The effect of cumulative stress on reef slope coral communities in the far northern and northern Great Barrier Reef: 2012 to 2016

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Contents

Terminology, definitions and abbreviations

Term	Definition
AIMS	The Australian Institute of Marine Science.
Benthic	Living upon or in the seabed.
Benthos	The flora and fauna found on the bottom, or in the bottom sediments, of a sea or lake.
Broadcast spawning	Eggs and sperm are released into the water column where fertilisation occurs externally.
Brooding	Eggs develop to planula larval stage in the gastro vascular cavity of the parent coral polyp.
Convoluted neural networks	A type of feed-forward artificial neural network in which the connectivity pattern between its neurons is inspired by the organisation of the animal visual cortex.
Coral	Marine organisms from the class Anthozoa that exist as small sea anemone-like polyps, typically in colonies of many identical individuals. Includes 'hard corals' within the order Scleractinia which secrete calcium carbonate to form a hard skeleton and form reefs; and 'soft corals' within the order Alcyonacea which have no hard skeleton and are not considered reef-building organisms.
Coral bleaching	The loss of intracellular endosymbionts (*Symbiodinium*, also known as zooxanthellae) from coral either through expulsion or loss of algal pigmentation.
Coral bleaching HotSpot	Region where the sea surface temperature (SST) is currently warmer than the highest climatological monthly mean SST for that location.
Corymbose	Coral growth form: flat-topped flower cluster in which the individual flower stalks grow upward from various points of the main stem to approximately the same height.
COTS	Crown of thorns starfish.
Crustose coralline algae (CCA)	Calcareous algae that can grow in a thin mat over rocks and other hard structures.
Deep learning	A branch of machine learning based on a set of algorithms that attempt to model high level abstractions in data. This is a novel and commonly used approach for automated image classification in computer vision.
DHW	Degree heating weeks (DHW). Accumulated thermal stress, measured as the product of magnitude and duration of sea temperature above the normal summer-peak temperature.
Digitate	Coral growth form: shaped like a spread hand.
Encrusting	Coral growth form: low spreading growth forms that usually adhere to hard rocky surfaces.
GBR	Great Barrier Reef.
GBRMPA	Great Barrier Reef Marine Park Authority.
GCI	The Global Change Institute.
Invertebrates	A group of animals that have no backbone. For example: hard corals, soft corals, clams, and crabs.
IPCC RCP8.5	Intergovernmental Panel on Climate Change, Representative Concentration Pathway 8.5, which represents a high-end emissions scenario or 'business-as-usual scenario'.
Heterogeneity	A measure of diversity.
Hispidose	Coral growth form: shaped like a bottlebrush.
Multivariate	Multiple variables; refers to a form of statistical analysis.
Convolutional neural networks	Neural networks are a computer system modelled on the human brain and nervous system that has the ability to learn to distinguish patterns and shapes. Convolutional neural networks are very similar to ordinary neural networks in that they are made up of neurons that have learnable weights and biases. Each neuron receives some inputs, performs a dot product and optionally follows it with a non-linearity. The whole network expresses a single differentiable score function: from the raw image pixels on one end to class scores at the other.
NOAA	National Oceanic and Atmospheric Administration. Operational section of the US government that focuses on

	weather and related issues.
PCO	Principal Coordinates Analysis.
PERMANOVA	Statistical software program that performs permutational multivariate analysis of variance based on any distance measure, using permutation procedures to obtain P-values for the tests for any balanced multi-factorial ANOVA design.
PRIMER	Statistical software program Plymouth Routines In Multivariate Ecological Research (Version 6.1.11, Primer-E Ltd).
P-value	In statistical hypothesis testing, the probability of obtaining a result at least as extreme as the one that was actually observed, assuming that the null hypothesis is true.
Resilience	The capacity to recover from disturbance or withstand ongoing pressures.
Recruitment	The process by which drifting planulae (tiny coral larvae) attach and establish themselves as members of the reef community.
Sessile	Fixed in one place; immobile.
Spatial	Relating to space.
SST	Sea surface temperature.
Substrate	The surface on which an organism (such as a plant, fungus, or animal) lives.
SVII	Customised diver propulsion vehicle designed by the XL Catlin Seaview Survey.
Tropical cyclone (TC)	Tropical Cyclone. Low-pressure systems that form over warm tropical waters and have gale force winds (sustained winds of 63 km/h or greater and gusts in excess of 90 km/h) near the centre.
Transformation	Parametric statistical tests require that a number of assumptions to be met prior to the analysis. These are that samples are drawn from normally distributed data and that variance among groups is homogenous. Data transformations help to meet these pre-requisites while maintaining the information provided by the data (e.g. patterns).
Turf algae	A broad category including many different forms of small and finely branched 'turf'-like algae.
XL Catlin Seaview Survey	Multidisciplinary survey of the world's coral reefs using innovative technologies to fast-track change and assess broad-scale patterns of coral reefs.
XL Catlin Global Reef Record	A global repository of the data collected by the Xl Catlin Seaview Survey intended to provide a curated archive of coral reef monitoring data, as well as to serve as visualization and data-sharing platform (www.globalreefrecord.org).

Executive Summary

In the recent years, the far northern and northern Great Barrier Reef suffered a category 5 tropical cyclone in 2014 (Ita), a category 4 tropical cyclone in 2015 (Nathan), and a significant coral bleaching event due to an underwater heatwave in 2016. Each of these events had severe implications for the health of coral reefs within the Great Barrier Reef Marine Park.

The Global Change Institute in collaboration with the Department of Environment and Energy undertook a large-scale survey in October 2016 to document the effect of these cumulative impacts on the outer reef slope communities at ~10 m depth in the far northern and northern Great Barrier Reef. The 2016 data was compared to data the Global Change Institute had collected at the same locations and depths in 2012 and 2014 as part of the XL Catlin Seaview Survey – totally 59 transects (~100 km of reef) per survey year. All surveys used imagery collected from a customised diver propelled vehicle and camera system, and the imagery was processed using artificial intelligence based on automated pattern recognition. Changes in coral cover and the abundance and composition of benthic organisms between 2012 and 2016 were evaluated to assess the extent of damage caused by tropical cyclones Ita (2014) and Nathan (2015), and the thermal induced coral bleaching event (2016), as well as to provide an indication of the cumulative impacts of both these recent stressors.

Coral cover on outer reef shelf communities at ~10 m depth in the far northern and northern Great Barrier Reef declined between 2012 and 2016, with an average loss of coral cover relative to the initial 2012 coral cover of ~25%. Between 2012 and 2014, the small losses in coral cover were restricted to sites affected by tropical cyclone Ita, with the highest and most widespread loss in coral cover occurring after the impact of tropical cyclone Nathan and the coral bleaching event between 2014 and 2016 (average 32% loss). In the majority of cases, the losses in coral cover were accompanied by increases in turf algal cover. Hard corals from the families Acroporidae and Poritidae with encrusting morphologies showed the highest mortality, followed by massive colonies from the families Faviidae and Mussidae, and branching and tabular Acroporidae, which is consistent with their published susceptibility to bleaching and robustness to cyclones. The 2016 coral bleaching was the most severe coral bleaching event recorded on the Great Barrier Reef to date and it had the greatest influence on the changes observed in the far northern and northern Great Barrier Reef between 2012 and 2016, when compared to the impacts of tropical cyclones Nathan and Ita alone.

The results of this study, and those from the National Coral Bleaching Taskforce and the Great Barrier Reef Marine Park Authority, have shown that the bleaching and subsequent mortality was not uniform across the Great Barrier Reef Marine Park, and there are numerous reefs throughout the Marine Park that still have abundant live coral cover and diversity. The results also provide important insights into the future of the Great Barrier Reef, given that climate change is considered the greatest long-term threat to the Great Barrier Reef, whereby the frequency of coral bleaching events are predicted to increase in conjunction with the intensity of tropical cyclones as a result of rising ocean temperatures. Adherence to the Paris Climate Agreement, to hold the increase in the global average temperature to well below 2°C above pre-industrial levels and to pursue efforts to limit the temperature increase to 1.5 °C above pre-industrial levels average global surface, is therefore crucial to ensure the long-term sustainability of the Great Barrier Reef and coral reefs worldwide.

1. Introduction

Despite their remarkable persistence in taxonomic composition and diversity over the past 500,000 years (Pandolfi 1999), there has been an unprecedented decline in the distribution and abundance of coral communities worldwide over the past 30 years (e.g. Caribbean - Pandolfi 2002, Pacific - Bruno and Selig 2007, Great Barrier Reef - De'ath et al. 2012). The decline of coral communities has been attributed to local, non-climate change factors such as over-fishing of key ecological functional groups (e.g. herbivores), declining water quality (pollution), and the physical degradation of coral reefs by human activities such as destructive fishing and unsustainable tourism. More recently, climate change from the burning of fossil fuels has joined the list, with most scientists concluding that unrestrained emissions will eliminate coral-dominated ecosystems within the next few decades (Hoegh-Guldberg 1999). By adding carbon dioxide to the atmosphere, physical and chemical aspects of the seawater environment changes (e.g. warmer, less alkaline, stronger storms, increases in sea level - many of which are expected to alter the distribution and abundance of reef-building corals (Hoegh-Guldberg et al. 2007, Hoegh-Guldberg et al. 2014, Hooidonk et al. 2014) and their vulnerability to disease (Maynard et al. 2015a).

These declines have been driven by sequences of individual 'disturbances' (Connell 1997) that occur too frequently in a given location to allow sufficient recovery between events – leading to a loss of resilience (Hughes et al. 2010). At some reefs, this has resulted in a permanent lack of recovery – a 'phase shift' where reefs are no longer dominated by hard coral (Hughes 1994). On Australia's Great Barrier Reef (GBR), field data from the Long Term Monitoring Program from 1985 to 2012 demonstrated that a region-wide trend of falling coral cover was caused by the combination of physical damage from tropical cyclone waves, predation from crown-of-thorns starfish (COTS) and thermal stress from warming oceans (De'ath et al. 2012). Some areas (e.g. central GBR) were more consistently exposed to their combined effects over this time period than others (Maynard et al. 2015b). Although the greatest proportion of coral loss over the recent past was attributed to cyclone waves (De'ath et al. 2012), the recent mass bleaching event on the GBR in 2016 demonstrates that this is likely to change as the climate continues to warm. As that occurs, models indicate that the time between mass bleaching events will decrease until they become an annual occurrence (van Hooidonk et al. 2013).

1.1. Mass coral bleaching and mortality on the Great Barrier Reef

Increasing sea temperatures have been directly linked to the occurrence of coral bleaching (Hoegh-Guldberg 1999), with the mass bleaching events of 1998 and 2005 reported to have had the most severe impact on reefs globally (Oliver et al. 2009). In Western Australia, up to 90% mortality was reported over an area of 10 km^2 that was surveyed at Scott Reef on the edge of the continental shelf (Gilmour et al. 2013) following the 1998 event. Along Australia's GBR, while only about ~5% mortality was reported, bleaching was detected across 1300 km of reef surveyed in 1998 (GBRMPA 2009, Osborne et al. 2011). Similarly, less than 5% mortality was reported across the entire 1300 km stretch of the GBR surveyed (Osborne et al. 2011) following a mass-bleaching event in 2002 (Berkelmans et al. 2004). However, punctuated cases of high mortality (~70%) were reported on certain reefs following these events (Berkelmans et al. 2004, AIMS 2014). Additional localised bleaching events were recorded in 2006 at the Keppel Islands (Diaz-Pulido et al. 2009), and at Lord Howe Island in 2010, which resulted in ~35% and ~25% mortality, respectively (Harrison et al. 2011, AIMS 2014).

As in 1998, strong El Niño in combination with climate change have driven record temperatures worldwide, with 2016 reported to be the hottest year in recorded history. As a result, corals around the world have bleached as part of the third global bleaching event, with anomalous sea temperatures in the GBR region during the 2015-2016 summer resulting in reports of widespread coral bleaching. The National Coral Bleaching Taskforce reported only 7% (68 reefs) of the 911 individual reefs observed during aerial surveys along the full 2300 km length of the GBR had escaped bleaching (ARCCoE 2016).

1.2. Physical damage from tropical cyclone waves

Tropical cyclones (TC) generate extreme winds that, given sufficient fetch and duration, drive heavy seas that can destroy entire reef structures (Done 1992, Fabricius et al. 2008). The spatial distribution of such damage, however, is typically very patchy due to local scale differences in coral vulnerability and exposure (e.g., Beeden et al. 2015). Nonetheless, such damage can be spread across hundreds of kilometres. This is particularly true for strong cyclones that span vast areas (Puotinen et al. 2016), such as category 5 TC Yasi that crossed the GBR in 2011 (Beeden et al. 2015). From 1969 to 2012, the strongest cyclone to affect the northern GBR near Lizard Island was category 3 TC Ivor in 1992 (Done 1992, Puotinen et al. 1997, Puotinen et al. 2016), though category 4 TC Ingrid damaged reefs north of this in Princess Charlotte Bay in 2005 (Fabricius et al. 2008). In 2014 and 2015, two strong cyclones crossed the GBR region: TC Ita (April 2014, category 5) and TC Nathan (March 2015, category 4).

In cases where successive strong cyclones track close to large numbers of coral reefs (e.g TC Hamish in 2009), or are unusually large in size (e.g. TC Yasi in 2011), the combined damage can be spread over

1000s of kilometres of coral reef or related habitat (Cheal et al. 2017). Cyclones like TC Yasi and TC Hamish were rare within recent historic records of cyclones on the GBR. However, recent modelling based on the time series 1985 to 2015 predicts severe cyclone damage to be possible every 5 to 10 years or less at reefs located between Cairns and Mackay (central GBR) and between Cooktown and Princess Charlotte Bay (far northern/northern GBR) (Puotinen et al. 2016), which if true, will have major implications for the resilience of the GBR (Cheal et al. 2017).

On a global scale, most studies support the likelihood of more cyclones reaching the strongest intensities in future due to warmer seas (Lee et al. 2016, Mei and Xie 2016, Walsh et al. 2016), while the total number of cyclones is generally either not expected to change or to decrease slightly (Knutson et al. 2010).

1.3. Cumulative impacts and the importance of robust baseline data

Many disturbances threaten coral reefs (Jackson 1991), with some (most notably coral bleaching) becoming more frequent as the climate warms (Hughes et al. 2003) - meaning that it is becoming increasingly likely that a given coral community may be affected by a new disturbance before recovery from the previous one is complete. Thus, understanding the effect of single stressors such as elevated sea temperature is often difficult without considering the cumulative effects of all relevant disturbances (Hoegh-Guldberg 1999, Hoegh-Guldberg et al. 2007). Addressing cumulative impacts is fundamental to meet the challenges faced by resource managers and policy makers attempting to build resilience and manage coral reefs into the future (Cinner et al. 2016). Robust baseline data is key to understanding the recovery potential of coral reef systems in the face of environmental change.

The capacity to generate rapid, yet detailed and accurate, field data at appropriate scales required by conservation planners and resource managers is limited. Gonzalez-Rivero et al. (2014, 2016) introduced a novel framework for large-scale monitoring of coral reefs using high-definition underwater imagery collected using customised underwater vehicles. Combined with computer vision and machine learning (based on neural networks), this approach enables fast and accurate data analysis of research imagery. Validation of this method indicated that it is highly robust, with most benthic categories being estimated with errors below 4% (González-Rivero et al. 2016). Overall, the framework enables quantitative and geo-referenced outputs of coral reef features such as habitat types, benthic composition, and structural complexity (rugosity) to be generated across multiple kilometre-scale transects with a spatial resolution ranging from 2 to 6 m^2 (González-Rivero et al. 2014).

Using this technology, the Global Change Institute (GCI) in partnership with the XL Catlin Seaview Survey (http://catlinseaviewsurvey.com/) established the most comprehensive baseline of offshore fore-reef environments at ~10 m depth globally. For the GBR, this has enabled assessment of the impacts of cumulative stress over the past four years, and the recovery process for the far northern and northern GBR. The implications for our understanding and insights into the rates of change have profound ramifications for understanding and responding to the impacts of climate change and other stresses.

1.4. Scope of study

From 2012 to 2016, coral reefs in the far northern and northern GBR were damaged by two major cyclones and more recently by the widespread and severe coral bleaching event in March 2016 – potentially damaging the health of what was previously considered a relatively 'pristine' section of the GBR (e.g., Maynard et al. 2015b) - due to the reduced influence of land-based stresses such as nutrients and sediments, and the influence of the clear oceanic waters that flow over the outer reef slopes lining the most outer edge of the GBR. Based on reports of extensive coral bleaching in 2016, the GCI entered into collaboration with the Department of the Environment and Energy (DoEE) under contract to undertake a repeat survey of the sites sampled by the XL Catlin Seaview Survey in 2012 and 2014. The partners in this study were interested in understanding measuring the impact of these stresses (either singularly or in combination with each other) as well as the potential for the new technology to undertake intensive, rapid, detailed, repeatable and robust analyses of how coral reefs are changing in response to rising stresses in recent years.

This report addresses six key research questions for the far northern and northern sections of the GBR from 2012 to 2016:

1. What were the spatial and temporal patterns of disturbance between 2012 and 2016?
2. What were the temporal and spatial changes to coral cover?
3. How did benthic assemblages change over time and space?
4. Did the disturbances affect all reef-building corals equally?
5. How did other benthic organisms respond to the disturbances?
6. Given the geographical variability of the recorded disturbances, can the individual and combined the effects of cyclones and increased sea temperatures be partitioned as drivers of coral loss?

Detailed quantitative ecological assessments of cumulative impacts are scarce, and the data provided in this report robustly documents changes in coral cover, community composition and reef mortality, which has allowed assessment of cumulative impacts across a broad spatial scale on outer reef shelf communities in the far northern and northern GBR, as well as providing a solid baseline from which to assess reef recovery.

2. Methods

2.1. Environmental data

2.1.1. Thermal stress

Sea surface temperatures (SST), and Degree Heating Weeks (DHWs) were obtained for 1 January 2013 to 30 June 2016 for the northern sections of the GBR from Coral Reef Watch (NOAA 2016). These products are generated daily with a spatial resolution of 0.25-degree (~25 km). Corals are sensitive to an accumulation of thermal stress over time (Hoegh-Guldberg and Smith 1989, Glynn and D'croz 1990, Strong et al. 1997). In order to monitor this cumulative effect, a thermal stress index called Coral Bleaching Degree Heating Week (DHW) was developed by the NOAA Coral Reef Watch in 2000 (Liu et al. 2004). DHW is derived from the Coral Bleaching HotSpot product that provides an instantaneous measure of thermal stress and highlights regions in which the SST is currently warmer than the highest climatological monthly mean SST for that location. The HotSpot value of 1.0°C is a threshold for thermal stress to begin to accumulate, leading to coral bleaching.

Mass coral bleaching is caused by prolonged periods of thermal stress and the DHW product accumulates any HotSpots greater than 1°C over a 12-week window, thus indicating how stressful conditions have been for corals in the last three months. It is therefore a cumulative measurement of the intensity and duration of thermal stress, where DHW >= 4 ^{o}C-weeks has been shown to cause significant coral bleaching, and DHW >= 8 ^{o}C-weeks has been shown to cause widespread bleaching and mortality (Eakin et al. 2010). While, the response of coral reef organisms to thermal stress can be variable and taxa specific (Marshall and Baird 2000), here we consider DHW >= 4 ^{o}C-weeks to indicate thermal stress.

2.1.2. Cyclone impacts

Prior studies often assume that cyclone damage occurs within a threshold distance of the cyclone track, with damage occurring increasingly further from the track as cyclone intensity rises. However, recent work using extensive field data from seven cyclones on the GBR shows that this fails to fully capture the spread of severe damage from cyclones, particularly if they are small or large in size, or long lasting near reefs (Puotinen et al. 2016). As such, we used the 4MW model (Graham et al. 2015), which predicts if and where a sea state capable of damaging most vulnerable reefs was possible during a given cyclone, based on the duration of cyclone winds of various speeds and estimates of fetch.

The 4MW model defines an *a priori* threshold of sea state capable of damaging reefs. The threshold is reached when the highest one-third of wave heights in a region over a sustained period of high winds are 4 m or greater (significant wave height; a very rough sea state, shown to move large reef blocks) with a maximum wave height of ~10 m. Severe damage to vulnerable coral communities is assumed to be possible when the threshold is reached or exceeded for at least one hour. In essence, the 4MW model provides the same enhanced capability to assess and respond to tropical cyclone impacts on coral reefs as the 5-km Hotspot and DHW products of NOAA Coral Reef Watch provide for responding to coral bleaching. As with the NOAA products, the 4MW predictions represent the potential for damage, recognising that actual damage will invariably be patchily distributed due to spatial variability in coral reef exposure and vulnerability (Puotinen et al. 2016).

2.2. Ecological data

2.2.1. Survey locations

A total of 59 transects (~1.8 km in length) across 27 reefs were surveyed in 2012 as part of the XL Catlin Seaview Survey 'global baseline' (Figure 2.1. The reef habitats surveyed were offshore fore-reef environments within a gradient of wave exposure. A subset of these transects was resurveyed in November 2014, following the impact of category 5 TC Ita and again in October-November 2016 after the mass coral bleaching event in March 2016 (Table 2.1). On both occasions transects were surveyed using the same methodology as in the 2012 baseline. Data was extracted from over 140,000 images and around 100 km of reef repeatedly surveyed across the outer GBR (Table 2.1), and can be accessed through the global repository, the XL Catlin Global Record (www.globalreefrecord.org).

2.2.2. Benthic survey method

A custom designed diver propelled vehicle and camera system (SVII; Figure 2.2) consisting of three synchronised Cannon 5D-MkII cameras were used to survey the fore-reef habitats at the 49 transects in the far northern and northern GBR. Images (21 Mp resolution) were collected every three seconds (~ every 2 m) following a linear transect (averaging 1.8 km in length) along the 10 m depth contour. All images were geo-referenced using a surface GPS unit tethered to a diver. Depth and altitude of the camera relative to the surface and the reef substrate were logged at half-second intervals using a Micron Tritech transponder (altitude) and pressure sensor (depth) – allowing for the selection of imagery within a particular depth and altitude range (9 to 10 m depth and 0.5 to 2 m altitude) needed to maintain consistency and address variable environmental conditions, as well as ensuring a spatial resolution for each image of ~10 pixels cm^{-1}, which facilitates the images to be cropped to standardised $1m^2$-photo-quadrats. Full details are provided in Gonzalez-Rivero et al. (2014, 2016).

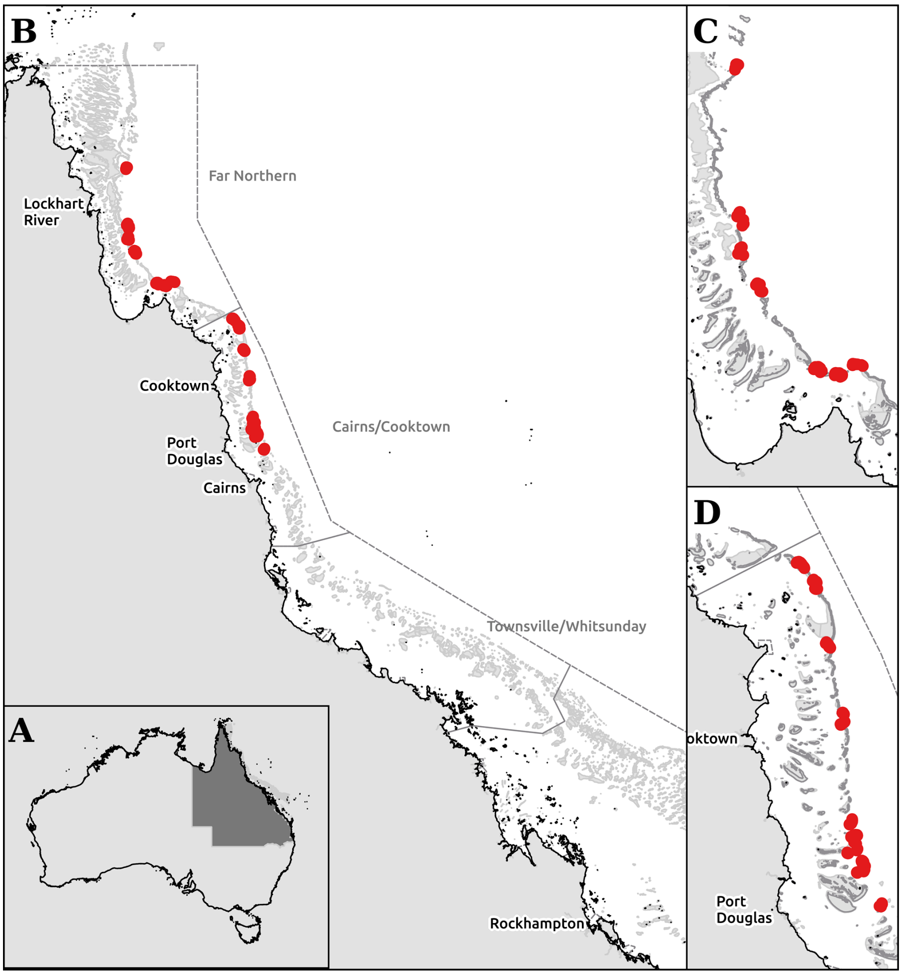


Figure 2.1. Locations surveyed by the XL Catlin Seaview Survey (2012, 2014) and this survey in the far northern and northern sections of the Great Barrier Reef (2016). Polygons delineate four management regions within the Great Barrier Reef Marine Park (B). In the report, studied regions are named as follow: Far Northern (C, Far Northern management zone) and Northern (D, Cairns/Cooktown management zone).

Table 2.1. List of reefs, number of transects, coordinates and years surveyed. (x = surveyed).

Region	Reef Name	Number of transects	Latitude	Longitude	2012	2014	2016
Far northern	Saunders Reef	3	-11.478	144.058	x	x	
	Great Detached	5	-11.749	144.04	x	x	
	Wishbone Reef	2	-12.049	143.934	x		
	Mantis Reef	2	-12.219	143.938	x		x
	Tijou Reef	5	-13.127	143.963	x	x	x
	13040 Reef	1	-13.284	143.951	x		x
	13050 Reef	1	-13.293	143.972	x		x
	13074 Reef	2	-13.467	144.062	x		x
	13116 Reef	1	-13.505	144.08	x		x
	14034 Reef	3	-13.923	144.629	x	x	x
	Wilson Reef	3	-13.947	144.405	x	x	x
	Tiedemann Reef	3	-13.977	144.52	x		x
Northern	Day Reef	3	-14.484	145.541	x	x	x
	Yonge Reef	3	-14.596	145.624	x	x	x
	Ribbon Reef 10		-14.664	145.666	x	x	
	14152 Reef	1	-14.933	145.689	x	x	x
	14153 Reef	1	-14.943	145.698	x	x	x
	Ribbon Reef 9	1	-14.958	145.707	x	x	x
	Ribbon Reef 5	2	-15.363	145.785	x	x	x
	15041 Reef	1	-15.399	145.771	x		x
	Agincourt Reef 4	2	-15.957	145.83	x	x	x
	Agincourt Reef 2b	1	-16.032	145.86	x	x	x
	Agincourt Reef 5	2	-16.04	145.836	x	x	x
	St. Crispin Reef	3	-16.108	145.842	x	x	x
	North Opal Reef	3	-16.185	145.895	x	x	x
	Opal Reef	3	-16.226	145.892	x		x
	Norman Reef	2	-16.431	146	x		x
Total number of transects					**59**	**41**	**49**
Total surveyed distance (km)					**106.2**	**73.8**	**88.2**
Total number of images analysed					**57,400**	**30,600**	**53,400**

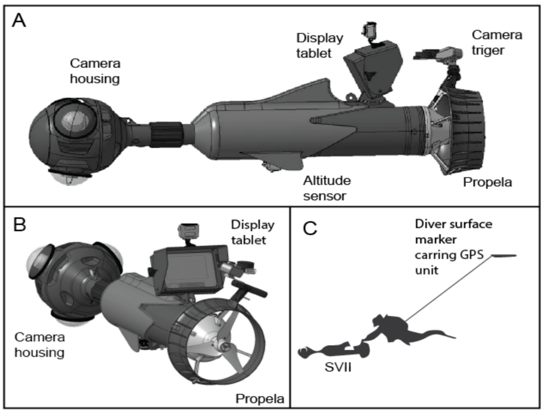


Figure 2.2. Schematic diagram of the customised diver propulsion vehicle (SVII) designed to gather benthic imagery of coral reefs. A) Lateral view of SVII illustrating the main components. B) Rear view of SVII where the display unit can be seen in detail. The propulsion unit allows conducting the surveys across nearly 2 km every 45 minutes. A display tablet allows the operator diver to adjust camera settings during the transect survey. Cameras are triggered using an automatic interval meter set to take images every 3 seconds. An altitude sensor on board SVII provides information regarding the distance from the substrate to the cameras, used to estimate the footprint area of each image. C) Schematic drawing to illustrate that while the diver controls the equipment underwater, a GPS unit is being tethered to the surface, capturing information to spatially reference each image.

2.2.3. Image analysis

A label set of 19 functional categories (Table 2.2) that was consistent with the 2012 and 2014 surveys was used (González-Rivero et al. 2016). These categories were chosen for their functional relevance to coral reef ecosystems and their ability to be reliably identified from images by human annotators. Four broad groups represent the main benthic components of coral reefs in the GBR: 'Hard Corals', 'Soft Corals', 'Algae', and 'Other Benthos'. Hard corals comprise eleven functional groups classified based on a combination of taxonomy (i.e. family) and colony shape (i.e. branching, massive, encrusting, plating, and tabular). These groups were derived, modified and simplified from existing classification schemes. Soft corals are classified by three main functional groups: 1) Alcyoniidae soft corals; 2) Sea fans and plumes from the family Gorgoniidae; and 3) Other soft corals. The main algae groups are classified according to their functional relevance: 1) Crustose coralline algae; 2) Macroalgae; and 3) Turf algae. The latter is considered a grazed assemblage of algae species of up to 1 cm in height. The remaining group, categorised as 'Other Benthos', consists of sand and other benthic invertebrates.

Manual image annotations using the 19 benthic categories were conducted using point-sampling methods (Coral Point Count Method) on a randomly selected subset. The training images were annotated at 100-point locations per image using CoralNet (http://coralnet.ucsd.edu/), where the substrate beneath each point was identified to one of the 19 categories. These manual annotations were used as calibration datasets to train the machine-learning algorithm for automated image annotation. A machine-learning framework, known as Deep Learning, was used to automatically classify or identify benthic substrate categories from images based on the training dataset provided by human annotators. Deep Learning is a branch of machine learning based on a set of algorithms within a convoluted neural network framework that attempt to model high-level abstractions in data using the human brain and nervous system as an example. These methods have dramatically improved the state-of-the-art in speech recognition, visual object recognition, object detection and many other domains such as drug discovery and genomics (LeCun et al. 2015), and more recently, marine sciences (Mahmood et al. 2016). The framework employs a number of convoluted filters (224 x 224 pixel regions around each point) that comprise attributes of texture and colour to identify the parameter space that best describe each of the benthic categories, based on the manual annotation dataset. Based on these filters, a weighted neural network architecture is built and optimised through numerous iterations, that allow predicting and assigning a label to each point in an image in microseconds (< 0.2 sec/50 points). While the automated annotation method can technically annotate every single pixel in every single remaining image, we followed the standard point sampling protocol of 50 randomly selected points per image to ensure straight-forward comparisons to percentage cover estimates from the human annotations, and because studies indicate that the estimation error is small if the number of points per image is sufficiently large (> 10 points per image).

Table 2.2. Label set defining of the benthic categories employed for the classification of coral reef benthos on the Great Barrier Reef.

Group	Short Name	Taxonomic Description	Overall functional attributes
Hard Coral	Acr. branching	Family Acroporidae, branching morphology (excluding hispidose type branching).	Major reef framework builders. Competitive life-history strategy: fast growing species, spawning reproduction, high susceptibility to thermal stress (bleaching) and wave action. Provide habitat to a range of other reef dwelling species.
	Acr. hispidose	Family Acroporidae, hispidose morphology	Competitive life-history strategy: fast growing species, spawning reproduction, high susceptibility to thermal stress (bleaching) and wave action.
	Acr. other	Other corals from the family Acroporidae (e.g. *Isopora*)	Brooding reproduction, severe/high susceptibility to thermal stress, and low/moderate susceptibility to wave action.
	Acr. encrusting	Family Acroporidae, thin plate and encrusting morphologies	Major reef framework builders. Competitive and generalist life-history strategies: fast/moderate growth rates, spawning reproduction, high/severe susceptibility to thermal stress, moderate to low susceptibility to wave action.
	Acr. tabular	Family Acroporidae, table, corymbose and digitate morphologies	Major reef framework builders. Competitive life-history strategy: fast growing species, spawning reproduction, high/severe susceptibility to thermal stress (bleaching), and high to low susceptibility to wave action. High to moderate susceptibility to disease outbreaks. Largely contribute to reef structural complexity.
	Massive meandroid	Families Favidae and Mussidae, massive and meandroid morphologies	Major reef framework builders. Stress-tolerant life history: slow-growing species, spawning reproduction, moderate susceptibility to thermal stress, and low susceptibility to wave action.
	Other corals	Other hard coral including all other groups not represented by the other coral categories of this label set.	Mixed attributes. Low/moderate susceptibility to thermal stress.
	Pocilloporidae	Family Pocilloporidae	Reef framework builders. Competitive and weedy life-history strategies: early colonisers in reef succession trajectories, fast growing species, brooding reproduction, highly susceptible to thermal stress, but moderate resistant to wave action. High prevalence of coral diseases.
	Por. branching	Family Poritidae, branching morphology	Weedy life-history strategy: spawning reproduction, high/moderate susceptibility to thermal stress.
	Por. encrusting	Family Poritidae, encrusting morphology	Brooding reproduction. Low/moderate susceptible to thermal stress.
	Por. massive	Family Poritidae, massive morphology	Major reef framework builders. Stress-tolerant life history: slow-growing species, spawning reproduction, low/moderate susceptibility to thermal stress, and low susceptibility to wave action.
Algae	CCA	Crustose Coralline Algae	Major reef framework builders and cementers. Provide key contribution to coral reef primary production. Facilitation of coral recruitment.
	Macroalgae	Macroalgae. All genera.	Key contribution to coral reef primary production. Provide food source and habitat to a range of other reef dwelling species. Critical role during phase shifts.
	Turf	Multi-specific algal assemblage of 1cm or less in height	Provide key contribution to coral reef primary production. Nitrogen fixation. Provide food source and habitat to a range of other reef dwelling species.
Other Benthos	Sand	Unconsolidated reef sediment	N/A
	Other Invert.	Other sessile invertebrates	Mixed attributes. This includes fire corals (*Millepora* spp), Ascidians, sessile invertebrates, excluding hard and soft corals)
Soft Coral	Alc. Soft coral	Soft coral, family Alcyoniidae, genera *Lobophytum* and *Sarcophytum*.	An important contributor to reef's structural complexity and biodiversity, providing habitat to a range of other reef dwelling species. Slow-growing and suspension feeders. Spawning and asexual propagation. Deplete large amounts of suspended particulate matter.
	Gorg. Soft coral	Sea fans and plumes	Provide habitat to a range of other reef dwelling species. Spawning and brooding reproduction. Suspension feeders.
	Other Soft coral	Other Soft corals	Mixed attributes.

2.2.4. Assessment of change

Changes in coral cover and the abundance and composition of benthic organisms between 2012 and 2016 were evaluated to assess the extent of damage caused by TC Ita in 2014, TC Nathan in 2015, and the thermal induced coral bleaching in 2016, as well as to provide an indication of the cumulative impacts of both these recent stressors.

In order to assess changes in community composition across time and space, and in a replicable and predictable fashion, a minimum sampling unit within the kilometre-scale transects was established using data collected from the surveys: sub-transects of 100 m in length and 4 m width within each ~2 km transect. The size of these sampling units or sub-transects was chosen to account for typical size at which benthic communities aggregate in the GBR and Coral Sea in order to maximise adequate representation of community assemblages and thus predictability across space (Gonzalez-Rivero et al. 2016). To estimate changes in the composition of benthic communities over time, estimated abundance (% cover) for each benthic category (Table 2.2) for all images contained within each sub-transect was averaged per survey year, and compared to other surveyed years. Each sub-transect represents a delineated area within each transect. Sub-transects are placed consecutively along the two-kilometre survey transect, summing up to about 20 sampling units per transect.

Because initial abundance of benthic organisms can heavily influence the observed effect of disturbances (McClanahan et al. 2007), changes in coral cover (*ΔC*) were measured as the difference in cover (C) between two periods (*a* and *b*), relative to the initial cover (*a*) (Equation 1).

$$\Delta C = \frac{(C_b - C_a)}{Ca} \cdot 100 \qquad \text{(Equation 1)}$$

In contrast to coral cover, Log Ratio was used as a measure of change for comparisons among and within functional groups due to high variance inflation of relative differences within rare or less abundant organisms. Log Ratio (*lr*) is calculated by the natural logarithm of ratio of cover for a given label or benthic category (C) for a given sub-transect between two survey periods (*a* and *b*) (Equation 2). Due to the scaled nature of the Log Ratio, it can be used as a more transparent metric of size effect to compare changes among benthic categories.

$$lr = \log\left(\frac{C_b}{C_a}\right) \qquad \text{(Equation 2)}$$

2.3. Statistical analyses

The independent and cumulative effect of disturbance on the observed spatial patterns of coral loss was evaluated using a linear multiple regression model. Linear regression is one of the most widely used statistical analyses for studying the relationship between a dependent variable and one or more explanatory variables. This model considered the zone of impact for each disturbance (explanatory variables) and evaluated their effect on changes in coral cover over time (dependent variable).

For the thermal stress, accumulated DHW of at least 4 ^{o}C-weeks were used to define the zone of impact. In the case of TC Ita (2014) and TC Nathan (2015), zones of impact were defined where the 4MW model threshold sea state was met for at least 12 hours. Changes in coral cover were considered separately for three different periods to isolate the effect and evaluate the interaction of disturbances: a) 2012-2014 (TC Ita), b) 2014-2016 (TC Nathan and coral bleaching), and c) 2012-2016 (cumulative impact of all three disturbances). Spatial heterogeneity and temporal autocorrelation, given the repeated measurements of the same sub-transects over time, were accounted for in a spatially nested mixed-effect regression model where the identity of each sub-transect was explicitly nested within transects within the random effect.

Log Ratio was used as a metric of change in order to account for variance inflation by evaluating the relative change of proportions and thus normalise the distribution and homogenise the variance of residuals in the model. Log Ratio was scaled and centred to zero prior to the analysis in order to use the regression coefficients as a better indication of the size of the effect attributed to each disturbance. This allowed us to infer the relative importance of each disturbance and their interaction in explaining the observed changes in coral cover. All analyses were conducted within R environment (R core team, version 3.2.3).

Spatial and temporal changes in benthic composition over time and across space were evaluated using a multivariate analysis of variance. This statistical analysis, similar to the regression analysis, evaluates the relationship between dependent and explanatory variables, with the difference that this approach tests differences among groups of multiple response variables (e.g. composition of benthic groups). In this case, we used a non-parametric approach (PERMANOVA) to account for the variable distribution of the response variables. Using the benthic categories described in Table 2.2, the benthic composition was compared among disturbance zones and time periods using PERMANOVA based on resemblance matrix using the Bray–Curtis similarity measure (Anderson 2008). The model included the effect of disturbance zones (a fixed effect), sites (a random effect) as a nested factor within disturbance zones, and time (2012, 2014 and 2016).

Ordination by principal coordinates (PCO) based on a resemblance matrix (Bray–Curtis similarity) was used to visualise dissimilarities in benthic composition among sites and temporal trajectories for each site, where similar sites or temporal stability for a site in terms of benthic composition will be spatially represented closer in the resulting plot (ordination space). Functional groups or functional categories characterising the sites were determined by Spearman correlations and then superimposed (vector overlay) on the ordination space. The PCO plot and the vector overlay therefore illustrate the relationship between community composition and the spatial and temporal patterns of the sites. Prior to analyses, percentage cover per benthic category was square root transformed to contribute to variance homogenization among groups. Analyses were conducted using PERMANOVA+ for PRIMER v6.

3. Results

3.1. Research question 1: Spatial and temporal patterns of disturbance between 2012 and 2016

Between 2012 and 2016, coral reefs in the far northern and northern GBR were impacted by TC Ita (2014), TC Nathan (2015), and by a severe coral bleaching event in March 2016 (Figure 3.1). Over 100 km of coral reefs in this section were surveyed in three different years at an unprecedented level of detail (i.e. centimetre resolution across 100 km).

3.1.1. Thermal stress

Anomalously high and sustained SSTs triggered the mass coral-bleaching event in the far northern GBR in early 2016 (Figure 3.1). SSTs were elevated above the NOAA Coral Reef Watch (http://coralreefwatch.noaa.gov) bleaching threshold for an extended period in early 2016 in the far northern section of the GBR and to a lesser extent in the northern section (Figure 3.1). Overall, 91% of the reefs in the north and far northern GBR were affected by at least 4 ^{o}C-weeks (Figure 3.2). Most of the far northern section accumulated between 4 to 8 ^{o}C-weeks, with some areas reaching up to 17.4 ^{o}C-weeks (Figure 3.2). Substantial portions of the northern section also experienced thermal stress of between 4 to 8 ^{o}C-weeks, with only a few areas reaching 10 ^{o}C-weeks (Figure 3.2).

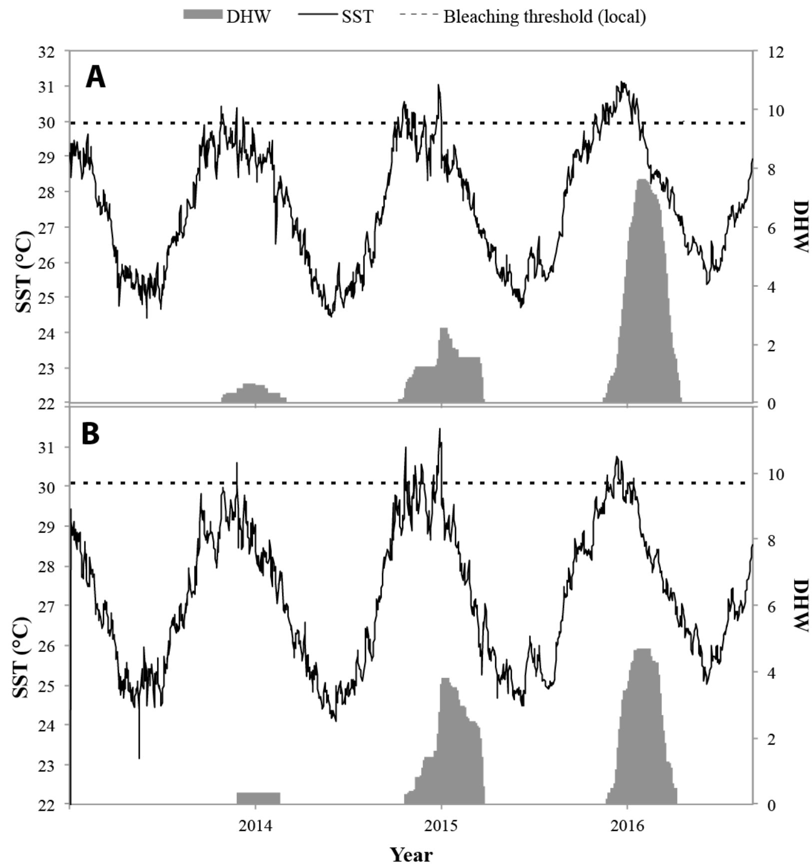


Figure 3.1. Seasonal variations in sea surface temperatures (SST, black continuous line) and cumulated Degree Heating Weeks (DHW, grey bars) for A) far northern and B) northern GBR between 2013 and 2016. Local temperature threshold, over which temperatures are considered anomalies and likely to induce coral bleaching, is represented by the horizontal dashed line. Data obtained from NOAA Coral Reef Watch.

3.1.2. Cyclone impacts

Catastrophic damage to vulnerable coral colonies was predicted to be possible within the zone of estimated 'very rough sea state' characterised by the potential for significant wave heights of 4 m or greater, using the 4MW wind model for TC Ita and TC Nathan (Figure 3.2). Within these zones, 1/3 of waves were predicted to be higher than 4 m, with an estimated maximum wave height of ~10 m.

TC Ita (category 5, April 2014) reached sustained winds of up to 220 km.h^{-1}, making it the second strongest tropical storm in the past decade to cross the GBR after TC Yasi (Figure 3.2). Seas capable of damaging the most vulnerable coral colonies were possible for up to 18 hours and for a threshold duration of 12 hours or more (dark pink to red – Figure 3.2-A).

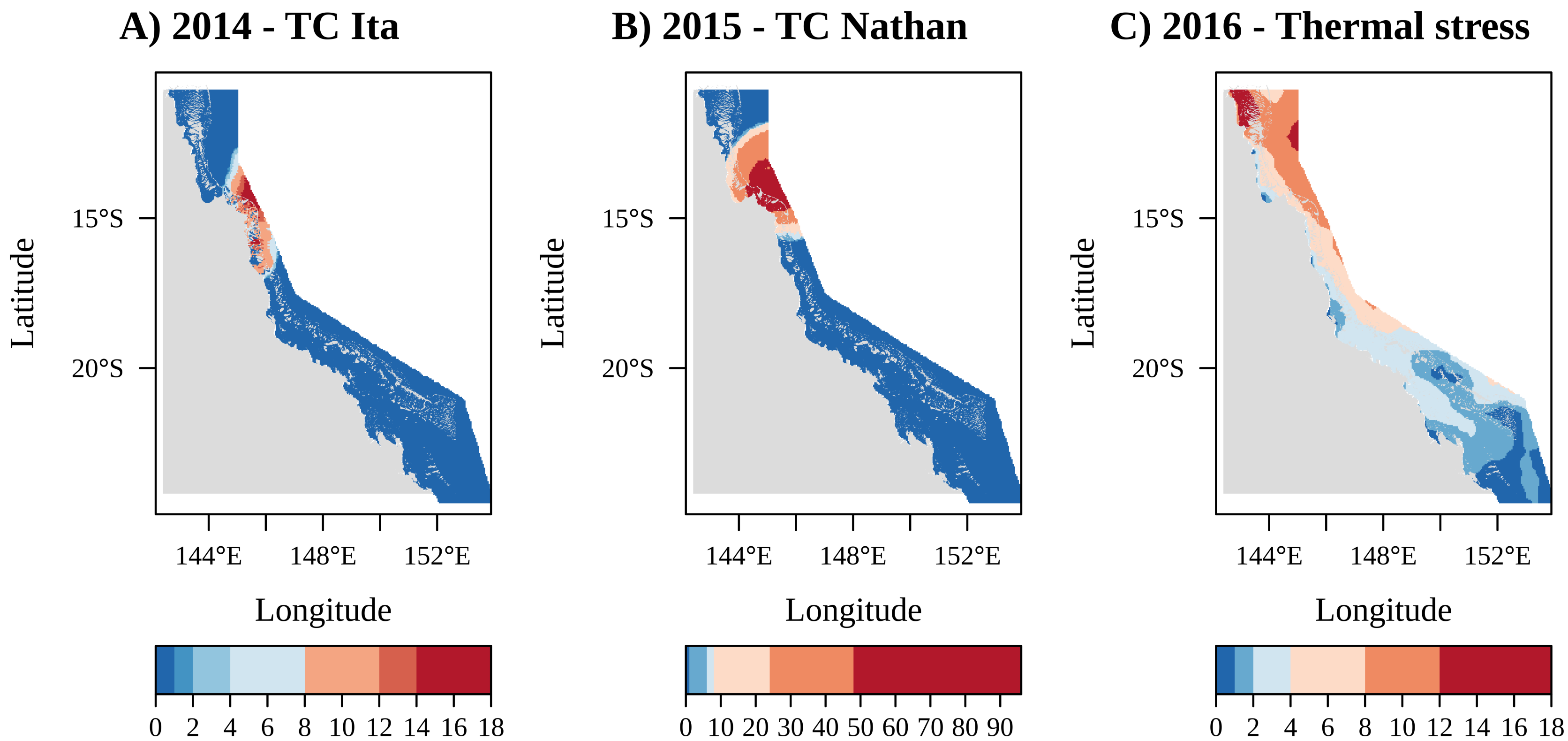


Figure 3.1. Spatial and temporal patterns of environmental disturbances on the Great Barrier Reef between 2012 and 206: A) TC Ita in 2014; B) TC Nathan in 2015 and; C) Thermal stress in 2016. Warm colours (reds) indicate regions where disturbance intensity posed moderate to very high impact on coral reef communities. In the case of cyclones (A and B), the intensity of disturbance was measured by exposure (hours) to very rough seas generated by gale force winds (4MW output). Degree Heating Weeks (DHW) as a cumulative metric of intensity (thermal anomaly) and exposure time (number of weeks) measures the intensity of disturbance generated by the thermal stress. DHW < DHW (blue) are associated with limited coral bleaching, between 4 to 8 DHW (light orange) are expected to cause significant coral bleaching, and values > 8 DHW (orange and red) are expected to cause widespread bleaching and mortality.

TC Nathan (category 4, March 2015) reached sustained winds of up to 201 $km.h^{-1}$, making landfall between Cape Melville and Cape Flattery (Figure 3.2). Seas capable of damaging the most vulnerable corals colonies during TC Nathan were predicted more than 5 times longer than TC Ita (> 90 hours). This was due to TC Nathan moving slowly near reefs and following a track that looped around near reefs (Figure 3.2-B).

3.2. Research question 2: Spatial and temporal patterns of coral loss

Coral cover on outer reef shelf communities at ~10 m depth in the far northern and northern GBR declined between 2012 and 2016, with an average loss of coral cover relative to the initial 2012 coral cover of ~25%. The highest and most widespread loss in coral cover occurred after the impact of TC Nathan and the coral bleaching event between 2014 and 2016 (average ~32% loss) (Figure 3.3). During this time, the majority of the reefs (90% of the sub-transects) showed a loss in coral cover – with the remaining 10% of the reefs showed no change or even an increase in coral cover (Figure 3.4). Although generalised across the region, the pattern of coral loss between 2014 and 2016 appears to follow, to a certain extent, the spatially heterogeneous pattern of exposure to thermal stress (i.e. DHW), which does not follow a completely consistent north to south gradient within the far northern and northern sectors of the GBR (Figure 3.2). Interestingly, coral cover on outer reef shelf communities at ~10 m depth in the far northern and northern GBR showed little change between 2012 and 2014, with the exception of sites affected by TC Ita (Figure 3.3). As such, the spatial and temporal patterns of change in coral cover appear to be associated with the delineated regions of expected impact caused by all three disturbances – and accentuated by cumulative disturbances (Figure 3.3).

3.3. Research questions 3, 4 and 5: Spatial and temporal changes in the composition of benthic communities

Significant changes in the composition of benthic assemblages were detected across outer reef shelf communities at ~10 m depth in the far northern and northern GBR between 2012 and 2016, with multivariate comparisons showing that the observed changes were location specific and also consistently different among years. The PERMANOVA (designed to compare changes community composition over time and among regions of impact by different disturbances) showed that there was a significant interaction between Transect, Disturbance and Year, indicating that the benthic composition of transects within the disturbance area changed over time (Table 3.1).

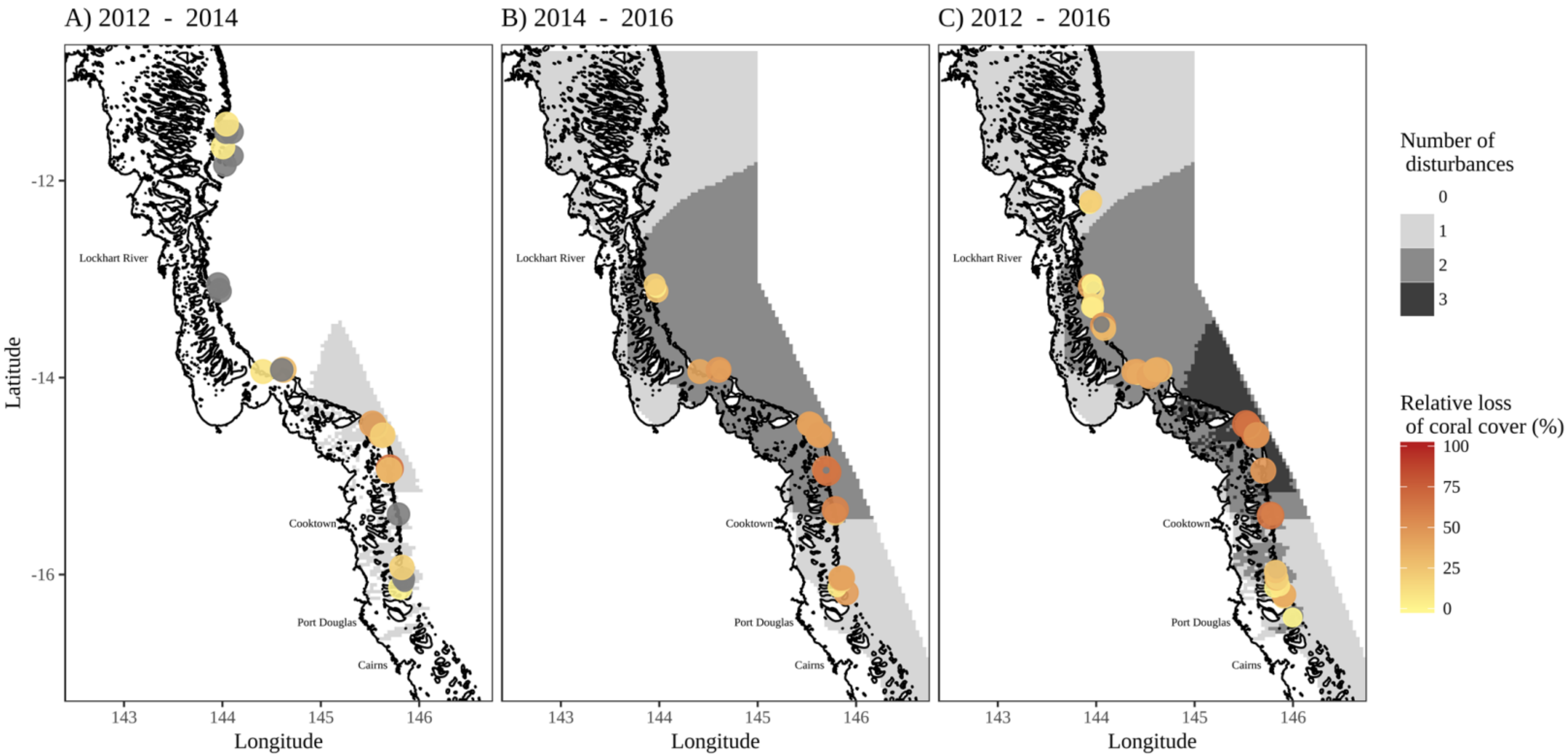


Figure 3.3. Patterns of coral cover over three periods, relative to existing coral cover at the beginning of each period: A) After TC Ita, B) After TC Nathan and the 2016 thermal stress, and C) After the cumulative impact of all three disturbances. Average coral cover loss is represented by the size and colour or points on the map, where larger points and warmer colours indicate a higher loss of coral cover. Note: grey circles indicate either no change or increase in coral cover.

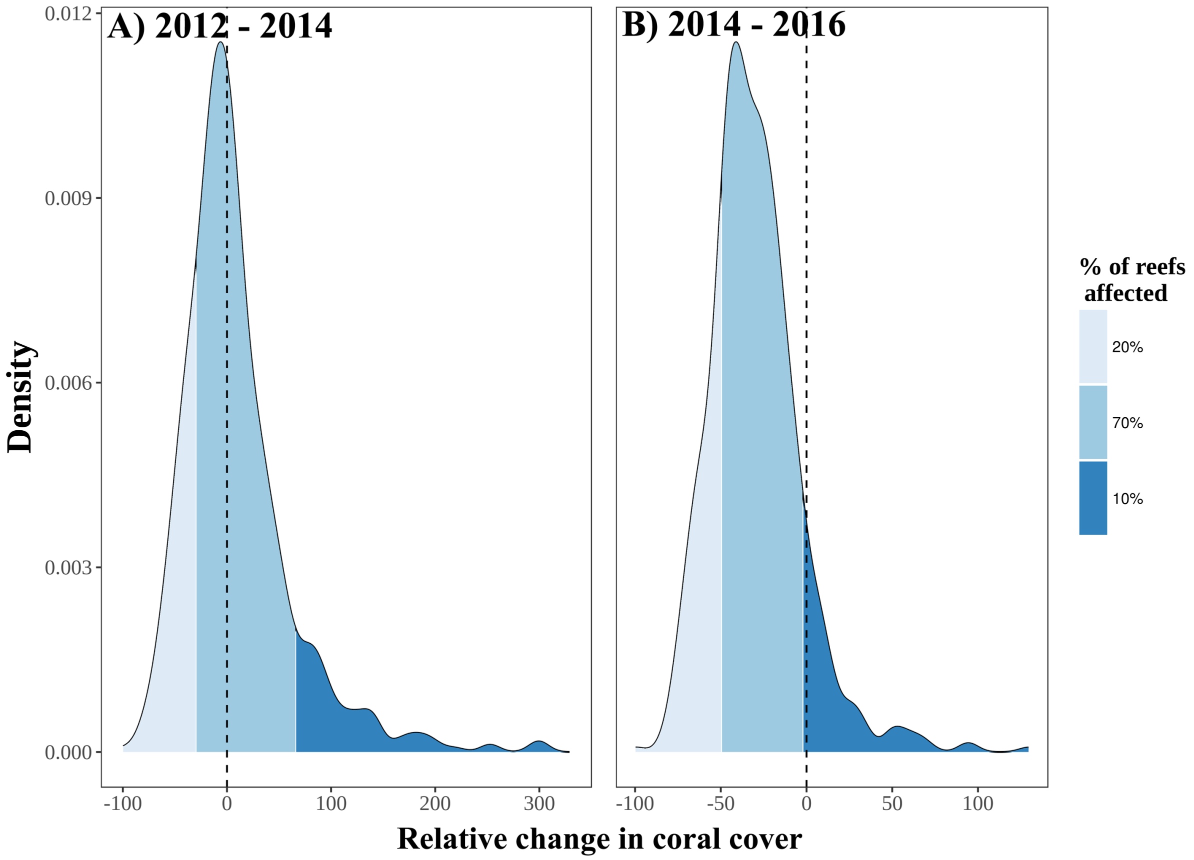


Figure 3.4. Density histogram of changes in coral cover across the far northern and northern GBR: A) Following the impact of TC Ita (2012 – 2014), and B) TC Nathan and the coral bleaching event (2014 – 2016). Blue shades divide the distribution into fractions to best represent the proportion of sub-transects affected (10, 20 and 70%). This comparative figure shows the number of reefs that showed either coral loss (left hand side from the dashed line) or recovery (right hand-side from the dashed line).

Table 3.1. PERMANOVA results examining the effect of disturbance zone and time on benthic composition of coral reefs in the far northern and northern GBR. df = degrees of freedom; MS = mean square.

Explanatory variable	df	MS	Pseudo-F	p-value	Pair-wise test
Disturbance zone	2	27378	2.2071	0.039	All pairs significantly different at <0.01, with the exception of one case.
Year	2	25340	14.924	0.001	
Transect	14	13618	131.04	0.001	
Disturbance zone x Year	4	3032.8	1.8239	0.022	
Transect x Year	28	1816.5	17.48	0.001	
Residuals	**1422**	**103.92**			
Total	**1472**				

Principal Coordinates Analysis (PCO) showed that the temporal changes at the transect level were not consistent across transects (Figure 3.5-A), although declines in hard coral were often matched with increases in algal cover (Figure 3.5-B). This pattern was reinforced at the community composition level, whereby the majority of transects (as represented by the cross and triangles in Figure 3.5-B) showed a loss of *Acropora* and a transition to increased algal cover post-2012, and only a few transects (as represented by the blue triangles) showed little change in benthic community structure between 2012 and 2016 (Figure 3.5).

Hard corals were the most affected of the major functional groups by the bleaching event, followed by other sessile invertebrates (Figure 3.6), such as *Millepora* spp. The loss in hard coral cover was accompanied by an increase in algal (mainly turf algae) cover (Figure 3.6).

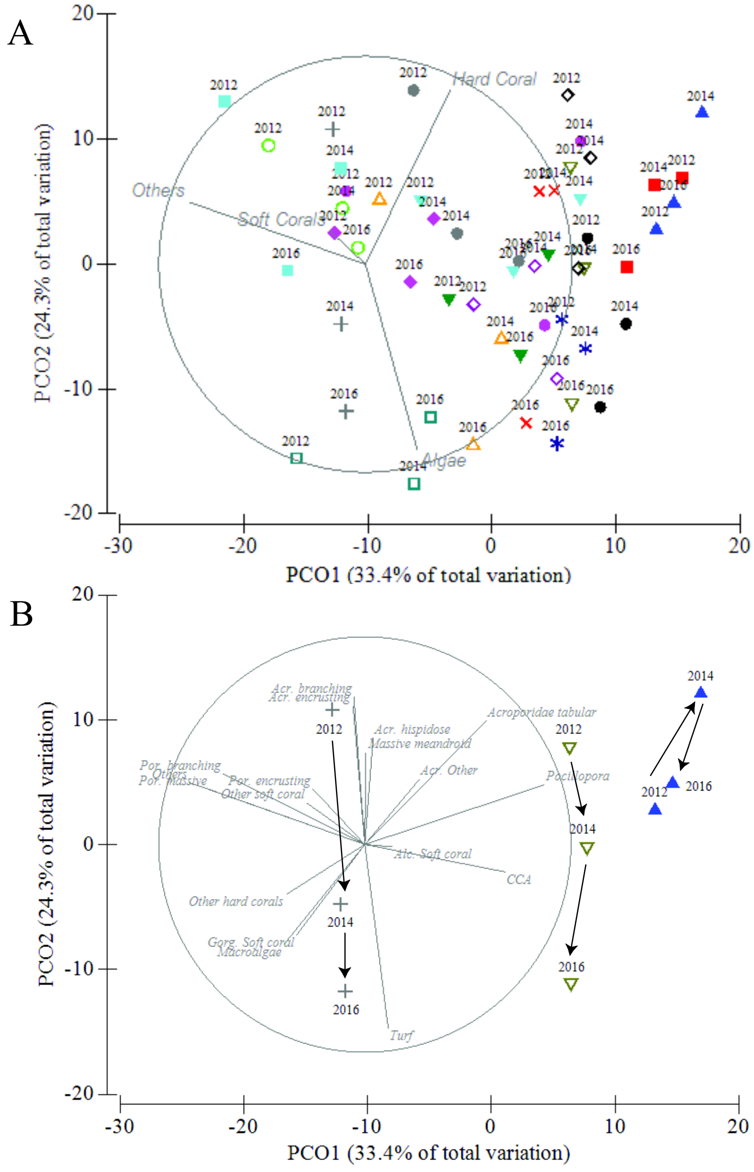


Figure 3.5. Principal Coordinates Analysis (PCO): A) PCO plot representing changes in benthic composition (Bray-Curtis distance) for each transect and across time, in relation to major functional groups. B) Detailed PCO to show changes for selected transects, in relation to functional categories. Grey vector lines show the correlation between functional groups (A) or functional categories (B) and transects over time. Each transect is represented by different symbols (colour and shape) and survey year is indicated above each symbol.

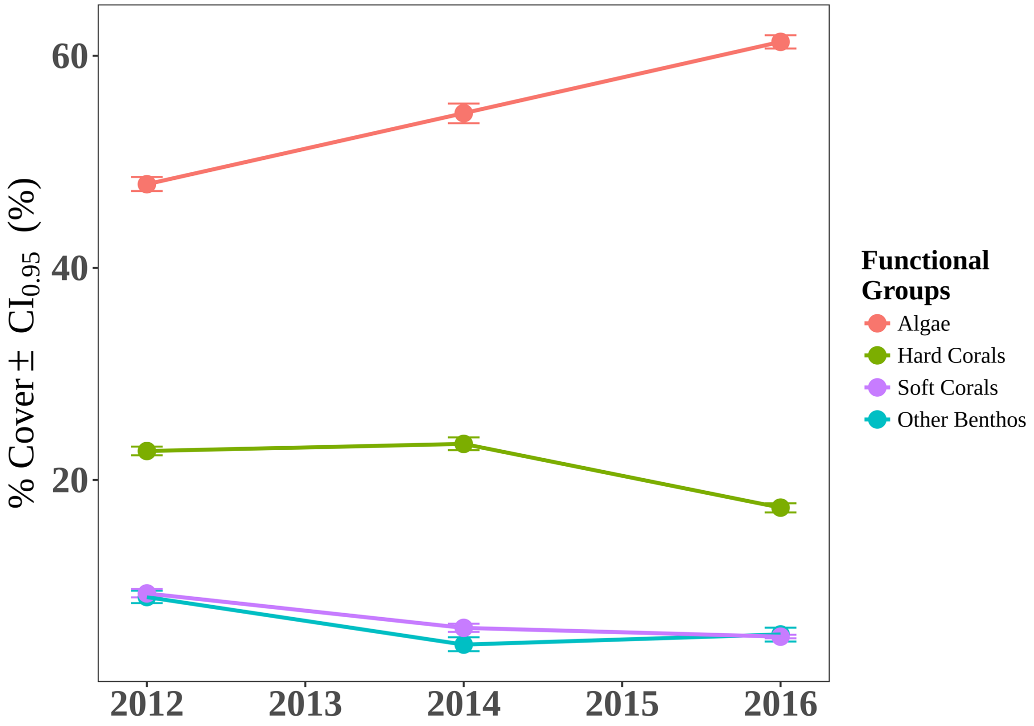


Figure 3.6. Temporal change among major functional groups in the far northern and northern GBR between 2012 and 2016. Filled circles represent averaged values of cover over time and error bars indicate the 95% confidence intervals. Other Benthos comprises sessile invertebrates such as fire corals (*Millepora* spp), ascidians, and sponges.

The response to the combined effect of TC Nathan and the coral bleaching event (2014 to 2016) was heterogeneous between functional groups of corals (Figure 3.7). In general, the bleaching susceptible corals were consistently affected across the region, which the exception of encrusting corals from the family Poritidae (Figure 3.7). [Note that the patterns shown in the Figure 3.7 are averaged across the entire area studied and therefore only represent the most common patterns (the spatial heterogeneity of the data is properly captured in the statistical analyses)]. Hard corals from the families Acroporidae and Poritidae with encrusting morphologies showed the highest mortality followed by massive colonies from the families Faviidae and Mussidae and branching and tabular Acroporidae, which is consistent with their known published susceptibility to bleaching and robustness to cyclones (Figure 3.7).

Comparative images illustrating key examples of temporal changes in benthic composition observed as a response of the patterns of disturbance between 2012 and 2016 are available in the Appendices.

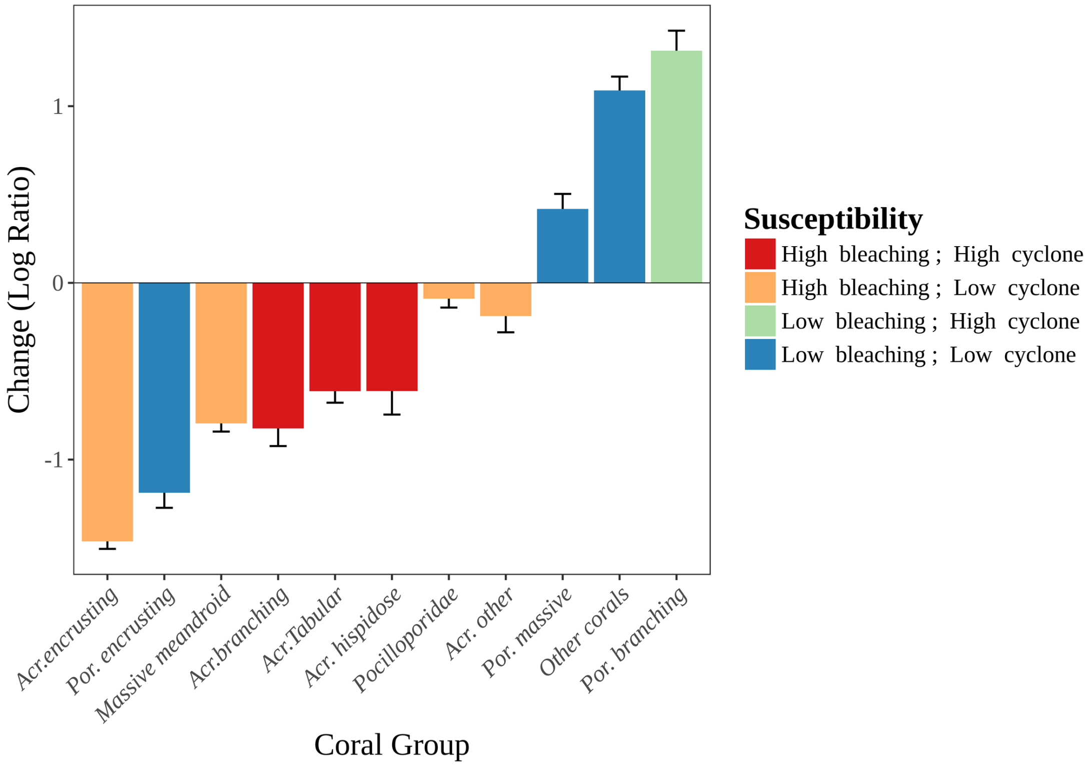


Figure 3.7. Average change of hard corals following TC Nathan and coral bleaching in the far northern and northern GBR. Change is measured as the natural logarithm of the coral cover ratio between survey years (Log Ratio). Negative values imply decline and positive values growth. Log ratio accounts for the natural skewness of the data, in particular for rare groups which coverage is considerably low (<5%). Error bars indicate 95% interval confidence. Bars are color-coded based on the reported susceptibility of these corals to bleaching, cyclone or both described in Gonzalez-Rivero et al. 2016.

3.4. Research question 6: Drivers of change in coral cover between 2012 and 2016

The three major disturbances and their interactions can be significantly correlated to negative changes in coral cover through the study region and over the past four years (Figure 3.8). Between 2012 and 2014, coral cover on outer reef shelf communities at ~10 m depth in the far northern and northern GBR did not change significantly across the whole study area, and only a weak effect of TC Ita was observed on the reefs within the area of cyclone impact, with the majority of reefs showing a positive trajectory of recovery from previous disturbances. Between 2014 and 2016, however, coral cover declined significantly throughout the studied area, and the magnitude of this change was significantly different among disturbances (Figure 3.8).

According to model estimates, the magnitude of coral loss between 2014 and 2016 was significantly higher within areas impacted by coral bleaching compared to those areas affected only by TC Ita (Figure

3.9). That said, the interactive effect of TC Ita, TC Nathan, and the coral bleaching event revealed that the cumulative impact of the three disturbances had the most significant negative effect on coral cover (Figure 3.8, Figure 3.9).

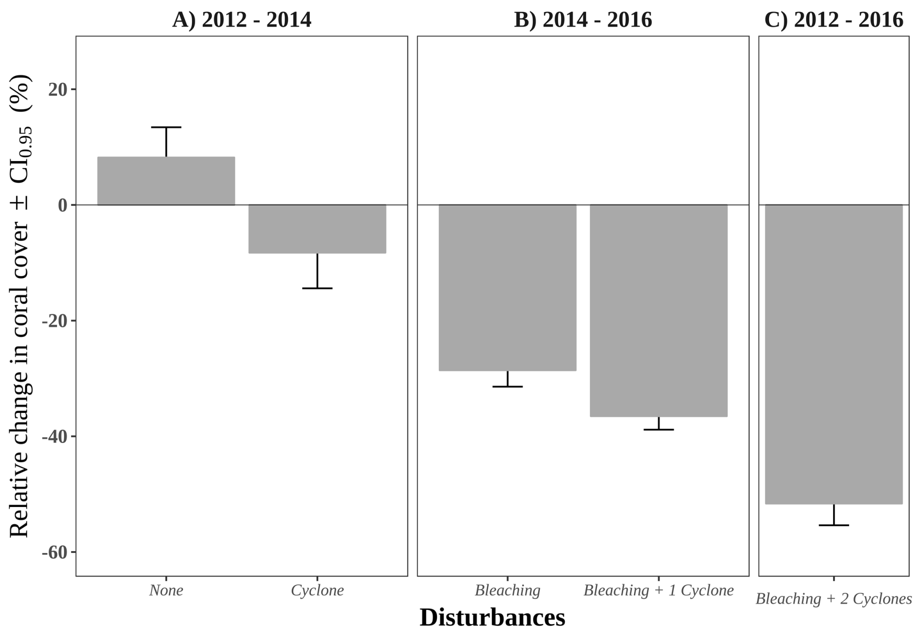


Figure 3.8. Relative change in coral cover within areas of disturbance. Change in coral cover has been averaged within regions impacted by each disturbance occurred within the evaluated periods: A) TC Ita (2012-2014), B) Bleaching and TC Nathan (2014-2016), and C) Cumulative impact over the past four years (2012-2016). Error bars represent the 95% confidence intervals.

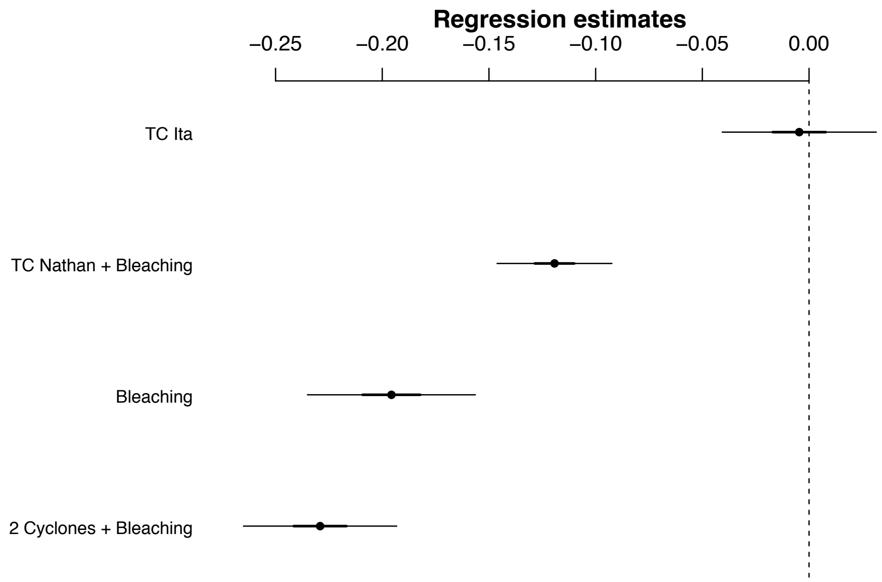


Figure 3.9. Regression coefficients from evaluating the change in coral cover among disturbance regions, as per Figure 3.8. Black dots represent the mean estimated coefficients of change (scaled log ratio) in coral cover compared to regions of no disturbance. Horizontal bars represent the estimated error, where the thin line show the Standard Deviation and the thick line the 95% confidence interval.

4. Discussion

Coral reefs are dynamic systems that are subjected to disturbance events that operate at a range of spatial and temporal scales. While COTS and tropical cyclones have recently been reported to be the two major contributors to the 50% decline of coral cover in the past 27 years on the GBR (De'ath et al. 2012), no COTS were recorded during our surveys of the far northern and northern GBR (2012 to 2016). Rather, the ~25% loss in coral cover between 2012 and 2016 on the outer reef shelf communities at ~ 10 m depth in the far northern and northern GBR is largely due to the coral bleaching impact in early 2016. The 2016 coral bleaching event had the greatest influence on the changes observed in the far northern and northern GBR between 2012 and 2016, when compared to the impacts of TC Nathan and TC Ita alone. While spatially isolated events of high coral mortality have been previously reported for the GBR following coral bleaching events (Berkelmans et al. 2004), the 2016 coral bleaching event was the most severe coral bleaching event recorded on the GBR to date, in terms of the attributed coral mortality (De'ath et al. 2012).

4.1. Temporal and spatial patterns of change in coral cover

In terms of both the footprint (extent, 90% of studied sites affected) and intensity (coral loss), the 2016 coral bleaching event in the far northern and northern GBR has had the greatest influence in the changes observed on outer reef shelf communities at ~10 m depth in the far northern and northern GBR between 2012 and 2016 when compared to the impact of TC Ita and TC Nathan. Consistently to this results, estimates of coral mortality, due to the mass bleaching event, between 11 to 83% for the far northern and northern GBR were recently reported by the National Coral Bleaching Taskforce (Hughes et al. 2016). While our results are consistent with these estimates – albeit on the lower range – the differences are likely attributable to the differences in the survey location, in terms of habitats and depth (outer reef slopes at 10 m depth). The outer reef slopes represent habitats with high water flow and few influences of land-based run-off or warming compared to the shallower, more affected, locations within the matrix of the GBR.

Thermal stress (Riegl and Piller 2003, Bridge et al. 2013) and the damaging effects of waves created by cyclones (Madin and Connolly 2006) generally attenuate with depth. Consequently, greater mortality was generally expected in shallower reef surveys (as per the National Coral Bleaching Taskforce surveys) compared to our study at 10 m depth. Moreover, contrasting differences in terms of dynamics of the oceanographic parameters (e.g. tides, currents, ocean front exchange), as well as patterns of water clarity, solar irradiance and temperature variability, across reef habitats can influence the severity of coral bleaching-induced mortality (Guest et al. 2012). Our surveys were conducted at offshore fore-reef environments at ~10 m depth compared to the broader range of reef habitats (inner, mid and outer shelf) surveyed by the National Coral Bleaching Taskforce.

The results of the current study are complementary to the shallower surveys across the inner to outer shelf of the National Coral Bleaching Taskforce, and together these surveys contribute to the assessment and understanding of the impact of the 2016 coral bleaching event in the far northern and northern GBR. These data combined with data from a broader range of habitats by the Great Barrier Reef Marine Park Authority's Eye-on-the-Reef Program, represent the most comprehensive post-bleaching assessment ever undertaken on the GBR.

4.2. Changes in community composition

While there is a general agreement that the far northern and northern GBR has suffered widespread coral mortality following the 2016 thermal anomaly event, not all members of the benthic community responded equality to the patterns of disturbance. Between 2012 and 2016, two different periods can be evaluated using the data from the XL Catlin Seaview Surveys: A) 2012-2014, when TC Ita occurred; and B) 2014-2016 when both the thermal anomaly event and TC Nathan occurred.

Sessile invertebrates (e.g. *Millepora* spp., ascidians and sponges) were among the most affected groups following the impact of TC Ita, between 2012 and 2014 (Figure 3.6). During this same period, the response of hard and soft corals was variable and non-significant. The observed region-wide patterns are perhaps attributable to the size of the disturbance (localised effect of the cyclone) and to the effect of local factors determining the variability of the response at the reef scale. For example, bathymetrical profile and geomorphological configuration of the reef can influence the wave patterns generated by the cyclone at local scales (10-100s m). Similarly patterns of wave exposure (chronic) and composition of benthic assemblages can strongly influence the response of the community, driving variable responses at higher aggregation levels (e.g., coral cover). Considering fine-scale covariates, as mentioned above, show that TC Ita had an important, yet localised, impact on the coral communities, which was not captured in the broad-scale generalizations of this study (Gonzalez-Marrero et al. 2015, Puotinen et al. 2016, Cheal et al. 2017).

Between 2014 and 2016, hard corals were the most affected group following TC Nathan (2015) and the thermal abnormality event in early 2016. This differential response could be explained by individual traits of susceptibility to bleaching and cyclone dislodgement. For example, corals belonging to the family Acroporidae, as well as other sessile invertebrates which includes fire corals of the genus *Millepora*, were among the most affected organisms and are classified as severely susceptible to thermal stress based on field observation (Marshall and Baird 2000). Concomitantly, complex and fragile morphologies of corals (e.g. branching, tabular, hispidose) were among the most affected groups, which are highly susceptible to dislodgment by wave generated from cyclones (Madin 2005). Other groups of corals (e.g. massive and branching Poritidae) showed no loss in abundance (cover) across the whole study area, which is consistent with published reports that these corals are classified within the range of low susceptibility to thermal stress (Marshall and Baird 2000) and robustness to cyclones (Madin 2005).

4.3. Coral reef resilience and recovery

Prior to the period of our study, the far northern and northern sections of the GBR reefs were considered the most 'pristine' part of the GBR, which had a consistent coral cover between 1985 and 2012 (De'ath et al. 2012) and were exposed to fewer broad scale disturbances (Maynard et al. 2015b). As such, these reefs were considered resilient due to their capacity to return to original conditions from perturbation, which is provided by the diversity in species composition and the limited human pressures (including water quality) associated to these remote locations (De'ath et al. 2012). However, the period between 2014 and 2016 has highlighted that the reefs in the far northern and northern GBR are not immune from the ocean warming due to climate change and strong El Niño conditions, plus strong tropical cyclones.

Under favourable environmental conditions, reef-building coral communities re-establish themselves following disturbances such as thermal stress and storm damage, although this make take decades. Following coral bleaching events in 1998 and 2001 at Sesoko Island in Japan, live coral cover increased from 3% in 2001 to 47% in 2010, and by 2007, species richness had recovered to levels similar to 1997 (van Woesik et al. 2011). Also, at Scott Reef in Western Australia where a coral-bleaching event in 1998 resulted in a 70% to 90% reduction in live coral cover, recruitment, genetic diversity, and community structure were similar to pre-bleaching years by 2010 (Gilmour et al. 2013). While it has been shown that live coral cover at Ashmore Reef in Western Australia increased from 10% in 2005 to 30% in 2009 following a coral bleaching event in 2003 (Ceccarelli et al. 2011), and reefs at Keppel Islands recovered in less than a year from a live coral cover of 20-30% to pre-bleaching levels of 77%-89% in 2006 (Diaz-Pulido et al. 2009), these rates are unusually rapid.

Recovery appears to be favoured when reefs are structurally complex and growing in clear water where the density of juvenile corals and herbivorous fishes are relatively high and when nutrient loads are low (Graham et al. 2015). That said, not all ecological attributes are always restored, and it appears that in the absence of future chronic stresses, coral communities have the ability to recover from chronic disturbance within 10 to 15 years. The recovery of live coral cover will depend on (i) the local survival of corals, (ii) whether corals on neighbouring reefs survived through the thermal stress, (iii) whether those neighbouring corals have the capacity to supply recruits, (iv) the survival of recruits from neighbouring reefs, and (v) the return frequency and intensity of thermal stresses and other impacts.

Global average sea surface temperatures have increased since both the beginning of the 20th century and the 1950s, and changes in the surface temperatures of the ocean basins are consistent with temperature trends simulated by ocean-atmosphere models with anthropogenic greenhouse gas forcing over the past century (Hoegh-Guldberg et al. 2014). Sea temperatures will continue to increase over the next few decades and centuries and under business as usual (IPCC RCP8.5), sea temperatures are projected to increase by 0.62°C to 0.85°C over the near term and 2.44°C to 3.32°C over the long term (Hoegh-Guldberg et al. 2014). This will increase the risk of thermal stress events. It only takes a temperature increase of 1-2°C to cause corals to bleach, and it is likely that coral bleaching and mortality will occur every 1 to 2 years by the mid- to late part of this century under low to high climate change scenarios (Hoegh-Guldberg 1999, Donner et al. 2005, Frieler et al. 2013). Moreover, the rising sea temperatures are projected to increase the number of more intense cyclones in the tropical Pacific, and implications for the GBR are yet unknown (Webster et al. 2005, Knutson et al. 2010). While it has been observed that the co-occurrence of cyclones and thermal stress have been shown to reduce the severity of bleaching in systems like the Caribbean and NW Pacific (Manzello et al. 2007, Carrigan and Puotinen 2014), this was not the case in this study, as they occurred in different years. TC Nathan and the 2016 thermal anomaly occurred almost a year apart; with enough time to isolate their antagonistic effect and prevent reef recovery. Based on this, it is expected that an increasing frequency of disturbance, such a more frequent bleaching events, coupled with a predicted increase in intensity of cyclone impacts will result in a faster degradation of tropical reef systems.

It has also recently been shown that three-quarters of past thermal stress events on the GBR have been characterised by a temperature trajectory that subjects corals to a protective and sub-bleaching stress (Ainsworth et al. 2016), before reaching temperatures that cause bleaching (Berry and Gasch 2008). However, as sea temperatures continue to rise, the sub-lethal bleaching temperature event of the protective trajectory will eventually exceed the bleaching threshold, switching events from being protective to becoming increasingly lethal (Ainsworth et al. 2016). As such, near future increases in temperature of just 0.5°C could result in this protective mechanism being lost on the GBR (Ainsworth et al. 2016). Mass mortality events that affect coral reefs (such as coral bleaching and tropical cyclones) will invariably result in more changes to community composition in the near term and a continuing downward trend in coral cover in the longer term (Gardner et al. 2003, Bruno and Selig 2007) – whereby the ecological recovery time will be less than the disturbance return time.

4.4. Novel techniques to support a better understanding of change

Variations in intensity, frequency and type of disturbance can strongly influence the fate of coral reefs communities (Nyström et al. 2000, Ostrander et al. 2000, Hoegh-Guldberg et al. 2007), and that climate change has a leading role in driving a sustained increase in intensity, size and frequency of broad-scale disturbances worldwide (Hoegh-Guldberg et al. 2014). As a result, there is general agreement that the effect of overlaying disturbances over time can accumulate impact, explaining a larger loss in coral cover compared to single disturbances (Darling and Côté 2008). Disentangling the effect of disturbance interactions over time to better forecast change is a complex task and often responds to the nature of these interactions (Côté et al. 2016), whether they are synergistic (more than the sum of the parts), additive (sum of the parts), or even antagonistic (different direction). Part of this complex nature of disturbance effects respond to challenges of adequately measuring change in underwater setting because of: 1) the broad extent of disturbances requires large extent of *in-situ* data; 2) accurate interpretations of change and their associations to disturbance requires robust baseline information to isolate intrinsic properties of each system; and 3) the clustered nature of disturbances over time or across space requires the need of highly frequent survey information to isolate each event and evaluate their overall contribution to change over time. Moreover, the individual response of reef communities can be masked by the previous history of disturbances, challenging the capacity to forecast change into the future; all in all, urging the need for a broad, standardised and repeatable approach to survey coral reefs.

This project demonstrated a novel, rapid and accurate technology for enabling large-scale surveys of coral reefs. Operating at speeds that are 100 fold higher than previous approaches (while maintaining precision and accuracy), this study enabled the detailed analysis of over 100 km of reef to be monitored three times. Using customised underwater vehicles to collect high-definition underwater imagery and a machine-learning framework for data analysis, interpretations of broad-scale changes over the last four years were possible in only seven weeks, instead of years. This novel framework for large-scale monitoring of coral reefs, which was introduced by the XL Catlin Seaview Survey, delivers a technology break-through in capacity to fast track the detection of change that offers a unique opportunity to guide timely management actions as disturbances are projected to increase in frequency and intensity. The importance of these technologies for reactive and integrating monitoring of coral reefs in a time of rapid change cannot be over-emphasized.

5. Conclusions

Significant declines in coral cover were recorded on the outer reef slopes of the far northern and northern GBR between 2012 and 2016. The interactive effect of tropical cyclones and a coral bleaching event in 2016 had the greatest effect on coral mortality in the far northern and northern GBR between 2012 and 2016 – with the 2016 coral bleaching the most severe bleaching event recorded on the GBR to date. That said, the results of this study and those from the National Coral Bleaching Taskforce and the Great Barrier Reef Marine Park Authority showed that the bleaching and subsequent mortality was not uniform across the GBR Marine Park, and there are numerous reefs throughout the Marine Park that still have abundant live coral cover and diversity.

Climate change is considered the greatest long-term threat to the GBR (GBRMPA 2009, 2014), whereby the frequency of coral bleaching events are predicted to increase in conjunction with the intensity of tropical cyclones as a result of rising ocean temperatures. The results of this study therefore provide important insights into the future of the GBR in line with recent projections that suggest that most coral reefs will experience extensive degradation over the next few decades given the present behaviour of corals to thermal stress (Donner 2009). Given the nature of the cumulative impacts over the past four years, it is clear that the GBR will experience further decline in the coming years, and repeated monitoring of locations, such as in this study, will be important to assess recovery and to get a better understanding of cumulative impacts in the face of rapid change.

That said, coral reef ecosystems face considerable challenges under even an ambitious mitigation scenario that constrains global warming to 1.5 °C above pre-industrial temperatures – whereby preserving >10% of coral reefs worldwide would require limiting warming to below 1.5 °C relative to pre-industrial levels (Frieler et al. 2013). Adherence to the Paris Climate Agreement, to hold the increase in the global average temperature to well below 2°C above pre-industrial levels and to pursue efforts to limit the temperature increase to 1.5 °C above pre-industrial levels average global surface, is therefore crucial to ensure the long-term sustainability of the GBR and coral reefs worldwide.

Disclaimer

The contents of this Report are solely the opinions of the authors and do not constitute a statement of policy, decision, or position on behalf of NOAA or the U.S. Government.

6. References

AIMS. 2014. Past bleaching events on the Great Barrier Reef. http://www.aims.gov.au/docs/research/climate-change/coral-bleaching/bleaching-events.html. .

Ainsworth, T. D., S. F. Heron, J. C. Ortiz, P. J. Mumby, A. Grech, D. Ogawa, C. M. Eakin, and W. Leggat. 2016. Climate change disables coral bleaching protection on the Great Barrier Reef. Science **352**:338-342.

Anderson, M. J., Gorley, R. N., and Clarke, K. R. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. Page 214 pp. PRIMER-E Ltd: Plymouth, UK,.

ARCCoE. 2016. Only 7% of the Great Barrier Reef has avoided coral bleaching. https://www.coralcoe.org.au/media-releases/only-7-of-the-great-barrier-reef-has-avoided-coral-bleaching.

Beeden, R., J. Maynard, M. Puotinen, P. Marshall, J. Dryden, J. Goldberg, and G. Williams. 2015. Impacts and recovery from severe tropical Cyclone Yasi on the Great Barrier Reef. Plos One **10**:e0121272.

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

Berry, D. B. and A. P. Gasch. 2008. Stress-activated genomic expression changes serve a preparative role for impending stress in yeast. Molecular biology of the cell **19**:4580-4587.

Bridge, T. C. L., A. S. Hoey, S. J. Campbell, E. Muttaqin, E. Rudi, N. Fadli, and A. H. Baird. 2013. Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery. F1000Research **2**:187.

Bruno, J. F. and E. R. Selig. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. Plos One **2**:e711.

Carrigan, A. D. and M. Puotinen. 2014. Tropical cyclone cooling combats region ‐ wide coral bleaching. Global Change Biology **20**:1604-1613.

Ceccarelli, D., Z. Richards, M. Pratchett, and C. Cvitanovic. 2011. Rapid increase in coral cover on an isolated coral reef, the Ashmore Reef National Nature Reserve, north-western Australia. Marine and Freshwater Research **62**:1214-1220.

Cheal, A. J., M. A. MacNeil, M. J. Emslie, and H. Sweatman. 2017. The threat to coral reefs from more intense cyclones under climate change. Global Change Biology.

Cinner, J. E., C. Huchery, M. A. MacNeil, N. A. Graham, T. R. McClanahan, J. Maina, E. Maire, J. N. Kittinger, C. C. Hicks, and C. Mora. 2016. Bright spots among the world's coral reefs. Nature **535**:416-419.

Connell, J. 1997. Disturbance and recovery of coral assemblages. Coral Reefs **16**:S101-S113.

Côté, I. M., E. S. Darling, and C. J. Brown. 2016. Interactions among ecosystem stressors and their importance in conservation. Page 20152592 *in* Proc. R. Soc. B. The Royal Society.

Darling, E. S. and I. M. Côté. 2008. Quantifying the evidence for ecological synergies. Ecology Letters **11**:1278-1286.

De’ath, G., K. E. Fabricius, H. Sweatman, and M. Puotinen. 2012. The 27–year decline of coral cover on the Great Barrier Reef and its causes. Proceedings of the National Academy of Sciences **109**:17995-17999.

Diaz-Pulido, G., L. J. McCook, S. Dove, R. Berkelmans, G. Roff, D. I. Kline, S. Weeks, R. D. Evans, D. H. Williamson, and O. Hoegh-Guldberg. 2009. Doom and Boom on a Resilient Reef: Climate Change, Algal Overgrowth and Coral Recovery. Plos One **4**:e5239.

Done, T. J. 1992. Effects of tropical cyclone waves on ecological and geomorphological structures on the Great Barrier Reef. Continental Shelf Research **12**:859-872.

Donner, S. D., W. J. Skirving, C. M. Little, M. Oppenheimer, and O. Hoegh ‐ Guldberg. 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. Global Change Biology **11**:2251-2265.

Eakin, C. M., J. A. Morgan, S. F. Heron, T. B. Smith, G. Liu, L. Alvarez-Filip, B. Baca, E. Bartels, C. Bastidas, and C. Bouchon. 2010. Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. Plos One **5**:e13969.

Fabricius, K. E., G. De'Ath, M. L. Puotinen, T. Done, T. F. Cooper, and S. C. Burgess. 2008. Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. Limnology and Oceanography **53**:690-704.

Frieler, K., M. Meinshausen, A. Golly, M. Mengel, K. Lebek, S. Donner, and O. Hoegh-Guldberg. 2013. Limiting global warming to 2 oC is unlikely to save most coral reefs. Nature Climate Change **3**:165-170.

Gardner, T. A., I. M. Cote, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. Science **301**:958-960.

GBRMPA. 2009. Great barrier reef outlook report 2009. Great Barrier Reef Marine Park Authority.

Gilmour, J., L. Smith, S. Pincock, and K. Cook. 2013. Discovering Scott Reef: 20 Years of Exploration and Research. Australian Institute of Marine Science.

Glynn, P. and L. D'croz. 1990. Experimental evidence for high temperature stress as the cause of El Nino-coincident coral mortality. Coral Reefs **8**:181-191.

Gonzalez-Marrero, Y., M. Gonzalez-Rivero, and O. Hoegh-Guldberg. 2015. Understanding the impact of the cyclone Ita on coral reefs of the Great Barrier Reefs: Novel approaches for broad scale unerwater surveys. Thesis report. ERASMUS MUNDUS - EMBC.

González-Rivero, M., O. Beijbom, A. Rodriguez-Ramirez, T. Holtrop, Y. González-Marrero, A. Ganase, C. Roelfsema, S. Phinn, and O. Hoegh-Guldberg. 2016. Scaling up Ecological Measurements of Coral Reefs Using Semi-Automated Field Image Collection and Analysis. Remote Sensing **8**:30.

González-Rivero, M., P. Bongaerts, O. Beijbom, O. Pizarro, A. Friedman, A. Rodriguez-Ramirez, B. Upcroft, D. Laffoley, D. I. Kline, C. Bailhache, R. Vevers, and O. Hoegh-Guldberg. 2014. The Catlin Seaview Survey - kilometre-scale seascape assessment, and monitoring of coral reef ecosystems. Aquatic Conservation: Marine and Freshwater Ecosystems:*In press*.

Graham, N. A., S. Jennings, M. A. MacNeil, D. Mouillot, and S. K. Wilson. 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature **518**:94-97.

Guest, J. R., A. H. Baird, J. A. Maynard, E. Muttaqin, A. J. Edwards, S. J. Campbell, K. Yewdall, Y. A. Affendi, and L. M. Chou. 2012. Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. Plos One **7**:e33353.

Harrison, P. L., S. J. Dalton, and A. G. Carroll. 2011. Extensive coral bleaching on the world's southernmost coral reef at Lord Howe Island, Australia. Coral Reefs **30**:775-775.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research **50**:839-866.

Hoegh-Guldberg, O., R. Cai, E. S. Poloczanska, P. G. Brewer, S. Sundby, K. Hilmi, V. J. Fabry, and S. Jung. 2014. Chapter 30. The Ocean.*in* V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, and L. L. White, editors. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Hoegh-Guldberg, O., P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C. D. Harvell, P. F. Sale, A. J. Edwards, K. Caldeira, N. Knowlton, C. M. Eakin, R. Iglesias-Prieto, N. Muthiga, R. H. Bradbury, A. Dubi, and M. E. Hatziolos. 2007. Coral reefs under rapid climate change and ocean acidification. Science **318**:1737-1742.

Hoegh-Guldberg, O. and G. J. Smith. 1989. The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals Stylophora pistillata Esper and Seriatopora hystrix Dana. Journal of Experimental Marine Biology and Ecology **129**:279-303.

Hooidonk, R., J. A. Maynard, D. Manzello, and S. Planes. 2014. Opposite latitudinal gradients in projected ocean acidification and bleaching impacts on coral reefs. Global Change Biology **20**:103-112.

Hughes, T. E., B. Schaffelke, and J. Kerry. 2016. How much coral has died in the Great Barrier Reef's worst bleaching event? The Conversation, http://www.theconversation.com.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science-AAAS-Weekly Paper Edition **265**:1547-1551.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. Jackson, and J. Kleypas. 2003. Climate change, human impacts, and the resilience of coral reefs. Science **301**:929-933.

Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. Trends in Ecology & Evolution **25**:633-642.

Jackson, J. B. 1991. Adaptation and diversity of reef corals. BioScience:475-482.

Knutson, T. R., J. L. McBride, J. Chan, K. Emanuel, G. Holland, C. Landsea, I. Held, J. P. Kossin, A. K. Srivastava, and M. Sugi. 2010. Tropical cyclones and climate change. Nature Geosci **3**:157-163.

LeCun, Y., Y. Bengio, and G. Hinton. 2015. Deep learning. Nature **521**:436-444.

Lee, C.-Y., M. K. Tippett, A. H. Sobel, and S. J. Camargo. 2016. Rapid intensification and the bimodal distribution of tropical cyclone intensity. Nature communications **7**.

Liu, G., S. F. Heron, C. M. Eakin, J. L. Rauenzahn, E. F. Geiger, W. J. Skirving, T. F. Burgess, and A. E. Strong. 2004. NOAA coral reef watch's next-generation 5 km satellite coral bleaching thermal stress monitoring. Reef Encount **2**:27-29.

Madin, J. S. 2005. Mechanical limitations of reef corals during hydrodynamic disturbances. Coral Reefs **24**:630-635.

Madin, J. S. and S. R. Connolly. 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. Nature **444**:477-480.

Mahmood, A., M. Bennamoun, S. An, F. Sohel, F. Boussaid, R. Hovey, G. Kendrick, and R. B. Fisher. 2016. Automatic annotation of coral reefs using deep learning. Pages 1-5 *in* OCEANS 2016 MTS/IEEE Monterey.

Manzello, D. P., M. Brandt, T. B. Smith, D. Lirman, J. C. Hendee, and R. S. Nemeth. 2007. Hurricanes benefit bleached corals. Proceedings of the National Academy of Sciences **104**:12035-12039.

Marshall, P. and A. Baird. 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs **19**:155-163.

Maynard, J., R. Van Hooidonk, C. M. Eakin, M. Puotinen, M. Garren, G. Williams, S. F. Heron, J. Lamb, E. Weil, and B. Willis. 2015a. Projections of climate conditions that increase coral disease susceptibility and pathogen abundance and virulence. Nature Climate Change **5**:688-694.

Maynard, J. A., R. Beeden, M. Puotinen, J. E. Johnson, P. Marshall, R. Hooidonk, S. F. Heron, M. Devlin, E. Lawrey, and J. Dryden. 2015b. Great Barrier Reef no ‐ take areas include a range of disturbance regimes. Conservation Letters.

McClanahan, T. R., M. Ateweberhan, C. A. Muhando, J. Maina, and M. S. Mohammed. 2007. Effects of climate and seawater temperature variation on coral bleaching and mortality. Ecological Monographs **77**:503-525.

Mei, W. and S.-P. Xie. 2016. Intensification of landfalling typhoons over the northwest Pacific since the late 1970s. Nature Geoscience **9**:753-757.

NOAA. 2016. Coral Reef Watch. http://coralreefwatch.noaa.gov/satellite/sst.php.

Nyström, M., C. Folke, and F. Moberg. 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends in Ecology and Evolution **15**:413-417.

Oliver, J., R. Berkelmans, and C. Eakin. 2009. Coral bleaching in space and time. Pages 21-39 Coral bleaching. Springer.

Osborne, K., A. M. Dolman, S. C. Burgess, and K. A. Johns. 2011. Disturbance and the Dynamics of Coral Cover on the Great Barrier Reef (1995–2009). Plos One **6**:e17516.

Ostrander, G. K., K. M. Armstrong, E. T. Knobbe, D. Gerace, and E. P. Scully. 2000. Rapid transition in the structure of a coral reef community: The effects of coral bleaching and physical disturbance. Proceedings of the National Academy of Sciences **97**:5297-5302.

Pandolfi, J. 2002. Coral community dynamics at multiple scales. Coral Reefs **21**:13-23.

Pandolfi, J. M. 1999. Response of Pleistocene coral reefs to environmental change over long temporal scales. American Zoologist **39**:113-130.

Puotinen, M., J. A. Maynard, R. Beeden, B. Radford, and G. J. Williams. 2016. A robust operational model for predicting where tropical cyclone waves damage coral reefs. Scientific reports **6**.

Puotinen, M. M., T. T. Done, and W. Skelley. 1997. An atlas of tropical cyclones in the Great Barrier Reef region: 1969-1997.

Riegl, B. and W. E. Piller. 2003. Possible refugia for reefs in times of environmental stress. International Journal of Earth Sciences **92**:520-531.

Strong, A., C. Barrientos, C. Duda, and J. Sapper. 1997. Improved satellite techniques for monitoring coral reef bleaching. Pages 1495-1498 *in* Proc 8th Int Coral Reef Symp.

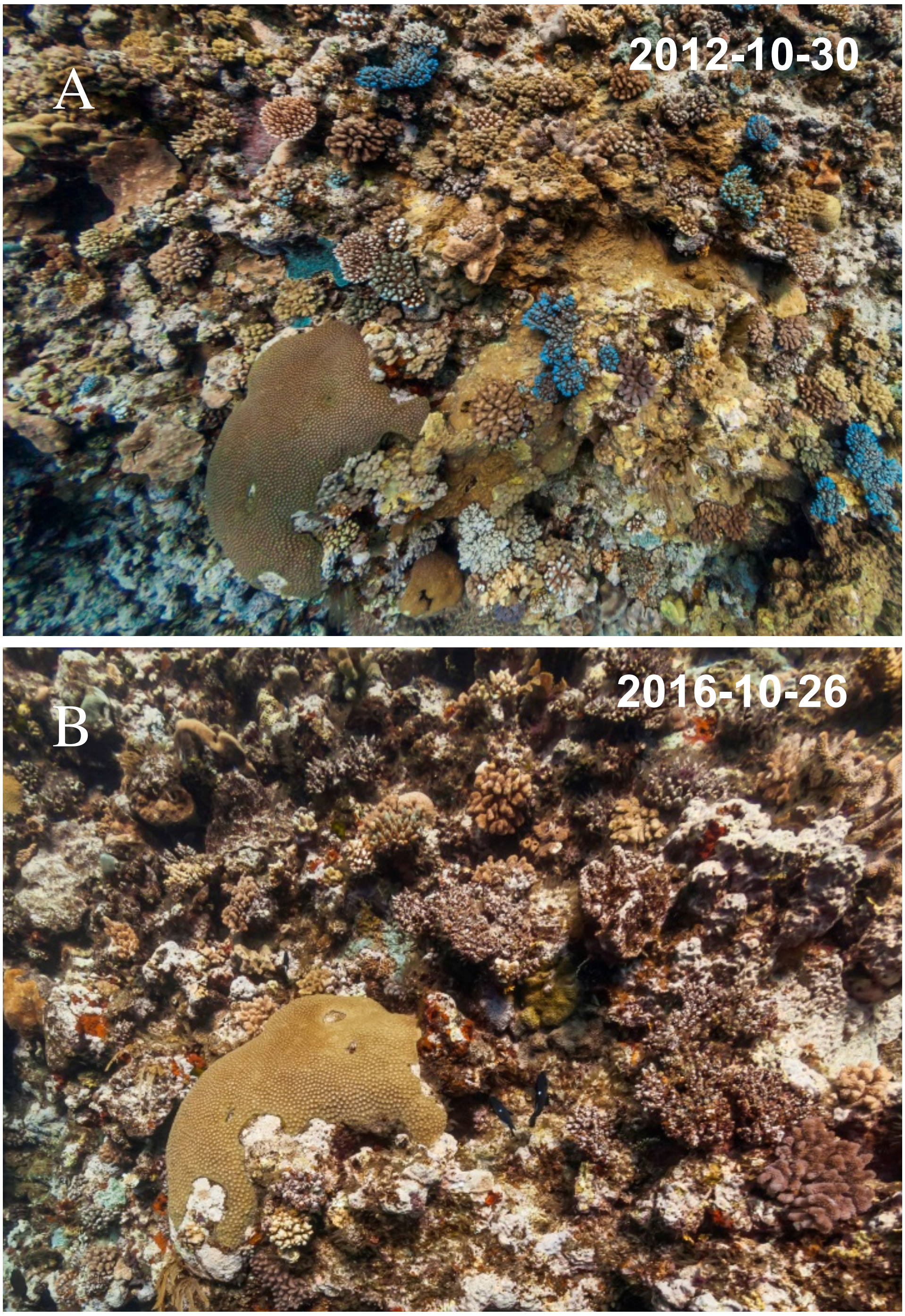
van Hooidonk, R., J. Maynard, and S. Planes. 2013. Temporary refugia for coral reefs in a warming world. Nature Climate Change **3**:508-511.

van Woesik, R., K. Sakai, A. Ganase, and Y. Loya. 2011. Revisiting the winners and the losers a decade after coral bleaching. Marine Ecology Progress Series **434**:67-76.

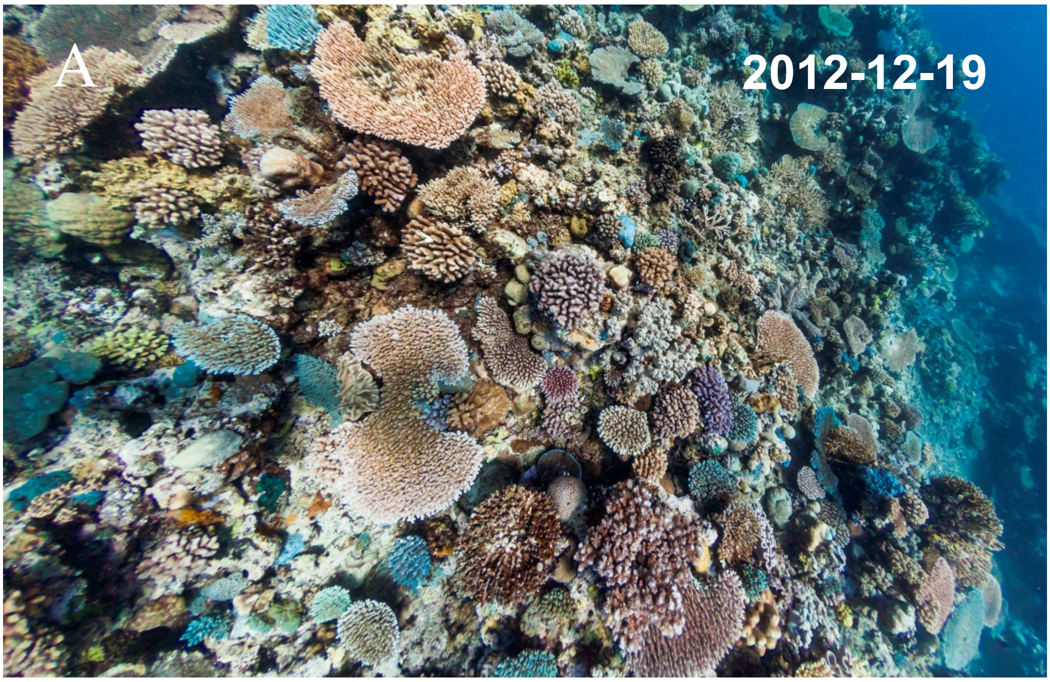
Walsh, K. J., J. L. McBride, P. J. Klotzbach, S. Balachandran, S. J. Camargo, G. Holland, T. R. Knutson, J. P. Kossin, T. c. Lee, and A. Sobel. 2016. Tropical cyclones and climate change. Wiley Interdisciplinary Reviews: Climate Change **7**:65-89.

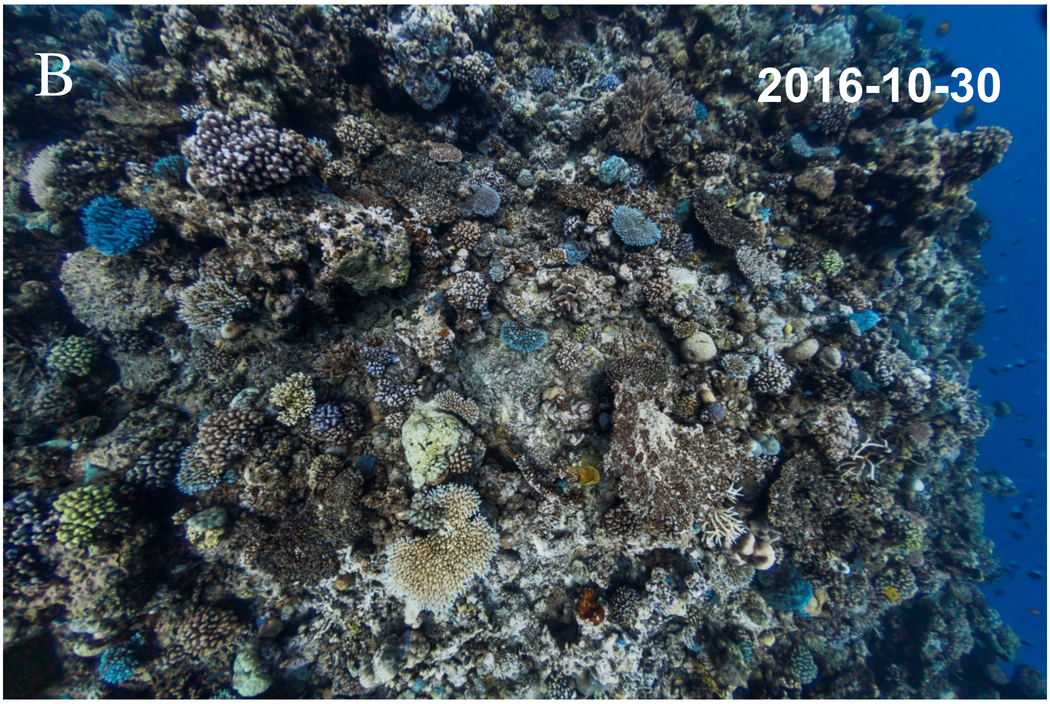
Webster, P. J., G. J. Holland, J. A. Curry, and H.-R. Chang. 2005. Changes in Tropical Cyclone Number, Duration, and Intensity in a Warming Environment. Science **309**:1844-1846.

7. Appendices

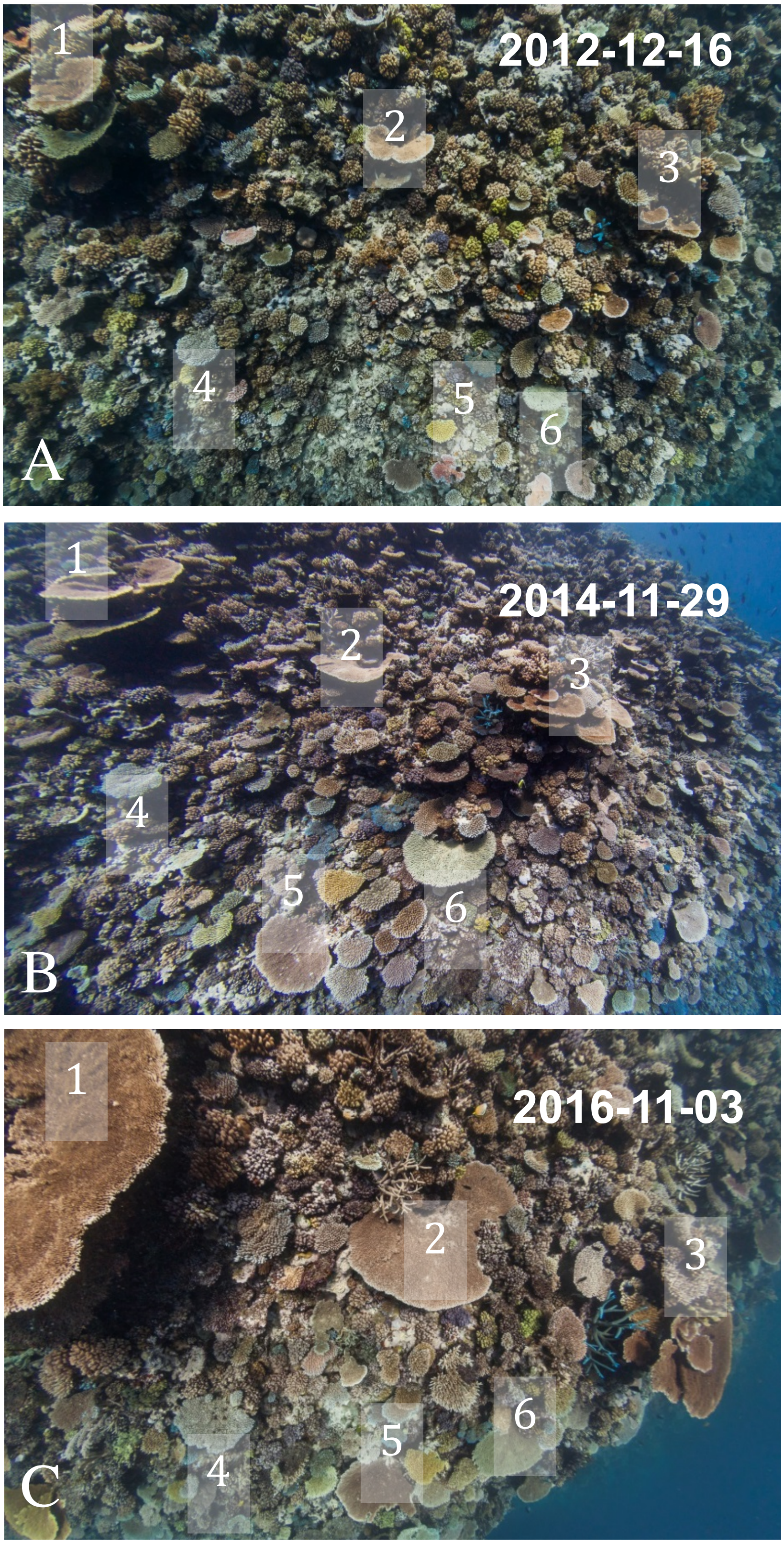


Appendix 1. Images illustrating changes in benthic composition between 2012 (A) and 2016 (B) at the same location on Ribbon Reef No. 9. Differences in the images are attributed to the combined effect of cyclones and bleaching. Acroporid hard corals, *Millepora* spp and soft corals showed the highest mortality.





Appendix 2. Images illustrating changes in benthic composition between 2012 (A) and 2016 (B) at the same location on Wilson Reef. Overall a significant reduction in coral cover (Acroporid hard corals) and significant increase in turf were observed on this reef, which could be attributed to the 2016 bleaching.



Appendix 3. Images illustrating no negative change (coral loss) in benthic composition between 2012 (A), 2014 (B) and 2016 (C) at the location on Tijou Reef. Overall an increase in coral cover (Acroporid hard corals) was observed in this reef between periods. Numbers indicate similar spots or the same coral colonies among images.