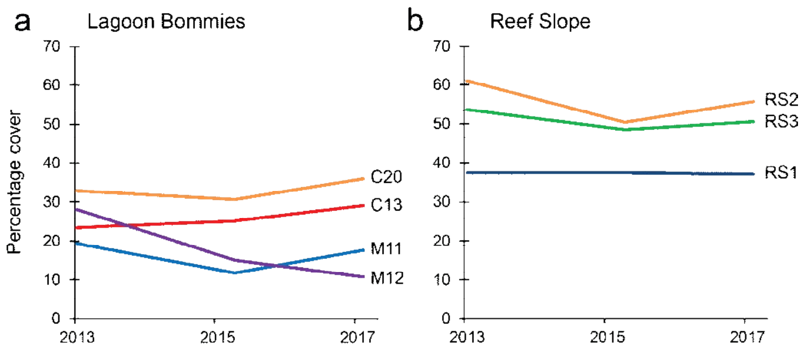



**Figure 12: Hard coral cover in (a) lagoon bommie and (b) reef slope habitats at the Rowley Shoals in 2013–2017. Lagoon bommie sites were at Mermaid Reef (M11, M12) and Clerke Reef (C13, C20). Reef slope sites were at Mermaid Reef (RS1), Clerke Reef (RS2) and Imperieuse Reef (RS3).**

# 4. Discussion

## 4.1 Twenty-three years of disturbances

Over 23 years, coral communities across Scott Reef underwent significant change, driven by two mass bleaching events and frequent moderate disturbances. During the same period, communities at the Rowley Shoals also changed in response to frequent moderate disturbances but did not suffer the severe and widespread impacts caused by mass bleaching. Damaging waves generated by cyclones caused mean decreases in coral cover three times at the Rowley Shoals and once at Scott Reef, but usually affected exposed communities and coral taxa with fragile growth forms. At Scott Reef, there were nine periods of heat stress, two mass bleaching events and at least two moderate bleaching events; at the Rowley Shoals, there were only two periods of heat stress and moderate bleaching events. Coral communities at Scott Reef experienced large variation in impact and recovery, with coral cover in 2017 near the lowest on record. Coral cover varied less at the Rowley Shoals and has remained high since 2014. The very different dynamics of these reef systems highlight the impacts of mass bleaching on coral reefs, and how these are mediated by local environmental conditions and coral life history traits.

## 4.2 Disturbances mediated by local environmental variation

Local environmental conditions play a fundamental role in structuring coral communities, even within a common habitat (Done 1982; Hughes et al. 2012; Schmidt et al. 2012; Zinke et al. 2018). Across the reef slope habitat at Scott Reef, variation in temperatures, wave energy, current speeds and water quality influenced the structure of coral communities, particularly in the absence of severe disturbances. The location on the reef and environmental conditions also mediated exposure to disturbances. For example, the Inner South West and Channel were most exposed to seasonal storms and cyclones, but are also flushed by internal waves bringing cool water from the deep (Bird 2005; Green et al. 2018; Rayson et al. 2018; Green et al. 2019). Cool water intrusions, higher current speeds and tidal mixing at the Channel and Inner South West communities reduced heat stress and bleaching in both 1998 and 2016 at Scott Reef. These localized reef hydrodynamics, singularly or in combination, have also been shown to reduce heat stress and bleaching at other reefs (Wall et al. 2015; Safaie et al. 2018; Page et al. 2019). Local reductions in heat stress and bleaching also occurred at the southern part of the Seringapatam lagoon in 2016 (**Figure 6**), following night-time cooling of water over the reef flat (Green et al. 2018). Conversely, more severe bleaching at other parts of the reef was due to the flow of warm water out of lagoons, low current speeds and limited tidal mixing. Fine-scale variation in hydrodynamics, water quality and light penetration all can influence local heat stress and the severity of coral bleaching (Nakamura and van Woesik 2001; McClanahan et al. 2007; Skirving et al. 2017; Page et al. 2019).

Local conditions also influenced the recovery of communities following severe disturbances. Reef structure and hydrodynamics determine patterns of larval connectivity among communities and rates of recruitment (Hughes et al. 1999; Becerro et al. 2006; Sato et al. 2018; Torda et al. 2018). All three atolls at the Rowley Shoals have similar shapes, which limits the dispersal of spawning and particularly brooding corals outside of each lagoon, but aids connectivity among the outer slope habitats at each reef (Thomas et al. 2019). At Scott Reef, local hydrodynamics are strongly influenced by the open lagoon at South Reef and the flow of water through the deep channel adjacent to North Reef (Green et al. 2018; Rayson et al. 2018; Green et al. 2019). The Outer South East and Channel at Scott Reef had consistently low recruitment because larvae were carried away by currents, while the Inner South East and Outer North East had the highest recruitment because larvae were concentrated by local eddies (Gilmour et al. 2013a; Rayson et al. 2018). Following larval recruitment, growth and survival of colonies were also influenced by local environmental conditions, and communities returned to their previous structure. There was no evidence of previously rare taxa becoming dominant at Scott Reef after the mass bleaching, or of major shifts in community structure towards less susceptible species. Long-term shifts in community structure on other reefs usually reflect the loss of susceptible taxa, rather than the proliferation of previously rare corals (Done et al. 2007; Hughes et al. 2018a; Torda et al. 2018; Edmunds 2019). More than a decade after the mass bleaching at Scott Reef, communities were distinguished by the loss of coral taxa whose life history traits (susceptability, growth reproduction) had made them most vulnerable to the heat stress.

## 4.3 Susceptibility, recovery and coral life histories

Both disturbances and routine environmental conditions structured coral communities through the life histories of their dominant taxa. At Scott Reef and Rowley Shoals, there were common patterns of susceptibility to cyclones and heat stress, with the *Acropora*, *Isopora,* Pocilloporidae generally most susceptible, and *Montipora*, Merulinidae, and massive *Porites* least susceptible. This variation in susceptibility is consistent with most other studies of coral reefs (Marshall and Baird 2000; Loya et al. 2001; McClanahan 2004; Hoey et al. 2016). However, the vulnerability of taxa depends on both their initial susceptibility (resistance) and capacity to recover (resilience) over many years (Van Woesik et al. 2011; Carturan et al. 2018). For example, when considering both the initial decreases in cover at Scott Reef following the 1998 mass bleaching and increases in cover over the following 12 years, taxa with very different life histories displayed similar levels of long-term vulnerability. Susceptible taxa recovered more rapidly while those least affected showed slower increases in cover. *Acropora* and Pocilloporidae were more susceptible to disturbances but had higher recruitment and growth rates (Harrison and Wallace 1990; Graham et al. 2011; Van Woesik et al. 2011). Their initial recovery was slow because most colonies were killed, but increased rapidly over several generations. Merulinidae, soft corals and massive *Porites* had lower susceptibility to disturbances and lower rates of sexual recruitment and growth (Harrison and Wallace 1990; Babcock 1991; Fabricius 1995; Fong and Glynn 2000; Van Woesik et al. 2011). Regrowth of injured soft corals and massive corals resulted in small initial increases in cover following cyclones and mass bleaching, but this slowed when recovery relied on recruitment.

The capacity for larval dispersal also influenced the recovery of different coral taxa following the 1998 mass bleaching. For the most susceptible taxa at the worst affected communities, recovery depended on the supply of recruits from other locations (Underwood 2009). Coral taxa with few local survivors and a low capacity for dispersal had not recovered a decade after the mass bleaching. This included the branching *Porites* and the hydrocoral *Millepora* that were already rare before the mass bleaching, and the soft corals and *Isopora* that were previously common. The slow growth of the dominant soft corals (*Sarcophyton, Lobophytum*, *Sinularia*) and their reliance on asexual replication (Fabricius 1995; Michalek-Wagner and Willis 2001; Bastidas et al. 2004) meant they remained at < 30% of pre-bleaching cover 10 years later. The recovery of *Isopora* also depended on local survivors, since their brooded larvae typically dispersed less than a few kilometres (Harrison and Wallace 1990; Underwood et al. 2009; Foster and Gilmour 2018; Thomas et al. 2019). Recovery had occurred within a decade at the two communities where the cover of *Isopora* was highest post-bleaching, but there had been little or no recovery at communities where few colonies had survived. Despite their susceptibility, broadcast spawning *Acropora* and *Pocillopora* produced many larvae that dispersed across the reef system, aiding the recovery of populations worst affected (Underwood 2009; Harrison 2011; Gilmour et al. 2013b; Thomas et al. 2019). As a result, *Acropora* were the only taxa whose cover was consistently higher at all communities more than a decade after the mass bleaching than before, with a similar transition observed on other reefs with a supply of larvae and several years without severe disturbance (Thompson and Dolman 2010; Johns et al. 2014; Torda et al. 2018). The ecological consequences of life history variation in corals is increasingly recognised (Darling et al. 2013; Done et al. 2015; Madin et al. 2016; Torda et al. 2018) and provides valuable insights into the viability of reefs through climate change. To successfully manage reefs through changing regimes of disturbance, life history variation must be considered in the context of functional importance to reefs (Darling et al. 2017) natural capacity for adaptation, and suitability for restoration efforts (Anthony 2016; McLeod et al. 2019).

### 4.4 Resilience of Scott Reef and the Rowley Shoals to past and future disturbance regimes

The 1998 global coral bleaching highlighted the threat of climate change to coral reefs (Hoegh-Guldberg 1999; Wilkinson 2000). Many reefs devastated in 1998 have not recovered, due to additional bleaching and local pressures (Baker et al. 2008; Sheppard et al. 2008; Graham et al. 2011; Bruno et al. 2018; MacNeil et al. 2019). Isolated reefs, including Scott Reef and the Rowley Shoals, are less exposed to local pressures (e.g. degraded water quality, pollution, depleted fish stocks), and have recovered faster, but the lack of larval connectivity with other reef systems also increases susceptibility to reef-wide reductions in population stocks (Graham et al. 2006; Sandin et al. 2008; Holbrook et al. 2018). At Scott Reef, there was a comparable decrease in coral cover and recruitment following the mass bleaching and this stock-recruitment relationship remained through the recovery period (Gilmour et al. 2013b). Recovery across the reef system relied on the surviving corals and their offspring, and not the supply of recruits from other reef systems (Underwood et al. 2009; Underwood et al. 2018). Nonetheless, high post-recruitment growth and survival was facilitated by high water quality, healthy fish stocks and a decade (1999-2009) with few disturbances (Gilmour et al. 2013b).

The heat stress in 2016 at Scott Reef was the worst on record and the mortality that followed was comparable to that in 1998, with similar variation among communities and coral groups. A recovery trajectory of 10–15 years would therefore be expected, if the future disturbance regime was also similar. However, the frequency and severity of disturbances at Scott Reef have increased since 2010, and a similar pattern is evident at many other reefs in Western Australia and around the world (Hughes et al. 2018b; Gilmour et al. 2019). With further climate change (Hoegh-Guldberg et al. 2018; Steffen et al. 2018), cyclones are expected to produce more damaging waves (Chand et al. 2017; Cheal et al. 2017; Simpkins 2018) and rising ocean temperatures (Raftery et al. 2017) are expected to increase outbreaks of coral diseases (Harvell et al. 2002; Maynard et al. 2015) and the frequency and severity of coral bleaching (Eakin et al. 2018).

Through the previous cycles of impact and recovery, the Scott Reef system transitioned through four general states indicative of the level of degradation and return times for severe disturbances. The healthier states had a much higher coral cover (> 40%) than degraded states (< 20%), but corals were replaced by crustose coralline that facilitates coral recruitment (Harrington et al. 2004). The space available for recolonization reflects the potential for the reef to recover, rather than permanently transitioning to a state in which algae or other benthic invertebrates dominate (Hoegh-Guldberg et al.

2007). Both degraded states also had a much lower cover of *Acropora, Isopora* and Pocilloporidae, which contribute most to the structure of the reef and micro-habitats used by fish and other organisms (Emslie et al. 2008; Wilson et al. 2009; Graham and Nash 2013; Darling et al. 2017; Richardson et al. 2017). These degraded states are indicative of the condition of the reef when recovery periods from severe mass bleaching are < 10 years. In contrast, at the Rowley Shoals communities maintained a healthy state through cycles of impact and rapid recovery from cyclones. Mass bleaching has not affected the reef system, but heat stress in 2016 was the highest on record and the severity of both coral bleaching and cyclones impacts are also likely to increase further at the Rowley Shoals.

The future condition of the Rowley Shoals and Scott Reef fundamentally depend on local water quality, fish stocks and regimes of disturbances, but also on local refuges from cyclones and heat stress, and the adaptive capacity of their corals. Contrasting susceptibilities and an increased understanding of the coral holobiont highlight the potential for coral adaptation to heat stress (Coles and Brown 2003; Baker et al. 2004; Maynard et al. 2008; Palumbi et al. 2014; Coles et al. 2018; DeCarlo et al. 2019). At all reefs, inferring coral adaptation to heat stress at the reef-scale is confounded by fine-scale variability, community structure, disturbance history and survey methods (percentage cover). Nonetheless, observations at the Rowley Shoals and Scott Reef suggest some adaptation to heat stress. Higher levels of heat stress at the Rowley Shoals in 2014 and 2016 caused similar or less bleaching to that in 2005. At Scott Reef, a similar level of heat stress in 2013 caused far less bleaching and mortality than in 1998, while bleaching was similar in 1998 and 2016 despite more severe heat stress in 2016. Among the coral taxa, the responses to heat stress were not consistent. For example, at Scott Reef the *Acropora* were among the worst affected by bleaching in 1998, 2010 and 2016, but not 2013; massive *Porites*, *Montipora* and Pocilloporidae had smaller relative decreases in cover in 2016 than in 1998, despite a higher level of heat stress. Other reefs also have consistent and contrasting patterns of bleaching susceptibility within and among groups (Pratchett et al. 2013; Palumbi et al. 2014; Hoey et al. 2016; McClanahan 2017; Coles et al. 2018).

Existing data for Scott Reef, the Great Barrier Reef (Hughes et al. 2017), and other reefs around the world, confirm that the current rate of adaptation by corals will not significantly reduce the likelihood of mass bleaching events in coming decades. Instead, reductions in the severity of mass bleaching at reef scales usually reflect a shift to a lower total coral cover and a higher proportion of less susceptible taxa (sliding baselines), rather than rapid and widespread adaptation (Osborne et al. 2017; Hughes et al. 2018a; Edmunds 2019). Management of Scott Reef and the Rowley Shoals must now focus on maintaining high water quality and healthy fish stocks, to aid recovery between acute disturbances (Diaz-Pulido et al. 2010; Jones et al. 2016; Johns et al. 2018; Richmond et al. 2018), and apply our emerging understanding of the reefs' natural capacity to adapt to future conditions (McLeod et al. 2019).

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# 6. Appendices

## Appendix I

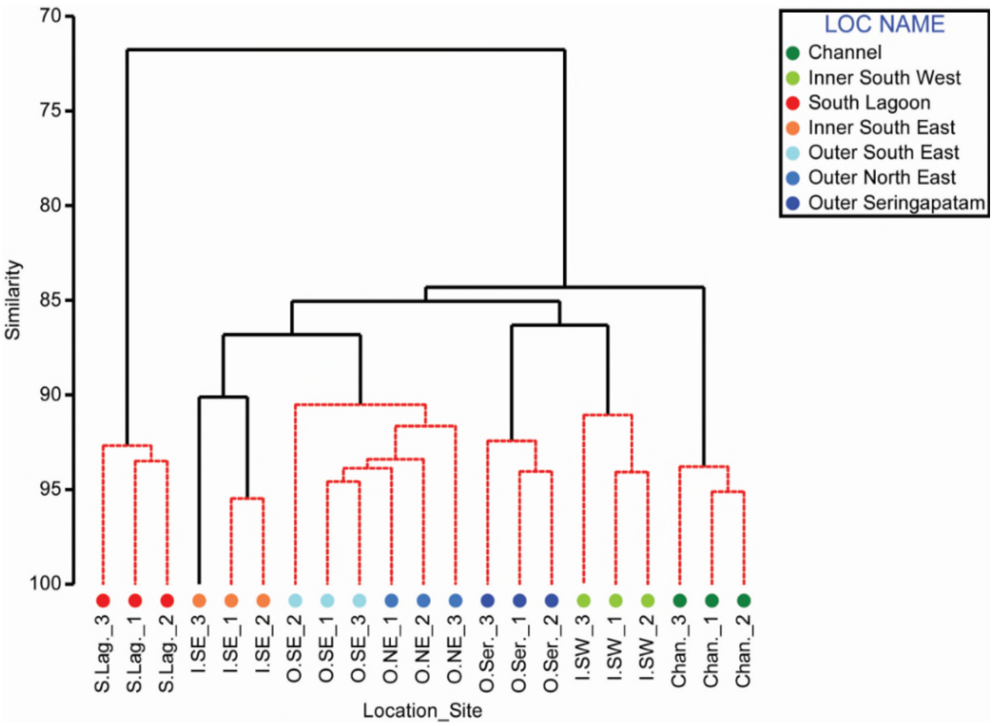


**Figure A 1: Grouping of the long-term monitoring sites surveyed at the Scott Reef system over the study period 1994 – 2014 based on similarities in benthic community structure. Spatial variation in the structure of coral communities at Scott Reef (1994–2014). Replicate sites (n = 3) consistently grouped together within locations (Figure 1). Sites linked by red lines are not significantly different, according to the SIMPROF procedure at a significance level of 5%. Data are Bray Curtis similarities for Log+1 transformed percentage cover of benthic groups (Table 1).**

## Appendix 2

The physical parameters that best distinguished locations at Scott Reef were associated with their regimes of sedimentation, water temperatures and current speeds, winds and waves, and concentrations of chlorophyll and turbidity (**Figure A2**).

The outer-slope locations at South Reef (Outer South East) and North Reef (Outer North East) 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 spanning a range of particle sizes, moderate current velocities and exposure to moderate winds and waves from the east (**Figure A2**). Although not quantified, the routine habitat conditions at Outer Seringapatam were similar to Outer North East.

Among the inner-slope locations, habitat conditions varied according to their proximity to the sheltered lagoon in South Reef and to the western side of the deep channel between North and South Reef. The South Lagoon was by far the most sheltered, having the lowest exposure to winds and waves, the slowest current speeds, a low deposition of fine particle sizes (silt, clay) and relatively high turbidity and chlorophyll concentrations. Consequently, its community experienced moderate temperature variation and was characterised by a fragile and gently sloping substrata with a low cover of sand.

Inner South West and Channel locations were the most exposed to winds and waves generated by seasonal storms from a westerly, south-westerly direction, and had high maximum current speeds and wave heights in summer (**Figure A2a, A2c**). 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. The Inner South West and Channel both had large temperature ranges and the highest 'cooling index' of all locations (**Figure A2a, A2b**). The Channel had steep substrata, while Inner South West was comparatively flat with patchy coral outcrops. Conditions at Inner South East were a mixture of the other locations, being exposed to winds, waves and cool water through the channel from the west, while also being sheltered from the open ocean to the east.

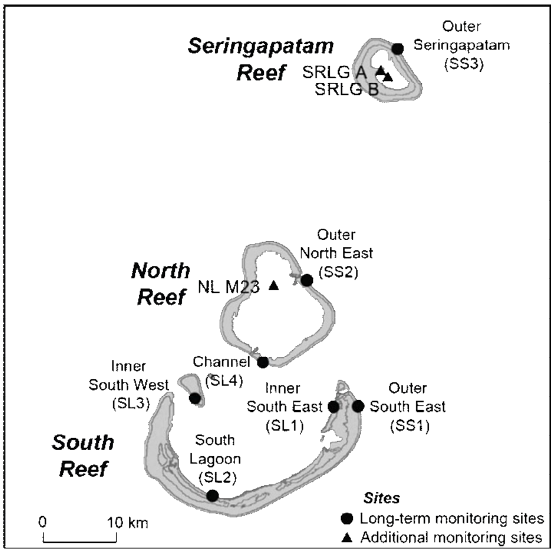


**Figure A 2: (a) Location of monitoring sites at Scott Reef. Long-term monitoring sites (black circles) have been surveyed since 1994 and additional monitoring sites (black triangles) since 2016**

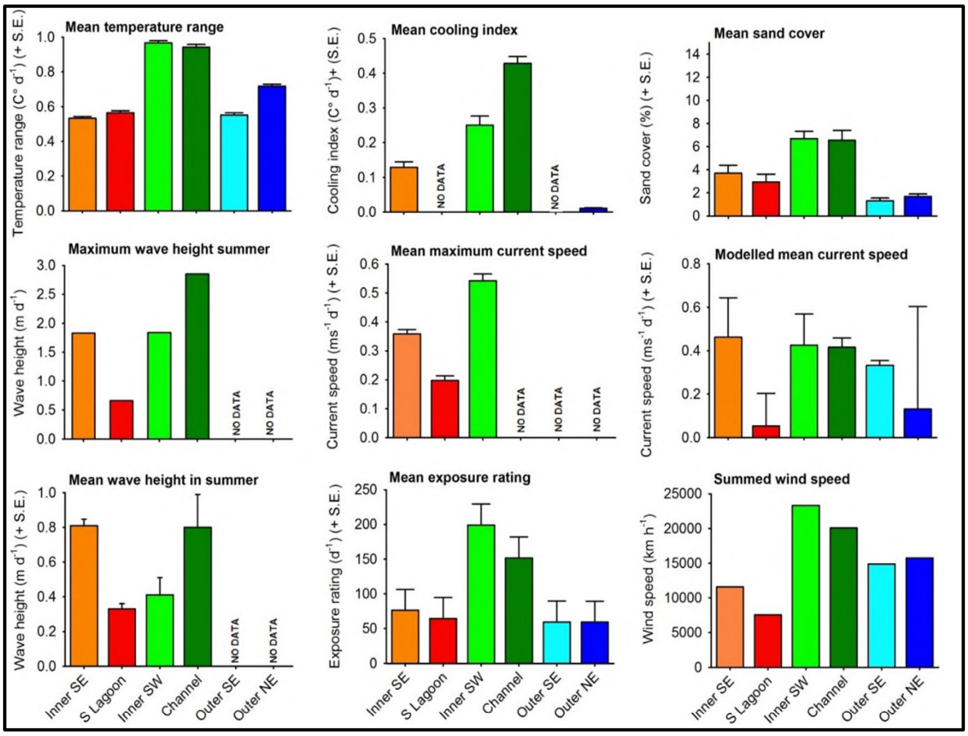


**Figure A 2: (b) Physical parameters measured at the long-term monitoring locations at Scott Reef. (c) Seasonal variation in physical parameters long-term monitoring locations at Scott Reef.**

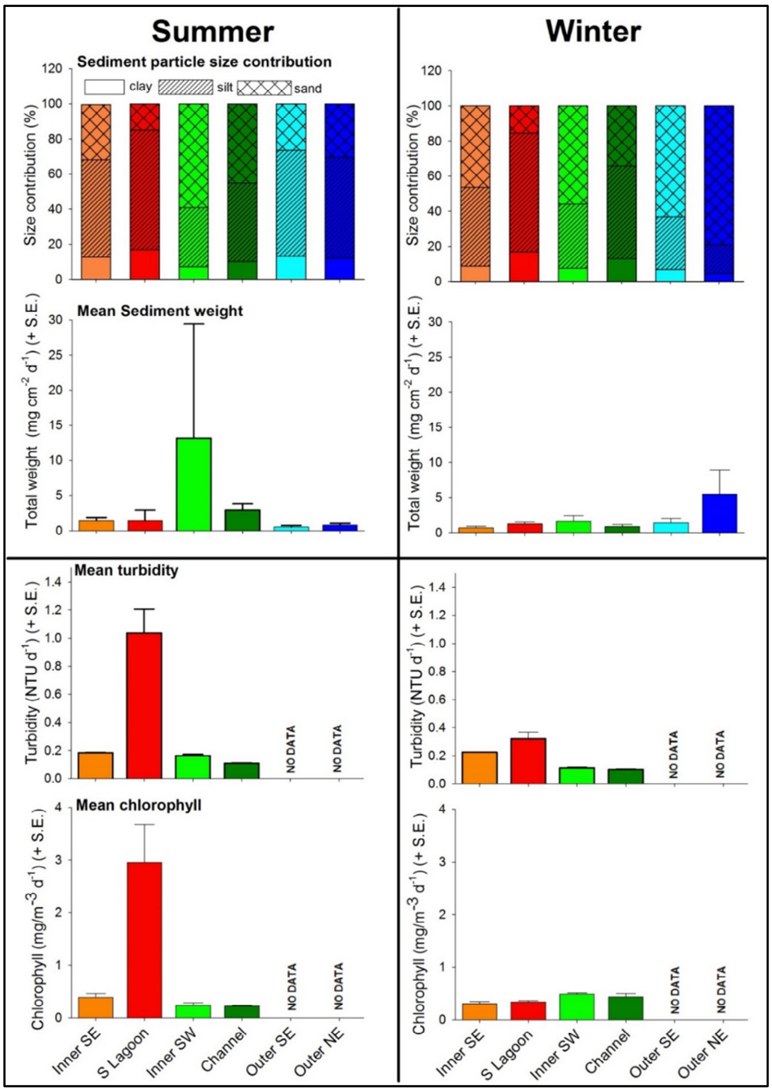


**Figure A 2: (c) Seasonal variation in physical parameters long-term monitoring locations at Scott Reef.**

## Appendix 3

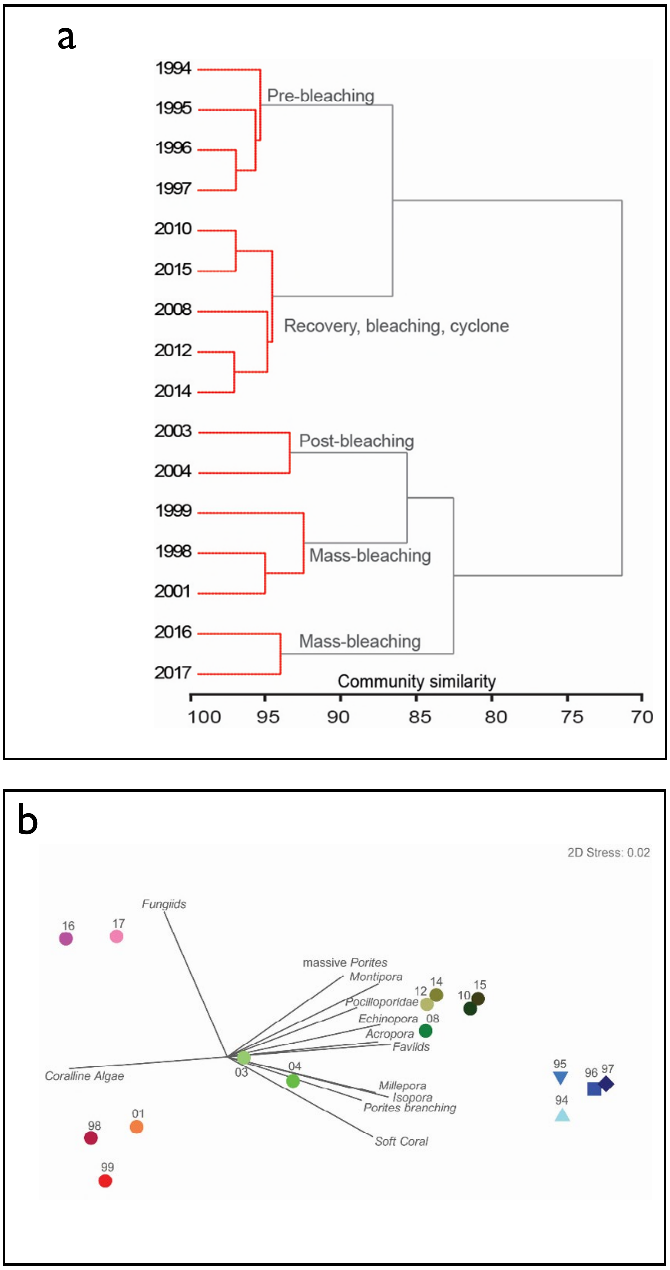


**Figure A 3: Temporal variation in community structure across Scott Reef grouped into five distinct periods, according to the cycles of impact and recovery from multiple disturbances, which were indicative of the state of the reef. a) Dendrogram showing years when coral community structure varied significantly (grey lines) across Scott Reef, according to the SIMPROF procedure at a significance level of 5%. Data are Bray Curtis similarities for Log + 1 transformed percentage cover of benthic groups. (b) Grouping of coral communities among years according to their differences in structure, with vectors indicating which coral groups are most abundant during the nearest years and distinguish communities from other years. Non-metric Multidimensional Scaling of coral community structure, using Bray-Curtis similarities of percentage cover of coral groups (square root transformed) by survey year.**

## Appendix 4

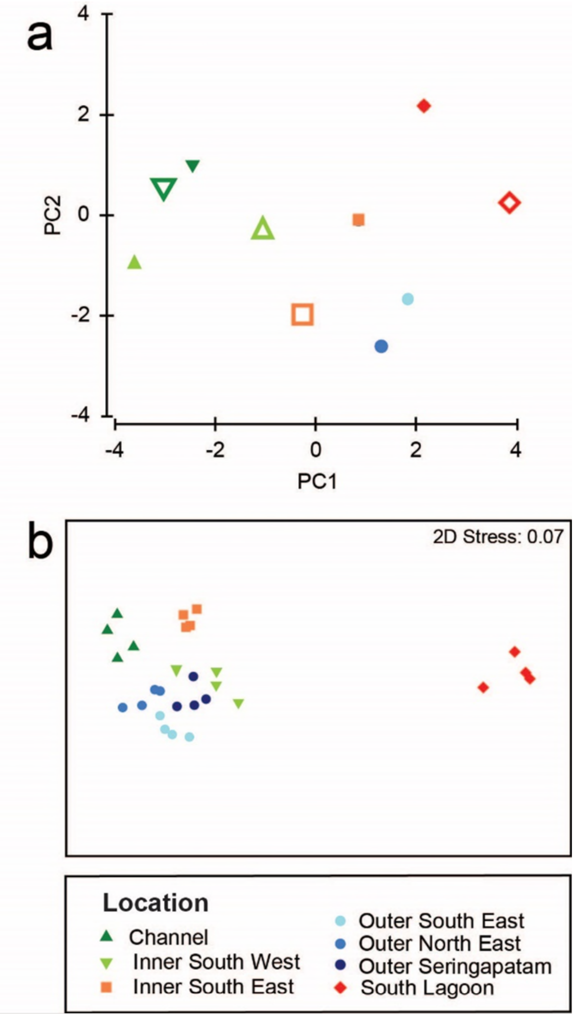


**Figure A 4: Physical conditions varied among locations across Scott Reef and caused comparable variation in coral community structure. (a) Principal Coordinate Analyses showing variation in physical conditions among locations (solid symbols) at North and South Reef, and additional parameters quantified only at the inner slope locations (hollow symbols). Physical conditions and their contribution to differences among location are in Appendix 1 and Appendix 5. (b) Non-metric Multidimensional Scaling, illustrating comparable variation in coral community structure among locations, during pre-bleaching (1994-1997) when the influence of physical conditions was not confounded by severe disturbances. Data are Bray-Curtis similarities of percentage cover of coral groups (square root transformed).**

## Appendix 5

**Table A 5: Variation in habitat conditions among locations at Scott Reef. Results of principal component analysis (PCA) of 10 variables quantified at all locations, and an additional 10 variables quantified at only the inner slope locations. Data for most parameters were first converted to daily averages and divided between summer (sum.) and winter (win.) months. More detailed parameter descriptions are in Table 2. Values indicate the strength of the correlation coefficient for each variable with the eigenvector of each PC. The first principle component (PC1) accounts for most of the variation among locations, and the contribution (positive, negative) of each parameter is ranked below each principle component.**

| **All locations** | | | | **Inner slope locations** | | | |
|---|---|---|---|---|---|---|---|
| Principal Component | Eigenvalue | %Var. | Cum.%Var. | Principal Component | Eigenvalue | %Var. | Cum.%Var. |
| 1 | 6.02 | 60.2 | 60.2 | 1 | 8.24 | 82.4 | 82.4 |
| 2 | 3.17 | 31.7 | 91.9 | 2 | 1.20 | 12.0 | 94.4 |
| 3 | 0.59 | 5.9 | 97.9 | 3 | 0.56 | 5.6 | 100.0 |
| Variable | PC1 | PC2 | PC3 | Variable | PC1 | PC2 | PC3 |
| 1. Sum. temp. range (ºC) | -0.377 | -0.078 | -0.103 | 1. Sum. mean current ($ms^{-1}$) | -0.331 | -0.277 | -0.083 |
| 2. Cover sand (%) | -0.378 | 0.192 | -0.074 | 2. Sum. max current ($ms^{-1}$) | -0.329 | -0.300 | -0.073 |
| 3. Sum. silt (%) | 0.39 | 0.152 | -0.02 | 3. Sum. mean wave (m) | -0.259 | 0.383 | -0.697 |
| 4. Sum. sand (%) | -0.394 | -0.079 | -0.25 | 4. Sum. max wave (m) | -0.346 | -0.054 | -0.114 |
| 5. Sum. course sand (%) | -0.274 | -0.288 | 0.681 | 5. Sum. mean turbidity (NTU) | 0.321 | -0.259 | -0.358 |
| 6. Win. silt (%) | -0.004 | 0.558 | 0.130 | 6. Win. mean turbidity (NTU) | 0.326 | -0.127 | -0.436 |
| 7. Win. sand (%) | -0.068 | -0.551 | -0.038 | 7. Sum. mean chlorophyll (mg $m^{-3}$) | 0.318 | -0.281 | -0.353 |
| 8. Win. Course sand (%) | 0.203 | -0.454 | -0.357 | 8. Win. mean chlorophyll (mg $m^{-3}$) | 0.296 | -0.466 | 0.175 |
| 9. Exposure (wind, wave) | -0.401 | 0.038 | 0.210 | 9. Sum. salinity range (PSU) | -0.306 | -0.435 | -0.016 |
| 10. Cooling (temp. ºC) | -0.356 | 0.151 | -0.517 | 10. Win. salinity range (PSU) | -0.322 | -0.339 | -0.127 |

## Appendix 6

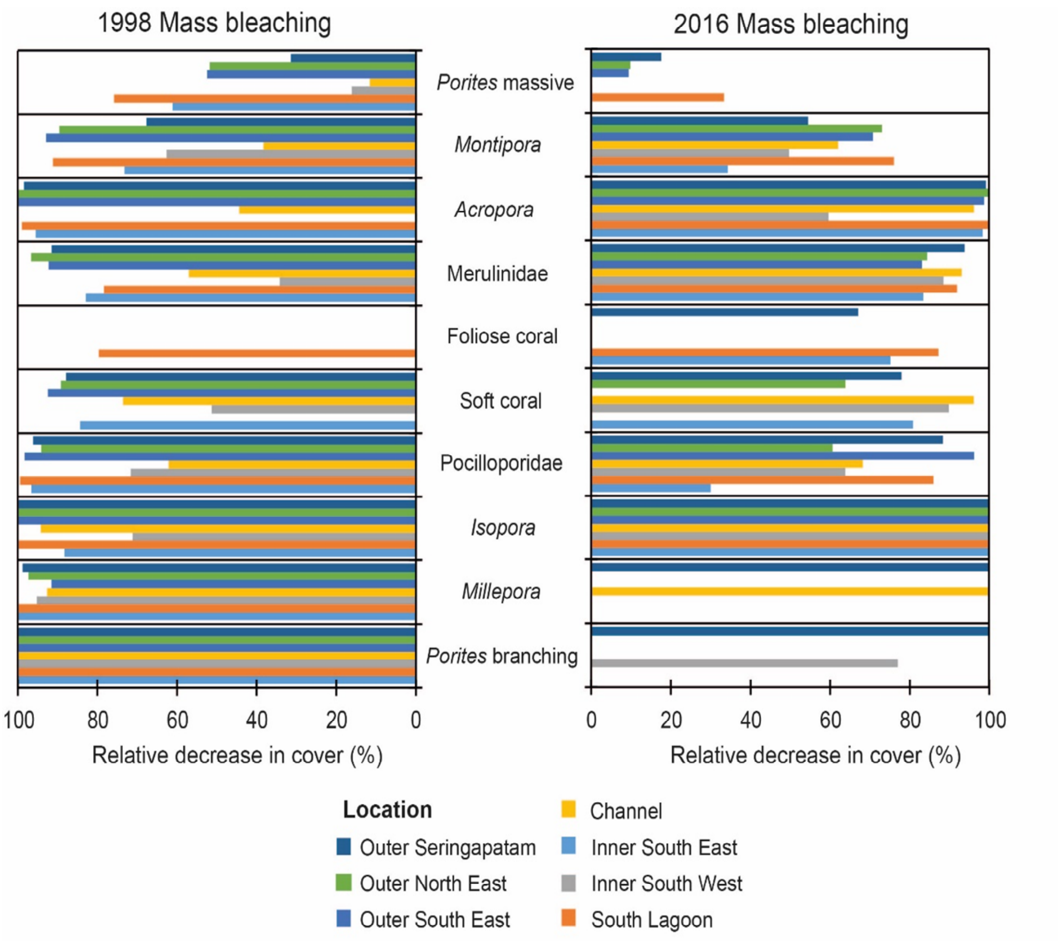


**Figure A 6: The variable impact of mass bleaching in 1998 and 2016 among coral groups and locations at Scott Reef. The mean (± SE) relative decreases (%) in coral cover before (October 1997, January 2016) and after (October 1998, October 2016) mass bleaching in March/April. Coral groups and locations were included only if their mean pre-bleaching cover was > 1%, as estimates of relative change are not accurate for rare corals. Not all coral groups were common (> 1%) at all sites prior to the mass bleaching in 1998 (e.g. Foliose corals), and others were rare prior to the mass bleaching in 2016 because they had not recovered from the 1998 mass bleaching (e.g. *Porites* branching, *Millepora,* Soft Coral). Coral groups are in Table 1 and locations in Figure 1.**

## Appendix 7

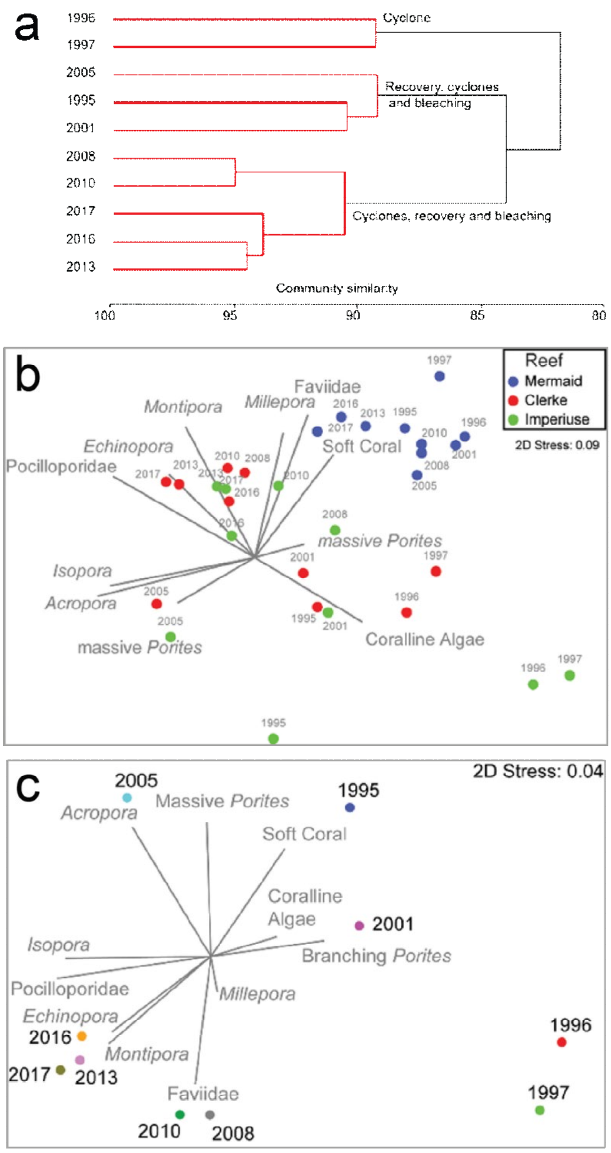


**Figure A 7: Temporal variation in community structure across the Rowley Shoals grouped into three distinct periods, according to the cycles of impact and recovery from multiple disturbances. a) Dendrogram showing years when coral community structure varied significantly (black lines) across Rowley Shoals, according to the SIMPROF procedure at a significance level of 5%. Data are Bray Curtis similarities for Log + 1 transformed percentage cover of benthic groups. The grouping of coral communities among years b) at each reef, and c) averaged across all reefs, according to their differences in structure. Vectors indicate which coral groups are most abundant at the nearest reefs and/or years and distinguish communities from other reefs and/or years. Non-metric Multidimensional Scaling of coral community structure, using Bray-Curtis similarities of percentage cover of coral groups (square root transformed) by survey year.**