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The Dynamics and Resilience of Coral Reefs

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ABSTRACT

A major goal in ecosystem management is to prevent shifts to undesirable states, and there is widespread interest in understanding, mapping, and quantifying resilience to support management decisions. With rapid changes taking place on coral reefs, managers and scientists are faced with a challenging task in prioritising interventions that help strengthen reef resilience. Resilience-based management (RBM) of coral reefs requires in-depth knowledge on the various components and feedback mechanisms of the ecosystem, and uses resilience theory to inform decisions. To date, there are mechanistic models that analyse and forecast the future of reefs, but being data intensive and requiring specialist knowledge, are not applicable to managers in most locations with limited data and analytical training. Hence, there is a need to develop approaches to acquire insights on resilience using monitoring data.

The global decline of reefs to varying extents, underscores the importance of understanding how biophysical factors influence and shape reef community dynamics. Multiple environmental factors affect reef functioning, either positively or negatively, and the diversity and complexity of responses make it difficult to predict future reef trajectories. My thesis addresses the need to improve retrospective analyses of time-series monitoring data to suit management goals, such as resilience, by focusing on the data collection and analytical components of long-term monitoring programmes. In this thesis, I trialled two state-of-the-art methods to extract useful ecological information and identified drivers of coral reef trajectories from long-term monitoring data collected in the Great Barrier Reef, arguably one of the most comprehensive coral reef monitoring dataset in the world.

In **Chapter 1**, I provide a theoretical overview of the issues related to resilience and identify the quantification approaches found within the coral reef field. By examining the current state of knowledge, a simple framework of resilience-related concepts is developed, followed by an analysis of approaches used to quantify reef resilience and vulnerability. Seven broad quantification approaches were identified under the three principle concepts of (1) ecological resilience (ecological resilience, precariousness and current attractor), (2) engineering resilience (short-term recovery rate and long-term reef performance), and (3) vulnerability (absolute and relative vulnerability) respectively.

Resilience-based management (RBM) is a new approach to reef management that is being adopted by governmental institutions globally. However, there are no quantitative studies on how this has changed coral reef monitoring and assessment. In **Chapter 2**, I conducted a critical evaluation of how RBM has changed the way we monitor our reefs. Through a comparison of metrics used in conventional programmes with those developed specifically for resilience assessments, I show that resilience metrics are much more diverse and have a strong focus on ecological processes and exposure to environmental drivers. Also, monitoring metrics focus on reef state, but seem less likely to predict the future responses of reefs.

To identify key drivers of coral trajectories in the inshore and offshore GBR, regions with fundamentally different biophysical drivers, I used multivariate autoregressive state-space approach (MARSS) and generalised additive mixed models (GAMMS) within a Bayesian framework using geoaddivitive coefficients in **Chapters 3 and 4** respectively. Key drivers identified in **Chapter 3** suggest that inshore reef coral trajectories are largely governed by episodic localised disturbances, alike their offshore counterparts. Surprisingly, no water quality variables emerged as key drivers, implying that the impacts of chronic water quality are more likely to affect reef dynamics over a longer time-scale and difficult to detect with a decadal dataset. In **Chapter 4**, I further examined the role of different disturbances on different *Acropora* morphologies, novel in the context of a large scale ecological dataset. Concurrent with the general literature, the impact of storms and crown-of-thorns starfish were found to be the key drivers of coral dynamics in the mid- and off-shore GBR, but there are significant differences on the relative disturbance impacts on coral growth forms.

This study has reviewed the field of coral reef resilience and captured the effects of biological and physical variables on inshore and offshore reef dynamics using a range of novel approaches. While coral reef dynamics seem to be driven mainly by acute disturbances, an important implication that stems from this research is on how one uses physical data (i.e. water quality, DHW) as predictors of resilience, and that the integration and scoring of variables into resilience assessments should be context dependent, contrary to current resilience assessments. The comparison of the last two chapters provides information to guide current reef monitoring programmes and delivers practical suggestions to improve future monitoring and resilience assessments.

DECLARATION BY AUTHOR

This thesis **is composed of my original work, and contains** no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

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PUBLICATIONS DURING CANDIDATURE

Lam, V. Y. Y., Doropoulos, C., & Mumby, P. J. (2017). The influence of resilience-based management on coral reef monitoring: A systematic review. PLoS ONE, 12(2), e0172064. doi: 10.1371/journal.pone.0172064

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<i>Contributor</i>	<i>Statement of contribution</i>
VYY Lam (Candidate)	Designed study (80%) Collected and analysed data (100%) Wrote the paper (100%)
C Doropoulos	Edited paper (40%)
PJ Mumby	Designed study (20%) Edited paper (60%)

CONTRIBUTIONS BY OTHERS TO THE THESIS

Chapter 1: Written by VYYL. PJM and CD provided feedback and comments on the manuscript.

Chapter 2: VYYL collected data, analysed the data and wrote the manuscript. PJM provided advice on framework design. PJM and CD provided feedback and comments to the manuscript.

Chapter 3: PJM provided advice on study design. CD provided statistical advice. VYYL collected and analysed the data and wrote the manuscript. All authors discussed results and edited the manuscript.

Chapter 4: PJM, MC and CD provided advice on study design and statistical analysis. Data was provided by AT from Australian Institute of Marine Science. VYYL cleaned the data, created models, ran analysis, interpreted results and wrote the manuscript. All authors discussed results and edited the manuscript.

Chapter 5: PJM and MC provided advice on study design and statistical analysis. Data was provided by HS (AIMS), NW, JC, KH and MD. VYYL cleaned the data, created models, ran analysis, interpreted results and wrote the manuscript. All authors discussed results and edited the manuscript.

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STATEMENT OF PARTS OF THE THESIS SUBMITTED TO QUALIFY FOR THE AWARD OF ANOTHER DEGREE

None.

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KEYWORDS

resilience, coral reefs, monitoring, time series, great barrier reef, state space models, bayesian regression, population dynamics, management, conservation, assessments

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ABBREVIATIONS

AICb - Parametric bootstrap Akaike Information Criteria

ASS - alternate stable states

BBN - Bayesian belief network

CBD - Convention on Biological Diversity

ForestGEO - Forest Global Earth Observatories

GAMM - generalised additive mixed regression model

GBR - Great Barrier Reef

GBRWhA - Great Barrier Reef World Heritage Area

GEOBON - Group on Earth Observations Biodiversity Observation Network

IPBES - Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

IUCN - International Union for Conservation of Nature

MARSS - multivariate autoregressive state-space model

MEI - multivariate ENSO index

nMDS - non-metric multidimensional scaling

NRM - natural resource management

PERMANOVA - permutational multivariate analysis of variance

RBM - resilience-based management

SE - standard error

SIMPER - similarity percentages breakdown

SST - sea surface temperature

STRI - Smithsonian Tropical Research Institute

UNESCO - The United Nations Educational, Scientific and Cultural Organization

1. GENERAL INTRODUCTION

Overview

Global natural system declines are occurring at unprecedented rates (Sato & Lindenmayer 2017). Reports of declines and collapses are increasingly widespread and found in diverse habitats, from freshwater systems (Vörösmarty *et al.* 2010) to tropical rain forests (Laurance *et al.* 1997) and seagrass habitats (Orth *et al.* 2006). In light of increasing biodiversity and ecosystem loss, it is of critical importance to be able to understand and predict the future of our ecosystems based on available data amassed by scientists, governments and conservation organisations alike. Degradation of the natural ecosystem are occurring at different scales including species, communities, functional groups, habitats and ecosystems and supported by evidence from an array of studies in geographic regions around the world (Butchart *et al.* 2010; Pereira *et al.* 2010).

To address the current biodiversity crisis, many international initiatives have been set up to contribute to and improve biodiversity conservation efforts around the globe. International research programmes such as DIVERSITAS and GEOBON were established, focusing on the integration of biodiversity science to address critical conservation issues (Loreau & Olivieri 1999; Larigauderie *et al.* 2012; Scholes *et al.* 2012). The Millennium Ecosystem Assessment was published in 2005 to document the impact of human disturbances on natural ecosystems, which in turn has major impacts on ecosystem services and human well-being (Millennium Ecosystem Assessment 2005). The Convention on Biological Diversity (CBD) has been publishing a periodic flagship report known as the Global Biodiversity Outlook on the status and trends of biological diversity and related information on conservation status and actions since 2010. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) was set up in 2012 by the United Nations to provide scientific information on status of biodiversity to support biodiversity conservation policies (Díaz *et al.* 2015). The International Union for Conservation of Nature (IUCN) established the Red List for Ecosystems in 2014 to assess the status of ecosystems around the world by investigating their

state of degradation and if the ecosystem is likely to remain functioning in the near future (Keith *et al.* 2013; Keith *et al.* 2015b).

The burgeoning development of conservation initiatives are centred on the importance of the status and trends in biodiversity and ecosystem function as a fundamental step before conservation actions can be designed and implemented to protect biodiversity and resources (Perrings *et al.* 2011). Declining trends in species abundance often serve as a warning that a population will eventually be extinct if declines continue, prompting further investigation on the drivers of decline (Keith *et al.* 2015a). Once drivers are identified, conservation efforts to minimise the harm of direct threats can be put in place, like harvest regulations in the case of the once abundant passenger pigeon (Stanton 2014). Additionally, status and trends are used for evaluating the effectiveness of conservation policies (Yoccoz, Nichols & Boulinier 2001; Nichols & Williams 2006). My thesis addresses the need to improve retrospective analyses of time-series monitoring data to suit management goals such as resilience (**Chapter 2**) by focusing on the data collection (**Chapter 3**) and analytical components of long-term monitoring programs illustrated by two case studies (**Chapters 4 and 5**).

Monitoring of iconic landscapes

Monitoring activities of ecological systems have long been conducted by natural resource managers, governmental departments and conservation organisations alike to obtain information on the status of and threats to ecosystems, species or habitat under concern or protection (Gray 1980; Callahan 1984). Monitoring will continue to be relevant and necessary if resources are to be managed, conserved and protected (Cowell 1978), and a review conducted by Lindenmayer and Likens (2010) found more than 5500 monitoring-related articles from 1985-2009. Numerous long term monitoring programs and initiatives on specific ecological habitats are in place, such as the Smithsonian Tropical Research Institute's (STRI) Forest Global Earth Observatories (ForestGEO) which started with a 50-hectare rainforest plot in Panama in 1980 and has now expanded to 59 sites internationally (Anderson-Teixeira *et al.* 2015). Similarly, the Long Term Ecological Research (LTER) program by the US Government monitors a variety of ecological habitats such as forests, deserts, lakes and coral reefs throughout the world (Hobbie *et al.* 2003). Apart from contributing to ecological research, monitoring also happens in places of special interest such

as UNESCO World Heritage Sites, a famous example of which is Australia's Great Barrier Reef (GBR) - the world's most extensive coral reef ecosystem (Great Barrier Reef Marine Park Authority 1981).

Several reasons make monitoring necessary. To assess whether a key species is in danger of extinction or a system in danger of degradation, there is a need for baseline information to evaluate population trends (Thomas, McKenzie & Eberhardt 1981). If trends show that species or habitats are in decline, further assessments can be used to identify threats, followed by the proposition of necessary actions for recovery or restoration (Hinds 1984; Nichols & Williams 2006). In addition, long-term monitoring data are a powerful and perhaps the only means of evaluating the success and effectiveness of conservation interventions to ensure conservation targets that have been set are met (Baillie *et al.* 2008). There is an increasing demand for long-term ecological monitoring data as short-term data are unable to detect complex ecosystem dynamics and interactions, such as nonlinear relationships and feedback mechanisms (Carpenter *et al.* 2006; Gitzen *et al.* 2012). Moreover, the combination of long-term and paleoecological data can help avoid the shifting baseline syndrome (Pauly 2005; Papworth *et al.* 2009) and to differentiate between natural variability and real change (Willis & Birks 2006; Willis *et al.* 2007). For example, the combined use of palaeoecological data with long-term monitoring data showed that woody vegetation cover in Kruger National Park South Africa has remained consistently higher than average over the past 5000 years and has not yet crossed the threshold of potential concern (Gillson & Duffin 2007).

Since the execution of long-term monitoring programs, much effort has been dedicated to improving its power and usefulness. Extensive research and analysis has been conducted to promote high quantitative standards for long-term monitoring and the subsequent analysis of the data for effective conservation and management (Pickett 1989; Müller *et al.* 2010; Gitzen *et al.* 2012). Although there is consensus that targeted monitoring to collect data to answer *a priori* questions is more effective than much of the existing monitoring known as passive or mandated monitoring for surveillance (Nichols & Williams 2006; Lindenmayer & Likens 2010), it is also important to explore statistical techniques that complement the growing availability of monitoring data from surveillance programmes. There is an increasing need for work addressing analytical approaches to generate understanding of ecosystem dynamics from data collected by existing monitoring programs (Yoccoz, Nichols & Boulinier 2001).

With the accumulation of monitoring data being collected from different parts of the world and from different systems, there is a need for parallel development in statistical techniques that allow us to use monitoring data effectively for conservation actions. In this thesis, I address the difficulty in using existing long-term monitoring data to understand the dynamics and drivers of an iconic landscape using the world's largest coral reef, the Great Barrier Reef, as a model system.

Reefs in a global context

Coral reefs are an important ecological habitat found in over 100 countries and are situated mostly in tropical regions between 30 degrees north and south of the equator (Birkeland 1997; Spalding, Ravilious & Green 2001)(Figure 1.1). Half a billion people are heavily dependent and up to 30 million are entirely dependent on the goods and benefits they provide (Wilkinson 2008). Reef ecosystem services are well documented and diverse, not only providing critical habitats that support fisheries, biodiversity and tourism, but also offering protection to coastal areas from wave exposure and erosion (Moberg & Folke 1999). In addition, coral reefs are sourced to synthesize pharmaceutical products and building materials (Carté 1996). It is estimated that a hectare of coral reef is worth 352,249 US dollars per annum (de Groot *et al.* 2012).

The Great Barrier Reef consists of more than 3,000 reefs that span 2,300 km along the coast of Australia covering an area of 348,700 km² (Hopley, Smithers & Parnell 2007). A variety of reef types are found in the GBR; including reef patches, fringing, submerged, crescentic, lagoonal, planar and ribbon reefs located in the inner, middle and outer cross shelf locations (Hopley, Parnell & Isdale 1989). Declared as a World Heritage Area in 1981, the GBRWHA was provided protection in 1975 under the Great Barrier Reef Marine Park Act by the establishment of the Great Barrier Reef Marine Park with multiple use zones and management plans (Great Barrier Reef Marine Park Authority 1975). Subsequently, one-third was designated as no-take zones under the GBR Marine Park Zoning Plan in 2004 (Wilkinson 2004). Despite being one of the most intensely managed reef systems in the world, extreme weather events and poor water quality has caused deterioration of the GBR in recent years demonstrated by a decline in total coral cover (De'ath *et al.* 2012; Great Barrier Reef Marine Park Authority 2014).

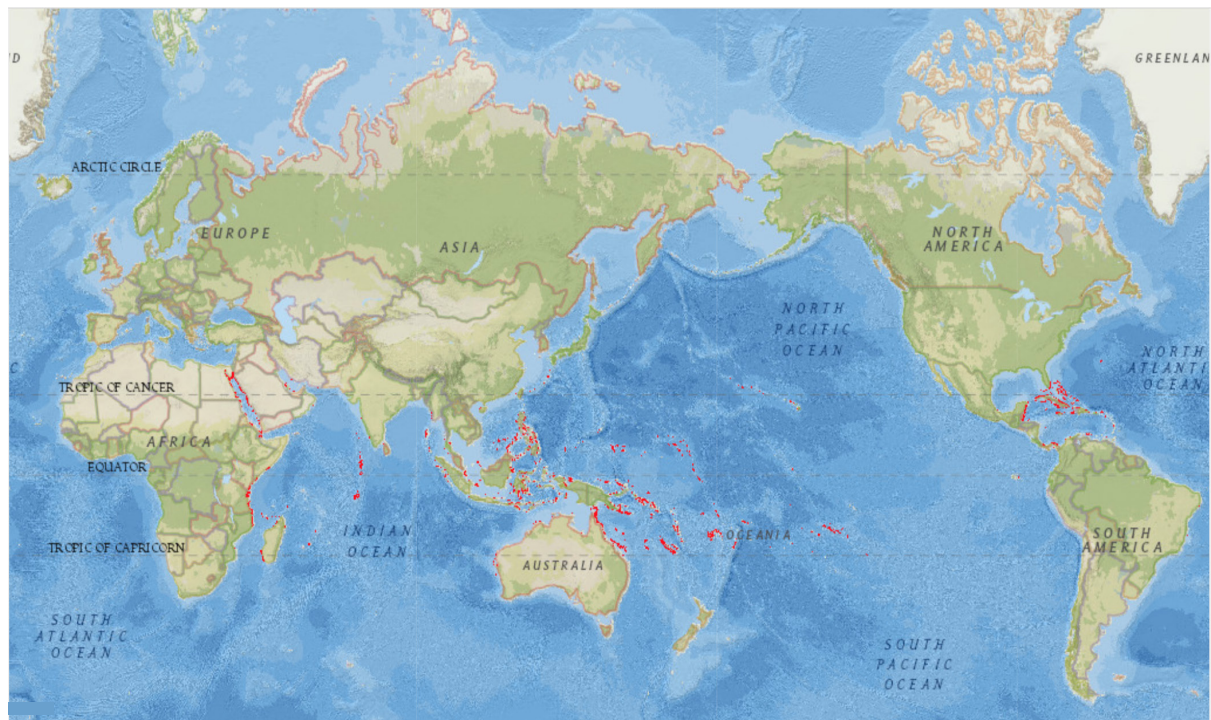


Figure 1.1 Distribution of the world's coral reefs.

Modified from UNEP-WCMC, WorldFish Centre, WRI and TNC 2010. URL: <http://data.unep-wcmc.org/datasets/1>

Trajectories of decline

The past decades have seen numerous reports on the global decline of coral reefs in the form of decreased coral cover, changes in community structure, alterations in system processes and/or transitions to depauperate ecosystem states (Bryant *et al.* 1998; Gardner *et al.* 2003; Pandolfi *et al.* 2003; Bruno & Selig 2007; De'ath *et al.* 2012; Jackson *et al.* 2014). These are caused by a wide range of disturbances such as cyclones and storms (Hughes & Connell 1999), bleaching, climate change and ocean acidification (Glynn 1993; Hoegh-Guldberg *et al.* 2007), disease (Weil 2004; Bruno *et al.* 2007), invasive species (Birkeland & Lucas 1990; Albins & Hixon 2011), overfishing (Jackson *et al.* 2001; Hughes *et al.* 2003; Hughes *et al.* 2007; Jackson *et al.* 2014), mining of corals (Bellwood *et al.* 2004), sedimentation (Rogers 1990; Fabricius 2005), eutrophication (McCook 1999), pollution from land-based runoff and discharges caused by coastal development, dredging, agricultural and deforestation activities (Fabricius *et al.* 2005; Pandolfi *et al.* 2005; Halpern *et al.* 2008) and destructive fishing

practices using dynamite or cyanide (Jennings & Polunin 1996; Wilson *et al.* 2006; Burke *et al.* 2011). Disturbances can impact various life stages of corals, from processes involved in recruitment (Connell, Hughes & Wallace 1997; Doropoulos *et al.* 2012a; Doropoulos *et al.* 2012b) to adult coral growth, survival, and ecological interactions (Carpenter *et al.* 2008; Mora 2008). Reefs can be impacted by one or multiple disturbances independently or synergistically (Karlson & Hurd 1993), and the interactions among multiple stressors may have complex effects on coral reefs (Hughes & Connell 1999; Ban, Graham & Connolly 2014). Moreover, reefs with different biophysical attributes are expected to respond differently to disturbances (Hughes & Connell 1999), especially reefs in different geographical regions (Graham, Nash & Kool 2011; Roff & Mumby 2012).

Multiple factors affect reef trajectories, either positively or negatively. Reef trajectories from empirical observations are a result of complex interactions between the biotic and abiotic components of the system (Pandolfi *et al.* 2003). Individual reefs respond differently to pressures influenced by factors such as coral community composition, population structure, herbivory levels, coral recruitment and even oceanographic conditions (Hatcher 1997). For instance, different coral taxa have different susceptibilities to disturbances of varying nature (Connell 1997; Knowlton 2001). For example, pocilloporids and acroporids are more susceptible to bleaching than *Cyphastrea*, *Turbinaria* and *Galaxea* (Marshall & Baird 2000) and branching and tabulate corals are often more vulnerable to storm damage (Madin & Connolly 2006). However, the most sensitive coral taxa are often found to be the most important for the recovery of reefs (Johns, Osborne & Logan 2014; Pisapia *et al.* 2016). Apart from individual susceptibilities to disturbances, the ecological balance between coral and algae is also key in determining reef trajectories (Bellwood *et al.* 2004; Hughes *et al.* 2007) which is largely influenced by herbivory (Burkepile & Hay 2010). Herbivory exerts a top-down control on reefs by ensuring sufficient grazing intensity to keep algae in a cropped state, thus preventing the proliferation of macroalgae which reduces coral recruitment, growth and fecundity (Hughes *et al.* 2007). In addition, grazing contributes to more available space for the settlement and recruitment of corals, and in turn keeps reefs structurally complex and dominated by corals (Mumby, Hastings & Edwards 2007).

Resilience of ecological systems

The perspective of resilience emerged in ecology through the study of predator-prey interactions and their functional responses in relation to ecological stability (Holling 1961; Lewontin 1969; May 1972). The resilience concept was introduced by Holling in 1973 and was described as "a measure of the ability of systems to absorb changes in state variables, driving variables, and parameters, and still persist" (Holling, 1973) and is further developed into two separate concepts known as ecological and engineering resilience respectively (Holling 1996). Broadly, ecological resilience is the magnitude of disturbance that a system can undertake while maintaining its structure and functions (Gunderson 2000; Walker *et al.* 2004), whereas engineering resilience refers to the speed and rate of recovery to the original system equilibrium (Pimm 1984). My thesis focuses on ecological resilience as engineering resilience is often difficult to apply to dynamic ecological systems as measurement requires an equilibrial reference that is hard to define and reach under current reef disturbance regimes (Mumby *et al.* 2014a). Engineering resilience also concentrates on the recovery component but not resistance which is equally important in determining reef resilience (Nyström *et al.* 2008).

An undesirable consequence of multiple disturbances on ecosystems is the event of a phase shift that can lead a system into an alternate basin of attraction (Scheffer *et al.* 2001). Examples of undesirable phase shifts include macroalgal-dominated reefs on coral reefs (Hughes 1994), turbid lakes with phytoplankton blooms instead of clear lakes with submerged vegetation (Carpenter, Ludwig & Brock 1999) and deserts with bare soil and ephemeral plants instead of perennial vegetation (Suding, Gross & Houseman 2004). Phase shifts occur when there is a conspicuous change to the community structure of a system, and the term was introduced when describing various coral reef systems that have switched from coral to algal domination (Done 1992b). Phase shifts can be an initial reaction to severe disturbance with subsequent reef recovery (Adjeroud *et al.* 2009; Diaz-Pulido *et al.* 2009; Manfrino *et al.* 2013), or reefs can remain in a permanent phase shift (Hughes 1994; McCook 1999; Mumby 2009). There is currently an on-going debate on whether phase shifts are evident in all systems and in different biogeographic regions (Scheffer & Carpenter 2003; Petraitis & Dudgeon 2004; Bruno *et al.* 2009; Fung, Seymour & Johnson 2011; Mumby, Steneck & Hastings 2013), with a discussion on whether field data alone (and not only theory

and models) can provide evidence for alternate attractors on coral reefs (Bruno *et al.* 2009; Möllmann *et al.* 2015). However, Mumby, Steneck and Hastings (2013) explained that it is unlikely that field data alone can provide the evidence for the existence of alternate attractors and there is a need for statistical and mechanistic approaches to make informed interpretations of trajectories.

One explanation for a permanent phase shift (also known as regime shifts) is the presence of alternate attractors (Lewontin 1969; May 1977; Connell & Sousa 1983; Petraitis & Dudgeon 2004) (also known as alternate stable states) reinforced by ecological feedbacks and nonlinear dynamics that drive the ecosystem towards these dominating attractors (Carpenter, Kinne & Wieser 2003) (Mumby, Steneck & Hastings 2013). A number of ecological processes and disturbance regimes determine the occurrence of a regime shift (Done 1992b; Knowlton 1992) and form complex ecological feedback loops that contribute to the occurrence of hysteresis (Scheffer *et al.* 2001; Hughes *et al.* 2010). Hysteresis describes a system that has different pathways when switching alternate attractors in one direction to that required to return (May 1977; Ludwig, Walker & Holling 1997; Petraitis & Dudgeon 2004) and has important implications for resilience as it marks a difficult reversal once a system shifts into an alternate attractor (Fung, Seymour & Johnson 2011). Even in the absence of disturbances, the presence of feedback loops will keep the system in the alternative basin of attraction (Scheffer & Carpenter 2003) (Mumby & Steneck 2011), and therefore the existence of alternate attractors has important ramifications on the conservation and management of ecological systems.

The most commonly illustrated example of alternate attractors in coral reef ecosystems are the coral- and algal-dominated reefs (Done 1992b), but other attractors are possible such as soft corals, sponges and urchin barrens (Norström *et al.* 2009). Reefs within the coral-dominated attractor basin will always exhibit a recovery trajectory after a disturbance because coral recruitment and growth is greater than coral mortality, whereas reefs in the algal-dominated attractor basin will move towards algal dominance as even background coral mortality is greater than recruitment and growth, caused by the presence of feedback mechanisms in the system (Mumby & Steneck 2008). Coral dynamics are also influenced by underlying feedback mechanisms, and one important feedback loop in reef systems is the interaction between herbivory, macroalgae and coral recruitment and growth (Hughes *et al.* 2007). Loss of herbivores results in an increase in macroalgal biomass which affects the

survival of corals in many ways (McCook, Jompa & Diaz-Pulido 2001) (Birrell *et al.* 2008), such as limiting space and interfering with recruitment (Kuffner *et al.* 2006; Doropoulos *et al.* 2016), suppressing coral growth (Tanner 1995; Lirman 2001) and even disease and mortality (Smith *et al.* 2006).

Operationalising coral reef resilience

A current critical challenge in the advancement of coral reef resilience science is to find ways to operationalise resilience-based management (Österblom *et al.* 2017). Difficulties in applying RBM in marine ecosystems have been noted, including both conceptual and practical issues, ranging from definitional problems (Brand & Jax 2007) to complications in measurement and data collection (Davidson *et al.* 2013). Some progress have been made with regards to undertaking ecological resilience assessments, such as the development of guidelines in the measurement and assessment of resilience indicators (West & Salm 2003; Grimsditch & Salm 2006; Maynard *et al.* 2010; McClanahan *et al.* 2012), and considerations for potential management interventions (Anthony *et al.* 2015). However, there remains a challenge in using existing monitoring programmes and the subsequent wealth of historical monitoring data in the application of RBM, and one of the key issues is the choice of reef metrics to monitor and its interpretation under a resilience context (Flower *et al.* 2017). Monitoring variables should include metrics on the recovery, resistance and disturbances to have adequate coverage on resilience (Nyström *et al.* 2008). To address this limitation, the identification of key drivers of coral reef cover trajectories from different habitats based on the analysis of long-term monitoring data may help establish key metrics for future consideration when adapting reef monitoring programmes to have a stronger focus on resilience.

Thesis aims

The overarching aim of this thesis is to identify the ways reef resilience is being measured, explore the links between monitoring and resilience and to improve the retrospective analysis of existing long-term coral reef data by using novel statistical techniques. To do so, I applied a range of techniques, including a systematic theoretical review of coral reef resilience literature and state-of-the-art statistical modelling (including state-space and Bayesian

geoadditive generalised additive mixed modelling) on two of the most comprehensive monitoring datasets in the world. Different analytical techniques were explored to address data limitations relevant to each dataset. Moreover, as reefs with different biophysical attributes are likely to exhibit dissimilar trajectories and dynamics, the use of the two datasets enabled different habitats from the inner, middle and outer-shelves of the GBR to be included in the analysis. Apart from the identification of key drivers of coral dynamics in different habitats, I hope my thesis results will inform and improve monitoring approaches, and in turn influence and advance the resilience-based management of coral reefs.

The specific aims of my PhD research are:

- 1) To provide a comprehensive review of the application, measurement and operationalisation of resilience to coral reef ecosystems (**Chapter 2**)
- 2) To assess how resilience-based management has influenced coral reef monitoring (**Chapter 3**)
- 3) To identify key drivers of coral trajectories in the inshore Great Barrier Reef (GBR) (**Chapter 4**)
- 4) To identify key drivers of coral trajectories and disturbance impacts on different *Acropora* morphologies in the inner, mid- and off-shore GBR (**Chapter 5**)

Thesis overview

The conceptual overview of thesis is presented in Figure 1.2, highlighting the focus of each individual chapter and the relationships between the different chapters to address the main aims of my PhD research. Here, I present the outlines of each individual chapter in order.

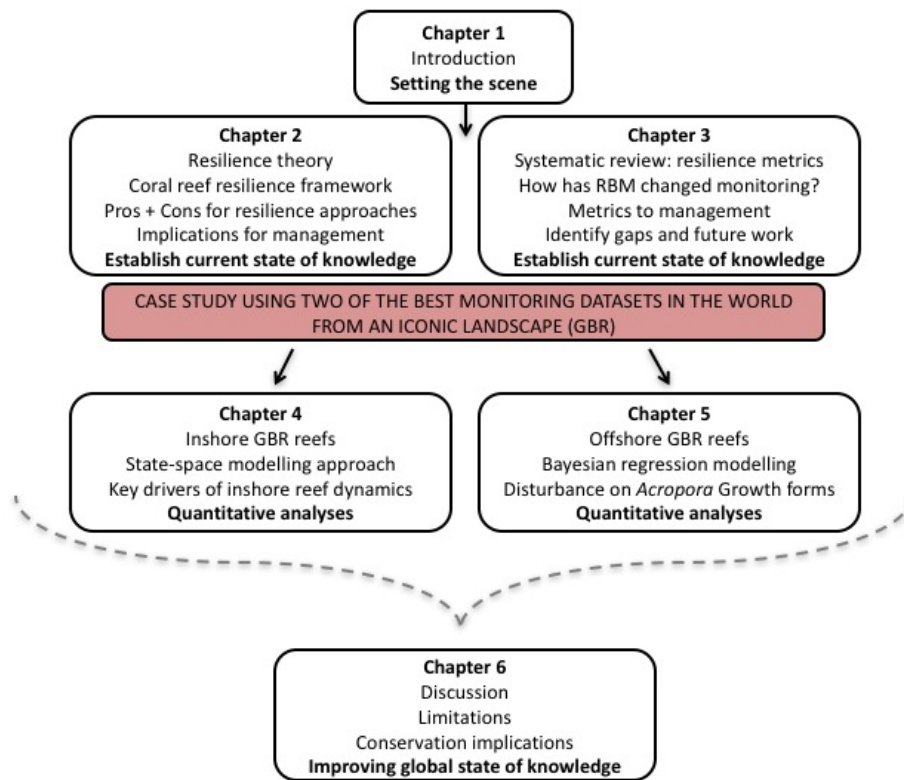


Figure 1.2. PhD overview flow chart

There has been an advent of resilience-based management when carrying out conservation and management of coral reef ecosystems. On one hand, it has been constrained by the confusing array of different resilience concepts and ideas which is explored in **Chapter 2**. On the other hand, it has led to some changes in the approaches of reef management, particularly on how people monitor and assess reefs. **Chapter 3** evaluates the influence of resilience-based management on monitoring, with a focus on comparing the metrics used by historical monitoring programmes against those developed for resilience assessments. Much of the understanding of what drives ecological systems has come from statistical analyses of long term datasets, perhaps with the combination of short-term experiment studies. In **Chapters 4 and 5**, I applied two cutting edge statistical methods to long-term monitoring datasets from the Great Barrier Reef to identify drivers of coral reef trajectories and to investigate disturbance effects on different *Acropora* growth forms. Despite uncertainty caused by the inherent variability coral reef ecosystems and data constraints, my thesis clearly demonstrates the issues involved in analysing long term monitoring datasets and highlights the spatial and temporal variation found in coral reef ecosystems. In **Chapter 6**, I conclude this thesis with the main findings and future implications of my research and how that might refine what we value when doing resilience and monitoring assessments.

2. CORAL REEF RESILIENCE FRAMEWORKS AND THEIR OPERATIONALISATION FOR MANAGEMENT

Abstract

The concept of resilience is long established across a wide-range of disciplines, but its evaluation in many ecosystems has been challenging due to the complexities involved in quantifying a somewhat abstract dynamical phenomenon. A framework of resilience-related concepts was developed and the methodological approaches described. Seven broad approaches were identified under the three principle concepts of (1) ecological resilience (ecological resilience, precariousness and current attractor), (2) engineering resilience (short-term recovery rate and long-term reef performance), and (3) vulnerability (absolute and relative vulnerability) respectively. Using specific examples, the strengths and limitations of each approach and their capacity to answer common management questions were assessed. The current synthesis provides new directions for resilience assessments to be incorporated into management decisions and has implications on the research agenda for advances in resilience assessments.

Introduction

From its early use in physical sciences and ecology, the concept of resilience is now ubiquitous across natural and social sciences including psychology (Luthar, Cicchetti & Becker 2000), urban planning (Eraydin & Tasan-Kok 2013), disaster management (Manyena 2006), resource-dependent industries (Marshall 2010), economics (Common & Perrings 1992; Brand 2009), and governance (Lebel *et al.* 2006). The concept has become increasingly malleable to fit different objectives and shows considerable variety in its application (Brand & Jax 2007; Martin-Breen & Anderies 2011; Davidson *et al.* 2016).

Quantification is critical for operationalising resilience, yet has remained largely conceptual and difficult to measure within ecosystems. Feature issues published in the *Journal of Applied Ecology* (Angeler & Allen 2016) and *Trends in Ecology and Evolution* (Hodgson, McDonald & Hosken 2015) demonstrate ongoing dialogue to quantify resilience and the relevant key questions. How can resilience be operationalised based on existing frameworks? What are the best quantifiable metrics to measure resilience in different ecosystems? Although recent studies advocate for generic indicators to achieve standardised quantification across systems, such as the measurement of resistance and recovery (Hodgson, McDonald & Hosken 2015; Nimmo *et al.* 2015), general metrics may not be easy to measure across all systems, each with distinct system dynamics exhibiting different behaviours and governed by different processes and mechanisms (Dakos *et al.* 2015; Yeung & Richardson 2015; Petraitis & Dudgeon 2016).

Recent reviews of resilience have focused on quantification approaches across multiple ecosystems (Scheffer *et al.* 2015; Allen *et al.* 2016; Quinlan *et al.* 2016), built on knowledge of model ecosystems for the development of the resilience theory such as lakes (Carpenter, Ludwig & Brock 1999), savannahs (Walker *et al.* 1981) and coral reefs (Hughes *et al.* 2003). Although a number of reviews have considered the processes that drive resilience and its application to management (Bellwood *et al.* 2004; Hughes *et al.* 2005; Nyström *et al.* 2008; Mumby *et al.* 2014a), a critical review of approaches is lacking.

Here, we synthesize progress on the measurement of resilience on coral reefs and identify several novel, additional concepts that might have utility. We begin with a brief historical perspective of reef resilience concepts and provide a framework to categorise approaches. We then assess the strengths and weaknesses of various approaches and identify appropriate management questions. Finally, new directions for resilience assessments are discussed, with an emphasis on improving the most common metrics-based approaches.

Historical perspective of coral reef resilience science

In the late 1960s, ecologists began to study the ability of ecosystems to exhibit alternative community states, each of which appeared to be stable over time, occurred in the same environment, and was fairly resistant to disturbance (Lewontin 1969; Holling 1973). The

term given to this phenomenon was ‘ecological resilience’ and ecosystems were said to be attracted to alternative equilibrial states (Holling 1973). Perhaps the first evidence that coral reefs might exhibit multiple states was the discovery of a stable patch of the unpalatable macroalga, *Asparogopsis taxiformis*, after a ship grounding and pollution event on the outer Great Barrier Reef (GBR, Hatcher 1984). Hatcher hypothesized that pollutants had provided an opportunity for the algae to bloom and once established, algae could persist by reaching a size escape from herbivory.

Nearly a decade later, the prospect of major shifts in coral community structure was revisited in a special issue of the journal *American Zoologist*. Done (1992b) coined the term ‘phase shift’ to describe a conspicuous change in community structure, referring to a drastic change from coral to macroalgal dominance. The term phase shift is symptomatic and has no explicit connotation of stability (Petraitis & Dudgeon 2004), and might involve alternative community states that become resistant to change owing to ecological feedbacks, or simply represent a reversible monotonic response of an ecosystem to a changing environment. In the same special issue of the journal, Knowlton (1992) published the first critical examination of mechanisms that might drive the existence of multiple alternative states on coral reefs. She mooted the idea that depleted herbivory could influence the competitive outcomes between corals and macroalgae and stabilise algal-dominated states. McManus and Polsenberg (2004) then proposed a conceptual model of key factors involved in reef phase shifts. To develop and reinforce the existence of multiple alternative states in reefs, Mumby and colleagues (2007) used a spatially-explicit and field-validated model of Caribbean coral communities. They proposed that the emergence of alternative states was a recent phenomenon in the Caribbean because reefs are not predicted to shift and lock when fast-growing acroporids or herbivory by sea urchins are returned to the ecosystem (Mumby, Steneck & Hastings 2013) yet both had been devastated from disease in the 1980s.

Although the existence of alternative stable states is a nuanced and by no means a universal phenomenon (Fung, Seymour & Johnson 2011; Mumby *et al.* 2013), the fact that some reefs have low resilience is beyond question. As more cases of reef decline and recovery were investigated, it became clear that reefs are profoundly dynamic systems that react and recover differently to perturbations and that resilience cannot be taken for granted (Pearson 1981; Brown & Suharsono 1990; Ginsburg 1993; Hughes & Connell 1999; Bellwood *et al.* 2004;

Graham *et al.* 2015). Moreover, Connell (1997) reviewed global patterns of reef recovery and found striking variability across the Pacific and the Caribbean; a pattern that persists today (Roff & Mumby 2012).

With growing awareness that the health of some reefs was experiencing persistent decline in the 1990s (Hughes 1994; Steneck 1994) – perhaps best marked by Bob Ginsburg’s ‘Colloquium on coral reef hazards and health’ (Ginsburg 1993) – science, management, and conservation agencies became increasingly engaged in understanding the processes determining the fate of reefs. West and Salm (2003) raised the idea of resilience-based management (RBM), albeit without coining the term, and proposed that interventions should be directed towards reefs less likely to be exposed to disturbance. They also proposed to focus interventions on the processes that confer resilience, facilitate recovery or help resist stress and disturbance.

Research into coral reef resilience continues to blossom and appears to follow five trajectories. The largest is the quest to understand individual processes underlying reef resilience, both in isolation and as cumulative stressors. This literature is too large to be summarised here but includes research into connectivity, demographic rates, ecological interactions and stress responses (Andres & Rodenhouse 1993; Roberts 1997; Cowen, Paris & Srinivasan 2006; Nyström *et al.* 2008; Fabricius *et al.* 2011; McClanahan *et al.* 2011; Doropoulos *et al.* 2016). Second is the identification of empirical resilience metrics that can be used to compare sites (West & Salm 2003; Obura & Grimsditch 2009; Maynard *et al.* 2010; Jouffray *et al.* 2015). Third is the use of statistical models to predict community trajectories and infer drivers of resilience trends (Zychaluk *et al.* 2012; Cooper, Spencer & Bruno 2015; Gross & Edmunds 2015). Fourth is the development of mechanistic ecological models to understand and integrate the processes of resilience and/or predict reef trajectories under multiple stresses (Mumby, Hastings & Edwards 2007; Anthony *et al.* 2011; Fung, Seymour & Johnson 2011; Blackwood, Hastings & Mumby 2012; Mumby *et al.* 2014b; Bozec & Mumby 2015). Finally, a broader set of frameworks has become available to link resilience science to decision-making (Game *et al.* 2008; McLeod *et al.* 2009; Mumby *et al.* 2011; McLeod *et al.* 2012; Anthony *et al.* 2015; Mumby & Anthony 2015).

Resilience concepts on coral reefs

There are three major usages of the term resilience in the coral reef and environmental literature. All three are introduced here in brief and then the behaviour of the most popular approach described in greater detail in a later section. The earliest usage of resilience considered the concepts of engineering and ecological resilience proposed by Holling (1996), which emerged from the modelling of predator-prey interactions revealing the ability of a system to undergo profound changes in community state (Holling 1961; Lewontin 1969; May 1972; Holling 1973). Engineering resilience refers to the time a system takes to return to a single equilibrium after a perturbation (Pimm 1984; Holling 1996). Ecological resilience considers the likelihood of the system [or social system, Marshall (2010)] to shift between multiple equilibria, separated by basins of attraction (Figure 2.1; Walker *et al.* 2002; Kinzig *et al.* 2006; Mumby *et al.* 2014b). Ecosystems can move towards different attractors because of the numerous reinforcing feedbacks that drive their behaviour even without external perturbations such as coral bleaching and storm damage.

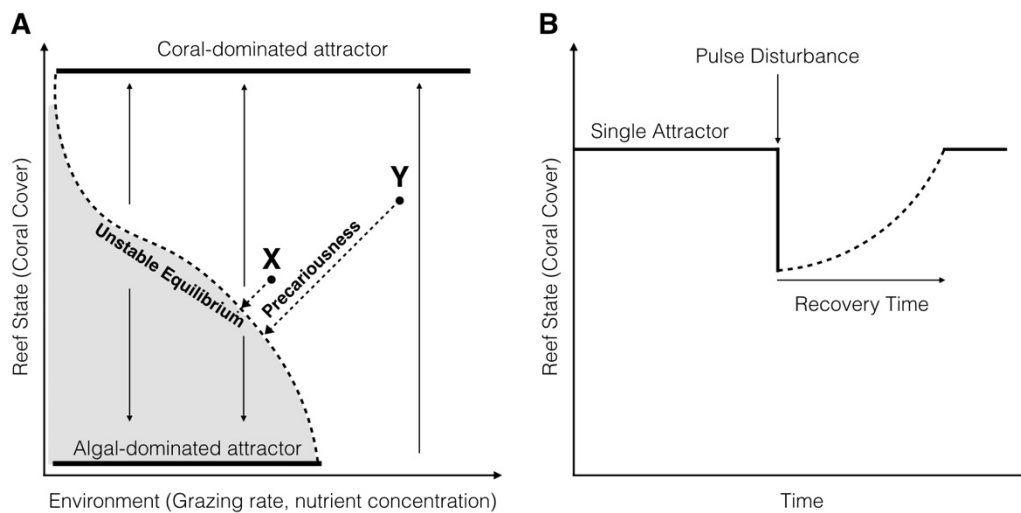


Figure 2.1. The differences between ecological (A) and engineering (B) resilience.

Precariousness is the distance of a reef to the suspected unstable equilibrium/tipping point.

The precariousness of Reef X is greater than Reef Y. Reefs that fall in the shaded grey area has an algal-dominated current attractor, and reefs are in the white area has a coral-dominated current attractor.

The second usage of the word resilience is an umbrella term and considers the behaviour of integrated socio-ecological systems, in which ecosystem dynamics might only be a single element amongst other components taken into consideration such as the role of human activity (Nyström, Folke & Moberg 2000; Folke 2006). Resilience in this context has been labelled ‘resilience thinking’ (Walker & Salt 2006) or ‘panarchy’ (Gunderson & Holling 2001), and provides a framework to consider the factors that stabilise and drive a system. The key aspects of resilience thinking include resilience, adaptability (adaptive capacity) and transformability (for more information please refer to Walker and Salt (2006); Folke *et al.* (2010); Bellwood *et al.* (2012)). The concept of panarchy refers to the hierarchical set of adaptive cycles at different scales and their effects across all scales (Gunderson & Holling 2001). These frameworks do not explicitly invoke ‘ecological resilience’, though multiple attractors may exist within the wider system or single components. Resilience thinking and panarchy provide a flexible framework to model complex systems and help identify metrics that confer resilience in social-ecological systems.

The third development of resilience on coral reefs is motivated by the ecological and social applications described earlier and seeks field-based metrics to ascertain the relative ‘resilience’ of sites (Hughes *et al.* 2005; McClanahan *et al.* 2012; Jouffray *et al.* 2015; Maynard *et al.* 2015). Because such snapshot metrics do not quantify dynamical aspects of the system – which is the preserve of engineering and ecological resiliences – they do not measure resilience directly; rather, they are useful in identifying sites that have a desirable set of metrics that indicate greater resilience. A major value of these approaches is that they do not depend on sophisticated models and are relatively easy to implement in the field. Since this approach does not quantify resilience *per se*, these approaches are better categorised as ‘vulnerability’ measures (Mumby *et al.* 2014a) and describe them hereon as a form of vulnerability.

Vulnerability as an alternative to the resilience concept

The concept of vulnerability emerged from the field of risk and hazard research (White 1974), and is the “degree to which a system, subsystem, or system component is likely to experience harm due to exposure to a hazard, either a perturbation or stressor” (Turner *et al.* 2003a). Because vulnerability is an encompassing concept warranting a number of measurement approaches (Alwang, Siegel & Jorgensen 2001; Eakin & Luers 2006), we discriminate between approaches that attempt to quantify the absolute vulnerability of a system versus those that create a relative measure of vulnerability. Obtaining an absolute vulnerability measure typically requires the specification of a critical threshold followed by an estimate of the probability of its transgression (Adger 2006). Examples might be the probability that coral cover falls below 10% within the next decade, or the risk of flooding in coastal cities in 2050 (Hallegatte *et al.* 2013). Estimation of absolute vulnerability requires a system model, whether it be statistical, analytical or simulation-based.

The second approach to measuring vulnerability, which in this chapter is termed ‘relative vulnerability’, often combines system metrics to compare vulnerability among sites or points in time. Here, the goal is not to calculate the absolute probability of an event occurring but rather to rank the relative vulnerability of sites and identify opportunities to reduce vulnerability (Eakin & Luers 2006). A common way to measure relative vulnerability is to

use the three components of the vulnerability framework: exposure, sensitivity and adaptive capacity (Adger 2006; Cinner *et al.* 2012). Vulnerability is calculated using the equation ‘exposure + sensitivity – adaptive capacity’, popularized by the Intergovernmental Panel on Climate Change (McCarthy 2001). Exposure is the nature and degree to which a system is exposed to stressors; sensitivity is the degree to which the stressors affect a system and is the opposite of resistance; and adaptive capacity is the ability of the system to adjust to the stressors or recover (Gallopín 2006). Metrics are chosen to represent exposure, sensitivity and adaptive capacity, and are measured and combined to provide a relative index for comparison of sites (Cinner *et al.* 2012). This method has been used to compare the vulnerability of fishing communities in face of climate change (Allison *et al.* 2009; Cinner *et al.* 2013) and to identify priority areas for management (Maynard *et al.* 2010; Maynard *et al.* 2015). Alternatively, many studies also seek to estimate the relative vulnerability of sites with a bespoke framework using specific components selected to suit the purpose of the study (i.e. resilience metrics).

These approaches are considered a form of vulnerability rather than resilience for three reasons. First, the measurement of static metrics cannot reflect the dynamical properties of a system (van Nes & Scheffer 2007; Nyström *et al.* 2008). Second, the definition of vulnerability is sufficiently flexible to be appropriate for the integration of ‘resilience metrics’ (Obura & Grimsditch 2009; Maynard *et al.* 2010). Third, empirical metrics alone are insufficient to make predictions and project trajectories into the future, a crucial element to measuring resilience (Standish *et al.* 2014).

Conceptual framework for measuring reef resilience and vulnerability

Following the major concepts of ecological resilience, engineering resilience and vulnerability, a framework of reef resilience quantification methods is proposed below and supported by case studies where applicable (Figure 2.2). Additional potential methods that have not been applied to reefs are also introduced under this framework.

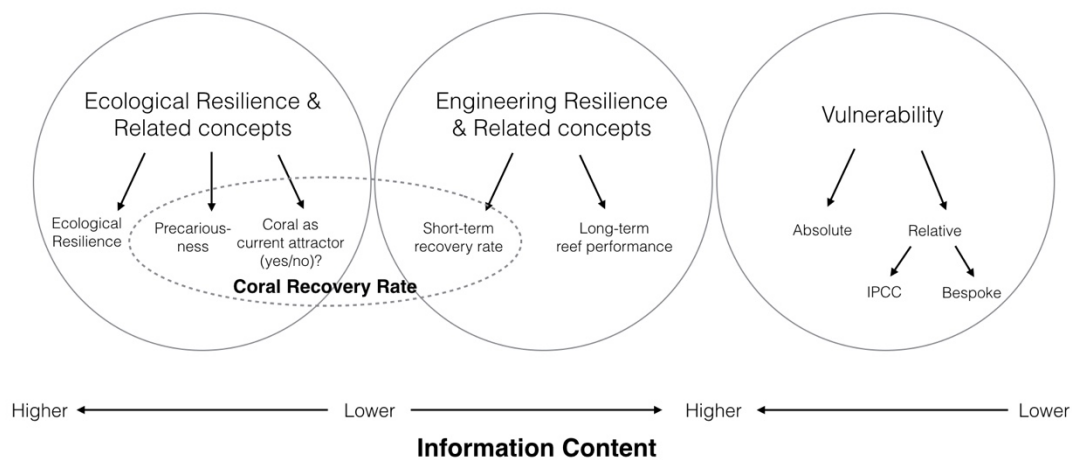


Figure 2.2 Conceptual diagram of resilience measurement on coral reefs.

Various methods of measuring ecological resilience, engineering resilience and vulnerability.

Dotted line represents cross-cutting methods that relate to coral recovery rate

Ecological resilience related approaches

1) Ecological resilience

An emerging approach to calculate the resilience of coral reefs uses mechanistic ecological simulation models to integrate available science. Mechanistic models can be used to ascertain whether multiple attractors are likely to exist and if so, predict the probability that a reef is pushed across tipping points within a specific period. This probabilistic approach embodies the original concept of ecological resilience (Holling 1973) and is an alternative to quantifying the ‘level of disturbance’ needed to tip a system, because the idea of measuring the ‘amount of disturbance’ across multiple disparate forms of disturbance (bleaching, cyclones, etc.) is impenetrable (van Woessik 2013). Rather, it is simpler to predict the probability of a system flipping attractor (also see van Nes and Scheffer (2007) who have developed a probabilistic approach in measuring the resilience of lake ecosystems).

An example of a mechanistic approach are models that have been tested against independent time-series data for the Caribbean (Mumby, Hastings & Edwards 2007) and the Pacific (Ortiz *et al.* 2014). For instance, the ecological resilience of the Belize Barrier Reef was modelled and mapped under two levels of local management action (business-as-usual vs. ban of herbivore fisheries) and two levels of action towards climate change (business-as-usual vs. a green economy; Mumby *et al.* 2014b). Resilience was calculated as the probability that individual reefs would still be exhibiting coral recovery by 2030 (i.e., remaining under the attractor of a coral-dominated state even though coral dominance is never actually attained). The study found that implementation of a herbivore fisheries ban enacted in 2009 might increase the resilience of the reef six-fold, although the benefits were variable among reefs. The concept was further operationalised by identifying thresholds of herbivore harvest and size limits that maintain resilience in face of external disturbances (Bozec *et al.* 2016). In a separate study, Graham and colleagues (2015) identified relationships of reef trajectory predictors and the probability of a regime shift and found that reef complexity and depth can correctly predict 98% of post-bleaching trajectories in their study sites within the Seychelles.

2) Precariousness

The prediction of resilience requires information on current system state, the location of underlying tipping points (unstable equilibrium, Figure 2.1), and predictive models of the disturbance regime. If the latter is unknown, an ‘instantaneous’ measure of resilience can be obtained by estimating the distance of the reef to suspected tipping points. This is termed precariousness (Figure 2.1; Walker *et al.* 2004) and can be used as a relative measure of resilience among sites. The closer a reef sits from the unstable equilibrium, the more precarious it is. The measurement of precariousness requires a comparison of the current system state to known tipping points. Although precariousness has been suggested in the wider ecological literature (Walker *et al.* 2004; Hodgson, McDonald & Hosken 2015), it has not been specifically measured for coral reefs. While the locations of unstable equilibria and thresholds have only been estimated for a very limited range of reefs, an interim approach might be to use the distance between a reef’s current state and the ‘tipping points’ identified for some Indian Ocean and Caribbean reefs for average system state against fish biomass (McClanahan *et al.* 2011; Karr *et al.* 2015). One advantage is that precariousness does not require the user to undertake modelling themselves. However, its shortcoming is the inability to account for exposure to external disturbances, such that two sites might lie equidistant

from tipping points (i.e. same precariousness) with one having a greater risk of being perturbed and hence lower resilience. In summary, the technique has its merits as a simple tool to compare relative resilience of sites that share a similar disturbance regime (Yeung & Richardson 2015).

3) Current attractor

An even simpler approach than precariousness is to know whether the reef is likely to exhibit recovery or decline before the next disturbance. The current attractor identifies whether a reef is attracted towards the coral or alternative state at a point in time (Figure 2.1). If a snapshot of the reef state is available, then, like precariousness, the identification of the current attractor requires existing knowledge on the unstable equilibrium to identify which basin of attraction the reef currently sits in (i.e. coral-, algal- or sponge-attractors). In the absence of models of the ecosystem, it might be possible to estimate the existence of tipping points from statistical analyses of monitoring data; i.e., community states where reef trajectories are uncertain and variable showing either recovery or decline between disturbances (Zychaluk et al 2011). Analyses of this type would require extensive data with at least short time series. The direction of each post-disturbance trajectory would allow the attractor to be identified at each initial state. Care must be taken not to confound this analyses with data from different physical environments where different attractors might occur (e.g., whereas a reef at 5 m might show recovery when coral cover is say 10%, a reef at 30 m might show decline when coral cover reaches an equivalent level).

Engineering resilience related approaches

The original definition of engineering resilience is impractical for coral reefs because reefs rarely attain a single coral-dominated equilibrium. However, two aspects of recovery rate can be operationalised. The first is a short-term recovery rate, usually measured directly from time-series. The second, termed reef performance, uses models to hindcast reef trajectories or project into the future, typically over longer periods of time (Mumby & Anthony 2015).

4) Short-term recovery rates

Rates of change and trends have commonly been used to examine coral reef recovery and decline by tracking changes in coral cover over time (Emslie *et al.* 2008; Graham, Nash &

Kool 2011; Johns, Osborne & Logan 2014). Despite being easily applicable, simple averaging is problematic as calculated rates are highly influenced by the initial coral cover and assumes linear growth rates (Côté *et al.* 2006). A more sophisticated way to obtain short-term recovery rate is through statistical models that can incorporate ecological processes and dynamics such as multivariate autoregression models (Zychaluk *et al.* 2012; Cooper, Spencer & Bruno 2015; Gross & Edmunds 2015). Recovery is usually quantified using exponential rates to reduce the dependence on initial state, such as the instantaneous growth rate of a logistic growth function (Haddon 2001), as there is a dependence of population growth rate (recovery rate) as a function of initial population size. Reefs with faster recovery rates have higher engineering resilience. In addition, it has been shown that recovery rates from disturbances reflect the distance to a tipping point, known as critical slowing down (CSD, Scheffer 2009; Veraart *et al.* 2012). In a coral reef context, Mumby (2009) demonstrated that recovery rates increase the farther the system sits from a tipping point. Thus, recovery rates can also be used as an instantaneous proxy of ecological resilience irrespective of future disturbance, and is correlated to precariousness. While short-term recovery rates cannot project reef state far into the future, they provide a useful basis for comparing the recoverability of reef locations.

5) Reef performance

In many cases, including the GBR, the state of the reef might decline despite significant investments in reef management such as improvements in water quality (De'ath *et al.* 2012). Here, the value of management is best viewed using counterfactual analyses that ask how much worse the system would look had management action been reduced (Mumby *et al.* 2017). Similarly, projecting how the reef might look into the future under different management scenarios provides a basis for management strategy evaluation. Mumby and Anthony (2015) proposed a framework that compares the trajectories of reefs under different levels of management and explicitly differentiates the degree to which local manageable stressors versus climate change and ocean acidification would contribute to loss of future reef state. Rather than calculating recovery rates based on the deviation from pre-determined equilibrium state (i.e. ideal amount of coral cover), this method allows for a shifting baseline considering ecological dynamics by projecting different scenarios. The approach is useful in systems where alternate attractors do not exist, since the metric is calculated by a comparison to the best possible trajectory given the disturbance regime (e.g. a site that is not frequently

hit by cyclones, with low influence of climate change but highly affected by a localised stressor such as crown-of-thorns starfish), and not a shift in alternate attractors. Moreover, modelling approaches like this have the power to project management effectiveness into the future but the spatial resolution of such patterns will be constrained by the finest scale of process information, which might be sea surface temperature (1-4 km), wave exposure (hundreds of metres), or larval connectivity (typically kilometres).

Vulnerability related approaches

Despite its roots in social science, the vulnerability concept is increasingly used in ecology (Beroya-Eitner 2016) and thus incorporated in the proposed resilience framework (Figure 2.2). Vulnerability is context-specific (Barnett, Lambert & Fry 2008) and its measurement can be grouped into two general categories. Absolute vulnerability allows comparisons across space and time, whereas relative measures only indicate rankings and are project/case-specific. It is useful to consider the suitability of using absolute or relative measures as data and skill requirements differ greatly (Alwang et al. 2001).

6) Absolute vulnerability

A measure of absolute vulnerability can be achieved through simulation or statistical models, providing data are available for the appropriate parameterisation. The measurement of absolute vulnerability requires an explicit benchmark (Alwang, Siegel & Jorgensen 2001), such as the vulnerability of corals to an increase of 1°C in seawater temperatures, to physical hurricane impact, or any other specific kind of disturbance. This approach is best implemented using models, be it statistical or mechanistic. System models are useful in quantifying vulnerability because the incorporation of explicit biological responses and ecological interactions lend themselves to projecting the response of a system into new environments (Scheffer & Carpenter 2003; Nyström *et al.* 2008). One example of an absolute vulnerability measurement in coral reef ecosystems is estimation of the number of years before coral cover fell below 10% in Belize (Mumby *et al.* 2014b). Statistical approaches offer an alternative to simulation models for understanding system dynamics. For example, Zychaluk *et al.* (2012) used a Markov process to project the average trajectory of coral reefs towards coral, algal or other endpoints. Alternative model formulations are also being used to incorporate a greater range of covariates (Cooper, Spencer & Bruno 2015), explore reef ecosystem stability in response to multiple disturbances (Gross & Edmunds 2015), and to

determine trajectories using Bayesian methods through reef accretion and recovery following disturbance (van Woesik 2013).

7) Relative vulnerability

Most published assessments of reef resilience utilised relative vulnerability and identified a series of reef attributes that confer resilience. Attributes are measured in the field, scored and aggregated to provide an overall ‘resilience metric’ at each reef location. Attributes are chosen by authors (Obura & Grimsditch 2009), collegial expert opinion (McClanahan *et al.* 2012), consultation of fishermen to anticipate social-economical responses to change (Marshall & Marshall 2007), literature review and relevance to geographic location (Maynard *et al.* 2010). Individual attributes are often weighted by importance prior to integration (Maynard *et al.* 2010; McClanahan *et al.* 2012). For example, Maynard *et al.* (2010) created an empirical framework where resilience attributes (indicators) were classified, ranked and weighted following scientific evidence. The final resilience score is simply the sum of all weighted scores. The great benefit of this metrics approach (i.e. relative vulnerability) is that it can be measured easily in the field and used to rank the vulnerability of sites (Beroya-Eitner 2016). Like all the approaches reviewed, it has some limitations and caveats (Table 2.1).

Table 2.1 Implicit underlying assumptions of the relative vulnerability approach

	<i>Metric Approach Analysis</i>	<i>Implicit assumptions / potential issues</i>	<i>References</i>
<i>Choosing Attributes</i>	1. Literature review	Ecosystem drivers in literature were from comparable system (physical environment, biodiversity, etc) to that being evaluated	Obura & Grimsditch 2009, Maynard et al. 2010, 2012
	2. Expert opinion ranking	Experts correct and that collective opinion is consistent and not a compromise such that attributes might not align with any individual opinion	McClanahan et al. 2010, Marshall and Marshall 2007
	3. Other management consideration of ecological services e.g. carbon sequestration	Will vary amongst approaches depending on the focus of programmes	Programmes within organizations
	1. Combining values of	Linear relationships	

	different attributes to get an overall resilience score	between attributes; score is a direct measure of resilience	
	a) Without weighting	All attributes contribute equally to resilience	Obura & Grimsditch 2009, Grimsditch et al. 2009
	b) With weighting	Weightings appropriate and attributes interact linearly	
	i) Ecological importance from literature	Ecosystem drivers in literature were from comparable system (physical environment, biodiversity, etc) to that being evaluated; relative importance of attributes appropriate	Maynard et al. 2010
	ii) Scientific evidence from literature/expert opinion	More studies on one attribute might elevate its perceived importance	McClanahan et al. 2012, Cinner et al. 2013
	2. Overall resilience scores classified into resilience categories (low, mid, high) based on predetermined ranges of overall scores	Linear relationships; overall scores directly translate to resilience categories	Maynard et al. 2012, Mamauag et al. 2013
	3. Comparison of individual attribute scores with no overall resilience score provided	No indication of the importance of each attribute to resilience	Bruckner 2012
<i>Link to Management</i>	1. Identified reef sites with the lowest to highest resilience	Score is a direct measure of resilience; does not link to further management actions.	Obura & Grimsditch 2009, Grimsditch et al. 2009, McClanahan et al. 2012
	2. Ranked 'management influence potential' to determine how management can influence the resilience of a reef site	The potential to be managed ranking directly influences the resilience of the systems	Maynard et al. 2010

A popular form of 'resilience assessment', one should note several issues when assessing resilience of reefs using the relative vulnerability approach. First, it does not project the likely future of reefs or quantify the expected impacts of management. Second, although the use of weightings can emphasise the disproportionate importance of some processes over others (Maynard *et al.* 2010), an implicit assumption remains that processes integrate linearly (Barnett, Lambert & Fry 2008). In reality, reinforcing feedback mechanisms are important

drivers of coral reef dynamics (Mumby & Steneck 2008) and tend to generate nonlinear interactions among processes (Birkeland 2004). For example, the outcome of having a ‘high’ value for coral larval supply depends strongly on the processes that influence settlement and post-settlement mortality, such as macroalgal cover (Dixon *et al.* 2015; Doropoulos *et al.* 2015) and corallivory (Doropoulos *et al.* 2016). The nonlinear and context-dependencies among processes are more easily dealt with using mechanistic models. Third, vulnerability assessments are sensitive to the number of metrics included in the analysis; the more metrics included, the less any particular attribute can influence the overall score. Yet an extreme value for one attribute (e.g., macroalgal cover) might be sufficient to reduce recovery severely (Mumby *et al.* 2015). An optimal number of metrics would likely sit between five and ten (Mayer 2008). Fourth, metrics are often assumed to be uni-directional, but factors can affect resilience in both directions depending on context and environment (Table 2.2). For example, ocean currents that contribute to connectivity may also become a threat to resilience by carrying pollutants, nutrients and diseases (Nyström, Folke & Moberg 2000; McClanahan, Polunin & Done 2002). Finally, while the empirical nature of vulnerability metrics approach is appealing, its dependence on field surveys tends to make it difficult to scale up. This is the converse problem with modelling studies which have large spatial extent but limited resolution at small-scales. Ultimately, the choice of approach (or approaches) will be determined, in part, by the scale or scales at which management is focused. Recent studies have advocated a nested approach that makes this explicit (Maynard *et al.* 2015).

Table 2.2 Variables used in resilience assessments that can have both positive and negative effects on resilience.

The signs + and - indicate a positive and negative effect on resilience respectively.

<i>Variable</i>	<i>Reason for affecting resilience</i>			
	(+)	<i>Reference</i>	(-)	<i>Reference</i>
Corals exposed at low tide	Promotes acclimatization and resistance	Obura & Grimsditch 2009; West & Salm 2001	Corals exposed to air for long periods causes mortality	Maynard et al. 2012
Currents	Larval transport;	Obura & Grimsditch 2009; West and Salm 2001	Wave action can cause colony breakage and	Maynard et al. 2012

	Temperature regulation; Prevent excessive buildup of toxins from bleaching	Obura & Grimsditch 2009 West and Salm 2001	result in injury of corals Carry pollutants, nutrients and diseases	Nyström et al. 2000
Mature colonies	Mechanically stronger; More recruits produced; Likely to have withstood a number a range of stressors and hence more resistant	McClanahan et al. 2011 Maynard et al. 2010 Maynard et al. 2010	More susceptible to bleaching	Mumby 1999; McClanahan et al. 2011
Sea urchins	Herbivory	Maynard et al. 2010; McClanahan et al. 2012; Obura & Grimsditch 2009; Graham et al. 2015	Bioerosion	Obura & Grimsditch 2009; West & Salm 2001
Turbidity/ Sedimentation	Less light penetration, less exposure to thermal stress	Obura & Grimsditch 2009; West & Salm 2001	Corals require physiological resources to tolerate sediments, which would increase its susceptibility to other stressors; Limits coral settlement	Maynard et al. 2010 Birrell et al. 2005; McClanahan et al. 2012

Upwelling	Reduces thermal stress during bleaching Cooling	Maynard et al. 2010;McClanahan et al. 2012 West & Salm 2001	Corals in upwelling areas more sensitive to temperature increases	West & Salm 2001
Wave exposure/energy	Increase oxygenation in water, enhances coral metabolism. Promotes water movement to flush toxins; Algal dislodgement	Obura & Grimsditch 2009 West & Salm 2001 Graham et al. 2015	Promotes algal growth	Graham et al. 2015; Mumby et al. 2014

Application of resilience assessments to reef management

The multiplicity of methods for resilience assessments has outpaced their incorporation into management. Each resilience method can be used to answer a suite of management questions (Table 2.3). Commonly, the end-point for many resilience assessments is a map of ranked vulnerabilities or ‘resilience metrics’, yet the pathway for these metrics to be incorporated into management decisions can be unclear. There has been some consideration on how to prioritise depending on the level of threats expected. Game *et al.* (2008) and Anthony *et al.* (2015) put forward comprehensive frameworks for the management process. What appears to be under-developed is formalising the link between the nature of a management intervention and its expected influence on resilience (or vulnerability).

Table 2.3 Management questions that can be answered using different resilience frameworks.

Note that 'precariousness' and 'current attractor' have not yet been implemented on coral reefs. * Requires a modified approach to simulate how the change in management will alter the final scores for relative vulnerability. ** Sensitive to how the integration of different attributes accurately represents the response of the reef ecosystem.

<i>Management Questions</i>	<i>Ecological Resilience</i>	<i>Precariousness</i>	<i>Current Attractor</i>	<i>Short-Term Recovery Rate</i>	<i>Long-Term Reef Performance</i>	<i>Absolute Vulnerability</i>	<i>Relative Vulnerability</i>
Will coral cover continue to increase given no disturbances?	✓	✓	✓	✓	✓	✓	x
What is the resilience of the reef at a future point in time?	✓	x	x	x	✓	x	x
What is the likely state of the reef in the next 2-3 years?	✓	✓	✓	✓	✓	✓	x
What is the likely state of the reef in the next 10+ years?	✓	x	x	x	✓	✓	x
How much greater is the resilience of reef X versus reef Y?	✓	x	x	x	✓	x	x
Which reefs are likely to have the greatest resilience?	✓	x	x	x	✓	x	✓
Where might no-take reserves have the greatest benefit on reef resilience?	✓	✓	✓	x	✓	✓	✓*
To what extent will improvements in water quality (or another management intervention) improve reef resilience?	✓	x	x	x	✓	✓	x
Which management intervention would improve reef resilience the most?	✓	x	x	x	✓	✓	✓**/**

A useful attempt to operationalise RBM utilized a metrics-based approach and identified metrics that were under potential management control and scored the likely ease of implementing such management at the site (Maynard *et al.* 2010). Another key consideration would be the degree to which management would improve the outlook or resilience score if implemented. Mumby *et al.* (2014b) specifically simulated the impact of a change in fisheries policy and mapped the expected increase in resilience across the reef. Mumby and Anthony (2015) went further and suggested management prioritisations would benefit from a simple framework that plotted current state or resilience on one axis and the degree to which management could improve that state or resilience on the other (Figure 2.3). A given management intervention would achieve the greatest ‘bang for buck’ where the scope for increasing resilience is maximised. Similarly, areas of low resilience that cannot be improved by management would receive a low priority for intervention.

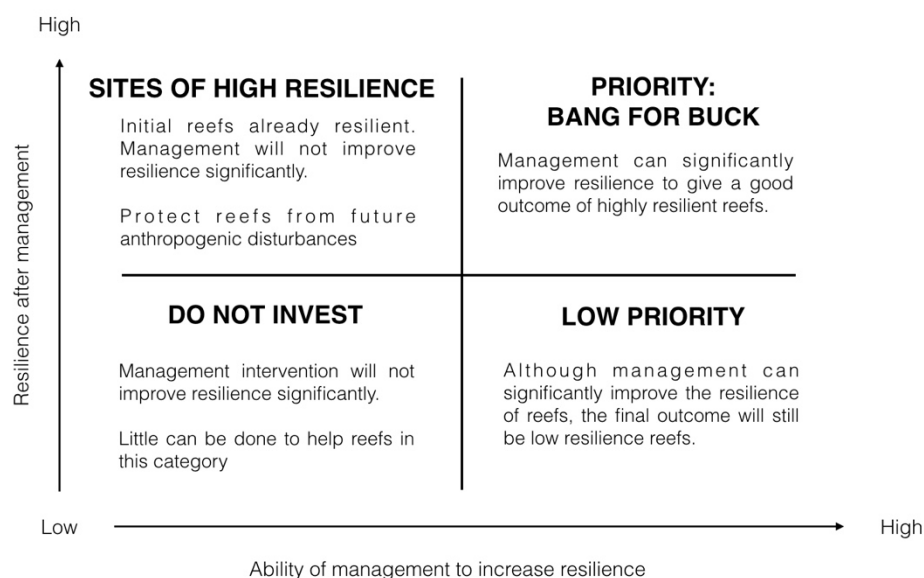


Figure 2.3 Decision making framework for investment strategy for locations with varying resilience levels and potential management impact.

Modified from Mumby and Anthony (2015).

A similar strategy to estimate the benefits of management implementation could be developed for metrics-based approaches. In addition to a site’s current vulnerability score, it would be possible to estimate the degree to which an intervention might increase that score, subject to local constraints. For example, a site might only have a standardised herbivory score of 0.5, implying intermediate herbivorous fish biomass. Were a marine reserve to be

established, herbivory would be expected to increase to the maximum score possible subject to limitations of the benthos, such as the local habitat complexity and the availability of food (cover of algal turfs). The researcher might turn to relevant analyses of bivariate relationships between variables to estimate these constraints; i.e., the relationships between herbivore biomass, habitat complexity, and algal cover (McClanahan *et al.* 2011; Karr *et al.* 2015). The outcome might be that herbivory could increase to a value of 0.8, which when combined with other influences of a reserve on other metrics, leads to a new vulnerability measure, ‘potential vulnerability if management enacted’.

To move towards strategic management planning, predictive approaches that link interventions to probable future reef responses would be useful. Given that the use of empirical metrics is the most widely-used resilience quantification approach, scientists need to facilitate the efficacy and predictability of metrics-based approaches. One challenge is to create a more sophisticated but accessible method for the integration of attribute values that captures the complex nonlinear interactions of physical, biological and ecological processes on reefs (Barbier *et al.* 2008; Nyström *et al.* 2008). This could be achieved by coupling ecological models with an interface that allows users to enter their attribute data and receive a prediction of resilience or recovery rate. An alternative is to combine the results of many monitoring assessments into a generic statistical framework that again allows users to input their metrics and receive a short-term prediction on the reef outlook (Eason *et al.* 2016). Creating a global reef knowledge-base and reanalysis of data would allow greater insight into the fate of reefs under different conditions, in which Bayesian Belief Networks (BBN) would be an appropriate tool (Renken & Mumby 2009).

3.

THE INFLUENCE OF RESILIENCE-BASED MANAGEMENT ON CORAL REEF MONITORING

Lam, V. Y. Y., Doropoulos, C., & Mumby, P. J. (2017). The influence of resilience-based management on coral reef monitoring: A systematic review. *PLoS ONE*, 12(2), e0172064. doi:10.1371/journal.pone.0172064

Abstract

With rapid changes taking place on coral reefs, managers and scientists are faced with prioritising interventions that might avoid undesirable losses in ecosystem health. The property of resilience captures how reefs react and respond to stressors and environmental changes. Therefore, in principle, management goals are more likely to be realised if resilience theory is used to inform decision making and help set realistic expectations for reef outcomes. Indeed, a new approach to reef management has been termed ‘resilience-based management’ (RBM). Yet, resilience concepts have often been criticised for being vague, difficult to operationalise, and beset by multiple definitions. Here, we evaluate how the advent of RBM has changed one aspect of reef management: assessment and monitoring. We compare the metrics used in conventional monitoring programs with those developed through resilience assessments and find that the latter have a stronger focus on ecological processes and exposure to environmental drivers. In contrast, monitoring tends to focus on metrics of reef state and has greater taxonomic resolution, which provides comprehensive information on the nature of changes but is less likely to predict the future responses of reefs. In addition, metrics measured by resilience studies are more diverse, owing in part to the reliance of state metrics as proxies of processes given the difficulty in quantifying key ecological processes directly. We conclude by describing practical ways of improving resilience assessments, and avenues for future research.

Introduction

The accelerating rate of change in many ecosystems (Millennium Ecosystem Assessment 2005; Hooper *et al.* 2012; Steffen *et al.* 2015) and apparent lack of recovery (Scheffer *et al.* 2001; Jones & Schmitz 2009; Gilljam, Curtsdotter & Ebenman 2015) has led to the perception that it is more appropriate to manage for ecosystem resilience rather than ecosystem state and condition (Walker & Salt 2006; Chapin III *et al.* 2009; Bestelmeyer & Briske 2012). This shift in management application has been termed ‘resilience-based management’ (RBM). RBM steers management actions towards the preservation of fundamental ecosystem functions, structure, identity and feedbacks (Chapin III *et al.* 2009). RBM departs from the classic view of steady-state resource management and instead attempts to focus on the processes that govern system dynamics (Anderies, Walker & Kinzig 2006). Contrary to the emphasis on the maintenance of a static perceived optimal state in traditional management approaches, RBM is closely tied to the prevention of regime shifts, whereby a conspicuous change to the structure and function of a system occurs once a threshold is surpassed (Scheffer & Carpenter 2003; Folke *et al.* 2004). Regime shifts involve complex feedback mechanisms that affect system dynamics, hence, a critical aspect of managing for resilience is a thorough understanding of ecological processes of the relevant ecosystems.

Monitoring and assessment are integral components of ecosystem management (Christensen *et al.* 1996; Nichols & Williams 2006), providing key information through empirical measurements and trend identification (Lindenmayer & Likens 2010). Historically, monitoring activities deliver a detailed account on ecosystem states with an emphasis on the abundance of important biological species. However, state indicators are not able to reflect important underlying system dynamics (Kupschus, Schratzberger & Righton 2016; Siddig *et al.* 2016). What is observed (i.e. the state) is the result of multiple interactions among the biophysical components of an ecosystem. Thus, in addition to ecosystem state changes, monitoring of ecological processes is fundamental to the successful implementation of RBM (Herrick, Schuman & Rango 2006; Crowder & Norse 2008; McLeod *et al.* 2013).

There is a long history of coral reef monitoring in different parts of the world (Wilkinson 1998; Jackson *et al.* 2014), with the majority of international programs initiated in the mid-

90s (Hill & Wilkinson 2004). The aim of these programs is to monitor and reflect the health of reef ecosystems, implemented through comprehensive surveys that record changes in the abundance of organisms and how they react to impacts (English, Wilkinson & Baker 1994). Conversely, metrics selected for resilience assessments aim to measure processes (Hughes *et al.* 2005), yet this is often difficult to achieve because many dynamic processes are not easily observable (Carpenter, Westley & Turner 2005), such as larval supply, settlement behaviour and post-settlement mortality.

Quantification is a crucial facet in the operationalisation of RBM, and efforts have concentrated on the identification of suitable resilience metrics (West & Salm 2003; Obura & Grimsditch 2009; Maynard *et al.* 2010; McClanahan *et al.* 2012). Although the focus on system dynamics for resilience assessments is apparent (Anthony *et al.* 2015), the extent to which RBM has transformed how reefs are evaluated and monitored is unclear. This study investigates how the introduction of RBM has changed the way reefs are surveyed. Specifically, we examine whether RBM has translated into an explicit change in the metrics surveyed and how it differs from earlier management approaches. To do so, metrics utilised by monitoring programs are compared to those adopted by more recent RBM approaches. Based on our results, new directions for resilience science are identified, in particular, on operationalising the metrics used for management and maximising the value of historical monitoring data.

Methods

A literature review was conducted to identify coral reef resilience studies that documented quantifiable metrics. A broad list of search terms was used to avoid missing any relevant research because resilience and monitoring studies often use different terminology. The search was conducted in July 2016 using the Web of Science service (ISI Thomson Reuters), with the key topics of “reef” and “resilience/regime shift” and “driver*/assess*/measure*/variable*/indicator*” and no limits on publication dates, which resulted in a total of 625 studies. A large proportion (95.8%) of the resulting studies included conceptual and theoretical research, and further analysis resulted in 10 resilience studies that contained quantifiable metrics suitable for analysis. Case studies using the same protocols were not included (total of 4 studies). For example, where Ladd and Collado-Vides (2013)

applied the resilience index developed by Maynard *et al.* (2010) in Mexico. Following, a snowball sampling technique was employed that expanded the search using reference lists from the initial pool of studies (Goodman 1961). Finally, twelve studies and six internationally recognised coral reef monitoring programs were identified that contained published protocols to represent resilience assessments and monitoring programs respectively. The classification of groups was based on the goals stated in each study, with the rationale behind the groupings outlined in Table S 3.1.

The initial stage of analysis included a thorough examination and documentation of metrics listed in each study, and the reasons for monitoring noted where applicable (Table S 3.1). Minor adjustments were made to the original terms describing metrics to minimise any biases resulting from heuristics (Table S 3.2). A total of 136 metrics were used to populate the data matrix, with a binomial response (present/absent) applied to each metric for each study in a multivariate data frame. Studies were visualised using non-metric multidimensional scaling (nMDS) and analysed for statistical significance among groups (resilience assessment, monitoring program) and locations (Caribbean, Pacific, Indian Ocean and global assessments) using PERMANOVA with 999 permutations to generate P values. Multivariate homogeneity of variance was tested using PERMDISP. SIMPER analysis was conducted to identify the key metrics that contribute to the similarities and differences between and within significant factors. Analyses were based on a Jaccard dissimilarity matrix, appropriate for presence-absence data (Clarke & Warwick 2001), and conducted using the software Primer-E v6 (Clarke & Gorley 2006) with the PERMANOVA extension.

The second analysis classified the full list of 136 individual metrics into 28 higher-level metrics (Table S 3.2), grouped into the general categories of biological community, disturbances, ecological processes and site characteristics for comparative analysis (Table 3.1). Abundance and diversity metrics were grouped under ‘biological community’, and include algae, corals, fish and other organisms found in the benthic community. Disturbance metrics that impacted the reef were grouped under ‘disturbances’, broadly separated into anthropogenic, biological, physical and physiological (Table 3.1). Process-oriented metrics were grouped under ‘ecological processes’, and include critical coral processes such as growth, recruitment and connectivity. Finally, metrics that reflected reef conditions were grouped under ‘site characteristics’, and contain information on the location, management

status and general environment of sites surveyed. Metrics were converted into presence/absence data for each study and the proportion of studies that measured the 28 higher-level metrics was calculated to indicate metric prevalence within the two groups (resilience assessment, monitoring program).

Table 3.1 Higher-level metrics classified under four general categories.

Classification used in Figure 2.2. For categorisation of original variables, refer to Table S 3.2.

<i>Category</i>	<i>Higher-level Metric</i>	<i>General areas covered</i>
Biological community (Richness, abundance, size, composition)	Algal cover	Size, diversity, growth form
	Algal biomass	
	Algal height	
	Coral community	
	Coral cover	
	Fish abundance	Diversity
	Fish size	
	Fish biomass	
	Fish community	
	Organisms (harmful)	
Disturbances	Organisms (unharmful)	Sponge, gorgonian, tunicate
	Other invertebrates	
	Seagrass	
	Anthropogenic	Development
	Biological	Human population
		Nutrients
		Water quality
	Physical	Bioerosion
		Invasive species
		Predation
Ecological processes	Physiological	Destructive fishing
		Hurricane/cyclone
		Physical impact
	Connectivity	Bleaching/thermal regime
		Disease
		Competition
		Growth
		Herbivory
		Mortality
		Recruitment
Site characteristics	Location & geomorphology	Depth
		Habitat
		Habitat complexity
		Location
		Reef type
		Reef zone

	Slope
Physical	Light conditions Temperature/thermal regime Salinity Wave exposure/tides/mixing Turbidity/visibility
Substrate	Rock, rubble, sand, silt, suitable for recruitment (substrate availability)
Management Status	Management

A final analysis was conducted to elucidate the potential of different metrics to provide information on reef processes used in the two groups of studies. Metrics from each study were classified into four broad categories: 1) state, 2) state/proxy, 3) proxy; and 4) process (Table S 3.2). ‘State’ represents static metrics (e.g., abundance), whereas metrics that directly measure rates and ecological processes are grouped under ‘process’ (e.g. recruitment, growth). Various state metrics are often used as proxies for ecological processes, such as herbivore biomass for herbivory, and these are grouped under ‘state/proxy’. Finally, metrics that were used directly as a proxy for a process within a study (i.e. indices developed to represent processes and disturbances such as coral submersion to estimate stress to corals when exposed to air, or number of boats to represent human impacts) were classified under ‘proxy’. When a state-only metric was explicitly used as a proxy for a process (42 out of 229 cases), metrics typically classified as ‘state’ (e.g., coral cover) were grouped under ‘state/proxy’. Metrics were considered on a case by case basis depending on how they were used in the particular study and the underlying measurement rationale (Table S 3.2). The proportion of metrics classified into each category were averaged to indicate differences between resilience assessments and monitoring programs.

Results

A total of 136 coral reef metrics was recorded, with monitoring programs and resilience assessments totalling 61 and 126 metrics respectively. Metrics used for resilience assessments differed significantly from those employed for monitoring ($p=0.01$, Table S 3.3, Figure 3.1), with an average dissimilarity of 75%. Despite the high dissimilarity between the two groups, metrics from resilience assessments encompassed many aspects observed by monitoring programs and had a higher multivariate dispersion (PERMDISP average

dispersion: resilience = 59.1; monitoring = 47.1, Table S 3.3), implying that resilience assessments measure a much wider range of metrics compared to monitoring programs. Two resilience studies in particular (AGRRA, Bruckner 2012), showed more similarity to monitoring studies than the other resilience assessments (Figure 3.1), and this may reflect their transitional nature. For example, AGRRA developed from monitoring methods in the late 1990s, but there was an explicit intent to include some process-level metrics, such as densities of coral recruitment and herbivore bite rates (Mumby, pers. obs. at AGRRA planning workshop). The influence of geographical location on measured metrics and the interaction between the two groups were both non-significant (Location: $p=0.18$; Group x Location: $p=0.534$; Table S 3.3).

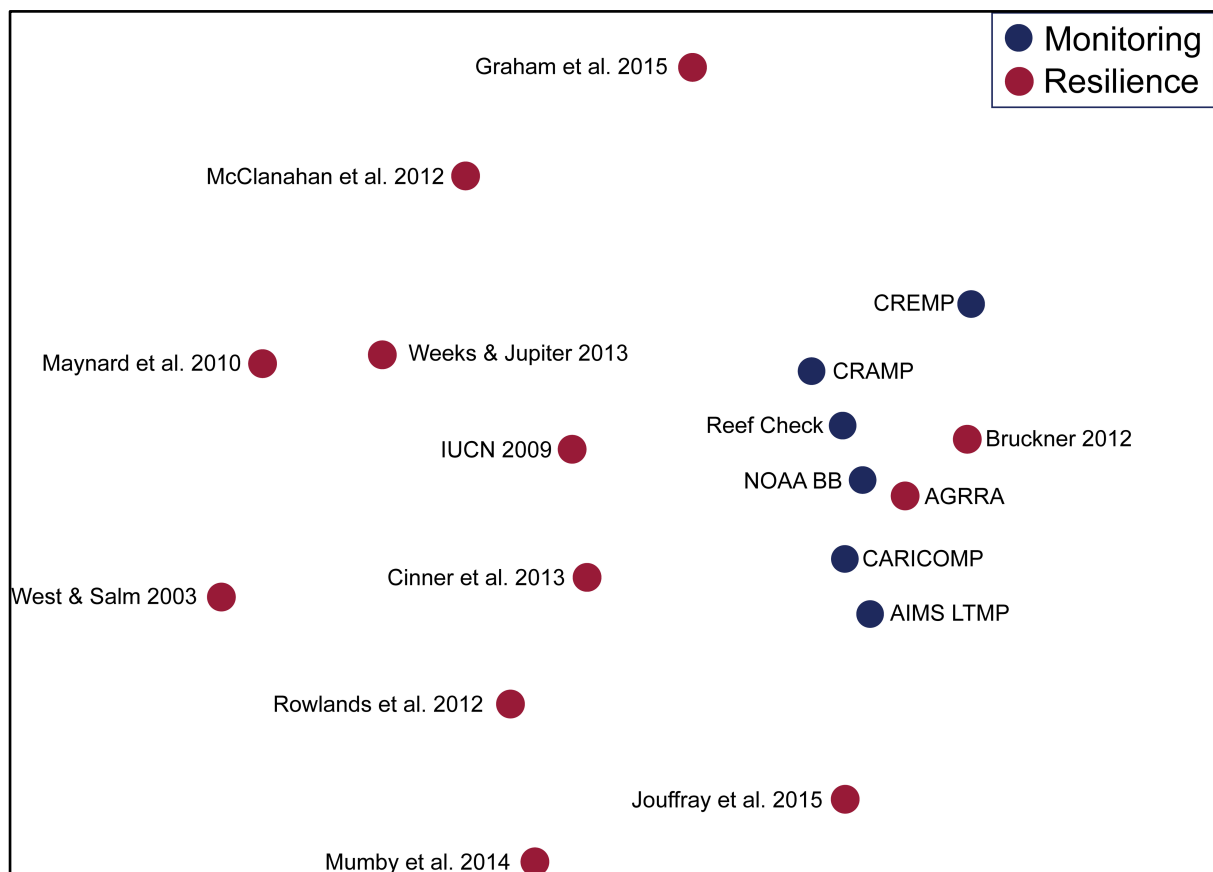


Figure 3.1 Non-metric multidimensional scaling plot (nMDS) comparing metrics used by studies with monitoring and resilience objectives.

AIMS = Long Term Monitoring Program, Australia Institute of Marine Science;
 AGGRA = Atlantic and Gulf Rapid Reef Assessment; CARICOMP = Caribbean Coastal Marine Productivity; CRAMP = Hawai'i Coral Reef Assessment and Monitoring Program; CREMP = Coral Reef Evaluation and Monitoring Project by Florida Fish and

Wildlife Conservation Commission; IUCN = International Union for Conservation of Nature (Obura & Grimsditch 2009); NOAA BB = National Oceanic and Atmospheric Administration, Center for Coastal Monitoring and Assessment, Biogeography Branch.

Monitoring studies had an average similarity of 42%. Key benthic state metrics such as coral cover (living, diseased, bleached and dead), algal cover (macroalgae, turf, crustose coralline algae), sessile invertebrate cover (soft coral, gorgonian, sponge, anemones, tunicates, ascidians) and substrate were used in more than two-thirds of the monitoring programs. Metrics reflecting biodiversity (coral and fish diversity) and site characteristics (location, habitat, temperature, depth, rugosity and turbidity) were also found in over half of the studies (Figure 3.2,

Table S 3.4). Metrics used in resilience assessments were more numerous and diverse, with a much lower average within-group similarity of 22%. Despite the high diversity of metrics being recorded, benthic components such as coral, macroalgal and substrate cover were used in more than half of the resilience assessments alongside drivers such as thermal regime, disease, fishing pressure and depth.

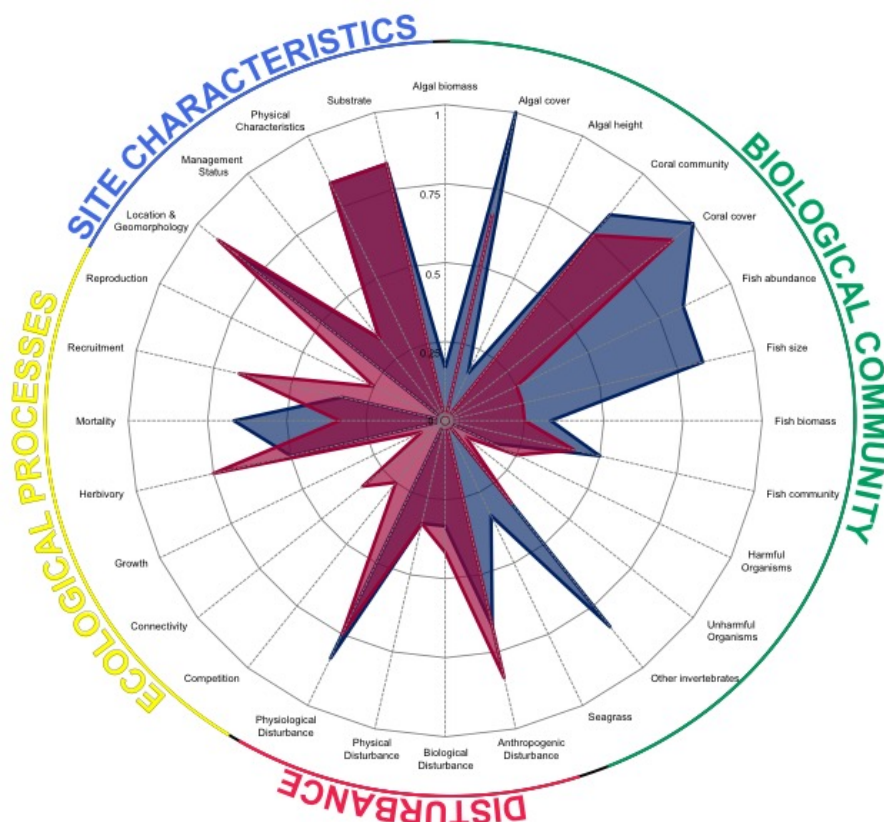


Figure 3.2 Higher-level metrics used by monitoring and resilience studies.

Blue and red areas represent monitoring programs and resilience assessments respectively. Axes points represent the proportion of studies within each study group that measured a given metric. Refer to Table S 3.2 for original metrics categorised under each higher-level metric.

Evidently, resilience assessments tend to focus on ecological and environmental processes, whereas monitoring programs concentrate on the biological community including benthic cover and organism abundances (Figure 3.2). Resilience studies tend to target specific functions, such as converting sea surface temperatures into thermal regime indices and identifying substrate categories suitable for coral recruitment (i.e. substrate availability). Monitoring programs tend to record sea surface temperatures changes and document all

substrate covers (i.e. sand, rubble and rock), leaving the analyst to determine the functions of the categories. Also, monitoring programs do not attempt to measure complex processes such as connectivity, competition and reproduction whereas most resilience assessments at least seek proxies for such processes. Monitoring studies often took note of other living organisms such as sessile and motile invertebrates, whereas resilience assessments focused on specific categories that are used as proxies for reef processes.

A more detailed examination of measurements by monitoring programs revealed that up to 35% metrics are state variables that can also be used proxies for processes (Figure 3.4), implying that scope exists to interpret monitoring data from a resilience perspective. Most metrics from monitoring programs are state variables (60%), with a strong focus on counts, abundances and diversity. In contrast, ~80% of the resilience assessment metrics fall under state/proxy, proxy and process categories. In resilience assessments, over half of the total measurements were states used as proxies for processes, signifying the critical role of surrogates in the development of RBM.

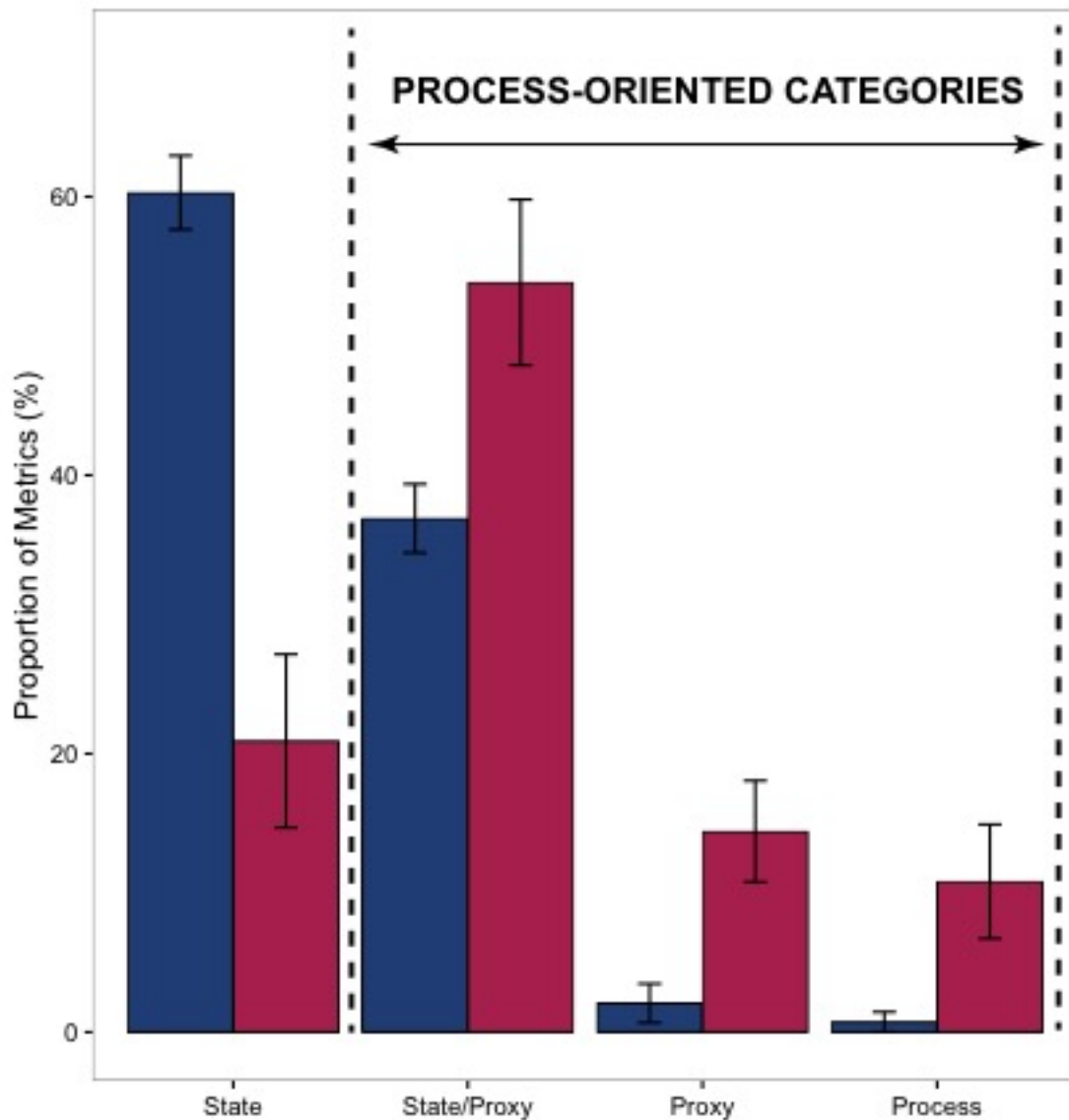


Figure 3.4 The potential of metrics to provide information on processes used in monitoring and resilience studies.

Blue and red bars represent monitoring and resilience assessments respectively. Error bars represent standard errors.

Discussion

Monitoring and resilience: “states” vs. “rates”

We found substantial differences in the metrics utilised by monitoring programs and resilience assessments and confirm that the introduction of RBM has influenced how reef surveys are conducted. Our study provides clear evidence that the intent of RBM has

translated into a real change in metrics surveyed, documenting a shift towards more process-oriented measurements as suggested by conceptual advice (Briske *et al.* 2008; Graham *et al.* 2013). The different foci of monitoring and resilience assessments reflect their respective objectives. Monitoring programs are concerned with the detection of detailed changes in the reef community, relying on state metrics that can be easily quantified. A strong emphasis on the biological community led to a higher degree of similarity within the monitoring group. Resilience assessments, on the other hand, have evolved from basic monitoring protocols to include additional ecological and environmental factors that provide insight on process dynamics (Allen *et al.* 2011; Bruckner 2012). Hence, resilience assessments often incorporate many of the metrics used in monitoring assessments, as shown in AGRRA (Lang 2003) and Bruckner 2012 (Bruckner 2012), as well as including a much larger variety of parameters.

Resilience assessments have a much higher variability of metrics used among studies than do monitoring programs. Results from the PERMDISP analysis show that multivariate dispersion observed for resilience assessments was 1.3 times more than monitoring programs, and there are reasons for this higher variability. First, resilience metrics include variables scored using systems such as the Likert scale to assign values rapidly in the field that would otherwise be complicated to quantify (e.g. self-, local- and distant-seeding that contributes to connectivity (Obura & Grimsditch 2009)), whereas monitoring programs do not attempt to quantify such variables. Second, metric variability within the resilience group occurs with the inclusion of modelling studies that incorporate the direct quantification of processes and rates such as growth, mortality and recruitment, which is hard to achieve in field-based resilience assessments, especially for snapshot surveys (Cinner *et al.* 2013; Mumby *et al.* 2014b). Third, monitoring studies have well-established protocols whereas resilience metrics are often modified and adapted to study sites or region (Maynard *et al.* 2010; Weeks & Jupiter 2013).

In line with literature advocating for the development of surrogates for processes measured in resilience assessments (Carpenter, Westley & Turner 2005), it is encouraging that resilience studies utilised a high proportion of state metrics, with the intent of using them as proxies for reef processes. Evidently, state metrics, when used appropriately, can provide valuable information on ecosystem dynamics (Flower *et al.* 2017). However, there are certain advantages and disadvantages associated with the use of proxies. Multiple proxies can be used to represent the same process or disturbance, and allows resilience assessments to be

more flexible in data acquisition. For instance, distance to the nearest river mouth or human population density are both used as proxies for human disturbance (Jouffray *et al.* 2015). However, proxies also contribute to the high diversity of metrics used in resilience assessments. High metric variability may add to the complexities of quantifying resilience using field-based measurements (Standish *et al.* 2014; Angeler & Allen 2016), thus, further work is needed to identify a uniform set of resilience metrics. Particular emphasis should be given to improving metrics for processes and drivers, as many of these are hard to observe using single proxies, making unification difficult (Quinlan *et al.* 2016).

From metrics to management

Despite finding clear differences between the metrics used in monitoring programs and resilience assessments, a substantial proportion of monitoring metrics have the potential to be used as proxies for processes and therefore help hindcast changes in ecosystem drivers. Relevant state metrics can be identified and interpreted using a resilience perspective to understand reef dynamics and assist with the interpretation of future reef trajectories based on mechanistic ecological relationships. The development of protocols on how state metrics can be interpreted to identify potential drivers and to estimate reef recovery based on ecological knowledge has recently been demonstrated by Flower *et al.* (2017). For instance, a decrease in juvenile coral density may imply a reduction of substrate availability, larval supply, or the occurrence of disturbance. However, if turf canopy height is also found to increase, a diagnosis can be refined suggesting that the substrate is becoming less hospitable for recruitment, either because of reduced herbivory and/or greater rates of primary production (nutrients). With appropriate tools and analyses, valuable information collected from historical monitoring programs can be used to apply RBM to coral reefs.

In all types of surveys, there exists a trade-off between the speed and ease of data collection, and the level of taxonomic resolution. Our results show that resilience assessments have deviated from documenting detailed changes in the biological community to focusing on a few metrics representing key reef processes (McClanahan *et al.* 2012). Examples include documenting coral functional groups instead of species (Graham *et al.* 2015), and omitting groups of organisms that have less well understood ecosystem roles such as sponges, ascidians and tunicates (McClanahan *et al.* 2012). Functional approaches were developed where species level is either too difficult to acquire, or so variable that it imparts little information (Steneck & Dethier 1994). Resilience assessments tend to take a functional

approach to the benthos, suggesting an implicit assumption that species-specific measurements are less relevant, such as focusing on branching coral cover (Graham *et al.* 2015) and in some cases, only using coral cover in total (McClanahan *et al.* 2012; Cinner *et al.* 2013).

Many high taxonomic level metrics currently assessed by monitoring programs contain valuable information for reef management and should not be left out (Flower *et al.* 2017). For example, if management is focused on conserving biodiversity, then species level taxonomic resolution is a necessity. While higher-level taxonomic data are more time consuming to collect, the data can be combined into functional groups if desired. Detailed benthic documentation is important even when simplified to major lifeforms, especially when results are linked to ecosystem functioning such as the critical role of plating corals in driving rapid reef recovery in the Pacific (Halford *et al.* 2004; Ortiz *et al.* 2014; Doropoulos *et al.* 2015) and the importance of branching *Acropora* as a nursery habitat for juvenile fishes (Floros & Schleyer 2016). The attempt to make resilience assessments logistically more feasible with lower resolution data may limit the insights that can be drawn with respect to reef functioning. To provide a comprehensive understanding for current and future RBM, it is critical to work out an optimal strategy to find a balance between monitoring state vs. process metrics, and the level of taxonomic resolution (Quinlan *et al.* 2016). A potential approach would be to adopt as detailed taxonomic resolution as is possible for some of the most important ecological processes driving resilience and compromise the taxonomic resolution on others.

Avenues for future research

Two of the continuing challenges for reef monitoring, whether with a taxonomic or more resilience-based focus, are incentivising data collection and linking the results to management actions. Greater synthesis and interpretation of monitoring data could help resolve both problems by adding interpretative value to the products. Currently, many monitoring programmes archive data, and while overall trends are plotted, there is often limited interpretation of patterns. Are the trends of concern or merely natural fluctuations? Can the trends be used to diagnose a problem and suggest a management intervention? Greater efforts to provide a diagnostic and interpretative interface, including the use of decision trees, can enhance the usefulness of data (Flower *et al.* 2017). Here, the

incorporation of process-orientated metrics along with changes in state can help provide diagnostic power.

Another opportunity to enhance the usefulness of monitoring data is in understanding and predicting reef dynamics. For example, statistical models such as Bayesian Belief Networks (Renken & Mumby 2009; Franco *et al.* 2016) can draw on individual case datasets to build predictive models. The more diverse the input data, in terms of environments and ecosystem states sampled, the stronger the predictions become. In an ideal scenario for coral reef monitoring data, it would be possible to imagine a central coral reef BBN being updated by multiple sets, with data providing new combinations of reef state and process and the ensuing trajectories. Individual practitioners could add their data and benefit from the functionality of the full reef model. A desirable outcome of this approach is that monitoring data are used to construct a dynamic model of the ecosystem that allows managers and scientists to run ‘what if’ scenarios, such as the likely consequences of reducing nutrient concentrations influencing reefs of a particular state and in a particular environment (Ban, Pressey & Graham 2014).

While utilising a global knowledge-base should improve predictions of reef state, it clearly raises concerns over heterogeneity in reef functioning. For example, processes influencing resilience, including the bottom-up and top-down drivers of macroalgal populations and the sensitivity of corals to algal interactions, can vary enormously between major biogeographic regions (Roff & Mumby 2012; Mumby *et al.* 2015). Therefore, there remains a need for studies to identify the proximate drivers of reef dynamics across a diversity of environments (Chollett *et al.* 2012). Some of this can be achieved through globally-replicated experiments (Steneck, Arnold & Mumby 2014; Mumby *et al.* 2015) and regional analyses of bivariate relationships (McClanahan *et al.* 2011; Karr *et al.* 2015), but it is critical that key processes are disaggregated and not lost as confounding effects in broad-scale studies (Williams *et al.* 2015).

This paper is written for both scientists and managers to identify promising new directions for RBM. There exists a wealth of monitoring data from different parts of the world that is highly fragmented and has rarely been analysed comprehensively (Jackson *et al.* 2014). While not specifically designed to measure processes, many monitoring variables provide a proxy of process. By using statistical approaches that consolidate monitoring data and

hindcast trends in reef health (Zychaluk *et al.* 2012; Cooper, Spencer & Bruno 2015), comparisons can be drawn between the observed trajectory of reefs and those predicted from novel metrics-orientated approaches.

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Supporting Information

Table S 3.1 The rationale behind the classification of studies into monitoring programs and resilience assessments.

<i>Study/Program</i>	<i>Stated goals</i>	<i>Rationale</i>
The Atlantic and Gulf Rapid Reef Assessment (AGRRA)	Goal: Provide a database suitable for comparative evaluation of current reef condition with a focus on ancillary observation on reef distribution, community structure, geomorphology and identification of localised threats. Approach: To characterise and compare reef conditions, distinguish between local and regional impacts and to recognise the effect of acute and chronic stressors on reef ecosystems through collecting data on key variables that reflect the structure and function of reef ecosystems. Methods: Collect relatively simple quantitative indicators of reef condition, and abundance and trends at specific depth intervals. Time period: 1997 – present Reference: Lang et al. 2003	Despite being a well-known monitoring program, the AGRRA protocol differs from other monitoring programs with greater emphasis on the link between key variables and ecological processes to provide an indication of reef resilience. In addition, Brucker (2012) has stated AGRRA as one rapid ecological approach that can provide an indication of the reef resilience together with the IUCN resilience assessment protocol (Obura & Grimsditch 2009). Hence AGRRA is classified under resilience assessments for this analysis.
Australian Institute of Marine Science, Long-Term Monitoring Program (AIMS LTMP)	Objective: Monitor status of benthic coral reef communities to quantify percent cover changes in benthos over time Time period: 1992 – present Reference: Jonker et al. 2008	The AIMS LTMP protocol focuses on monitoring the status of benthic coral reef communities and cover changes, and hence is classified as a monitoring program.
Bruckner 2012	Objective: Determine the history of disturbance and resilience of reef sites using static measurements of resilience using a rapid assessment technique.	This study focuses on variables that will help determine the resilience of a site, despite acknowledging its limits as a one-off study that relies on static metrics. This is

	Approach: Focused on coral population dynamics and is a hybrid strategy between AGRRA and IUCN resilience protocols with a few modifications. Data collected in 2010. Methods: Characterise colony size structure, partial mortality, recruitment and whether juvenile corals represent growing recruits or remnant colonies.	classified as a resilience study based on the intention of the study.
CARICOMP	Goal: A regional scientific program to study land-sea interaction in the Caribbean coastal zone and create a network of observers that can collaborate on region-wide events. Approach: Record changes in coral reef ecosystems by the regular monitoring of physical and biological factors and to distinguish between natural and human impacts. Time period: 1992 – present Reference: Alcolado et al. 2001	CARICOMP is a long-term regional monitoring program in the Caribbean, with a focus on the regular recording of the changes in physical and biological parameters. Hence CARICOMP is classified as a monitoring program.
Cinner et al. 2013	Goal: To assess and compare the key ecological and social components of coastal social-ecological systems. Approach: Used three categories including environmental exposure, ecological sensitivity and ecological recovery potential, to represent the ecological components of the coastal social-ecological system. Data collected in 2009, 2011-2012. Methods: Developed metrics to represent key characteristics of ecological exposure, ecological sensitivity and recovery potential of reefs to bleaching. Recovery potential was represented by ten indicators of ecological sensitivity and recovery potential.	Although termed as a vulnerability study, this study developed metrics for ecological exposure, ecological sensitivity and recovery potential of coral reef ecosystems which are compatible with the resistance and recovery concepts in resilience. In addition, the study used the resilience metrics weighting proposed by McClanahan et al. (2012), hence is classified as a resilience study using the relevant ecological metrics.
CRAMP	Goal: Established in 1998 to monitor the long-term changes	CRAMP focuses on repeated measurements of organisms

	of reef benthic communities in Hawaii, and to evaluate the reef condition. Methods: Monitoring of the abundance and cover of organisms, in addition to environmental parameters at permanent sites over time. Time period: 1998 – present Reference: Jokiel et al. 2001	and environmental parameters to evaluate the condition of reef communities in Hawaii, and hence is classified as a monitoring program.
CREMP	Goal: To monitor trends of reefs in the Florida Keys National Marine Sanctuary (FKNMS). Methods: Monitoring assessments conducted annually at permanent sites on changes in benthic cover and diversity of corals and other reef organisms Time period: 1996 – present Reference: Ruzicka et al. 2009	CREMP focuses on the collection of state metrics such as changes in benthic cover, trends and diversity, and hence is classified as a monitoring program.
Graham et al. 2015	Goal: To use site-level factors to predict whether sites would experience a regime-shift or recovery. Methods: Site factors were chosen based on evidence from literature that targets key processes or key roles in structuring coral reef ecosystems globally. Data collected in 1994, 1998, 2005, 2008 and 2011.	In this study, 11 factors were chosen based on existing literature to represent key processes in coral reef ecosystems that will allow the prediction of a regime-shift. As resilience can be defined as the probability of a system shifting into a different regime, this is classified as a resilience study.
Jouffray et al. 2015	Goal: To detect and define potential multiple ecosystem regimes using a comprehensive coral reef dataset in Hawaii. Methods: Tested and identified key human and environmental variables that were associated with different coral reef regimes. Data collected in 2010.	A number of predictor variables were identified to define multiple ecosystem regimes in a Hawaii coral reef ecosystem in this study. As resilience can be defined as the probability of a system to shifting into a different regime, this is classified as a resilience study.
Maynard et al. 2010	Goal: To develop a framework towards the	This paper introduces a framework that outlines metrics

	operationalisation of coral reef resilience. Methods: Identified 19 indicators of coral reef resilience with weighting based on evidence and management effectiveness. The framework provides a method to generate scores for individual sites based on the evaluation of the identified indicators. Data collected in 2007, 2008.	for assessing resilience, and hence is classified as a resilience study.
McClanahan et al. 2012	Goal: To develop selection criteria for prioritising coral reef resilience indicators and to identify reefs with the greatest resilience to climate disturbance. Methods: Analysed a suite of resilience indicators and Identified priority resilience indicators based on scientific evidence and expert opinion.	The goal of the study is to prioritise key indicators for quantifying resilience based on literature evidence and expert opinion, and hence is classified as a resilience study.
Mumby et al. 2014	Goal: To quantify the ecological resilience of the Belize barrier reef under different scenarios of climate change. Methods: Integrated biophysical data and modelled complex interactions among coral reef processes and different types of disturbance. The model was used to measure/calculate resilience, which is defined as the probability that a reef remained in the coral-dominated regime.	This paper uses biophysical data to model ecological processes and disturbances to derive measurements of resilience for reefs in Belize, and hence is classified as a resilience study.
NOAA Center for Coastal Monitoring and Assessment, Biogeography Branch	Goal: To characterise and monitor the distribution, abundance and size of marine coral reef organisms and develop data collection and management protocols. Methods: Long-term measurements of coral reef organisms and relate it with habitat data to establish a knowledge base. Time period: 1990 – present Reference: Pittman et al. 2010	NOAA’s Biogeography Branch focuses on monitoring state metrics such as disturbance, abundance and size of marine fauna found in reefs, and hence is classified as a monitoring program.
Obura & Grimsditch 2009 (IUCN)	Goal: To develop protocols to understand resistance and resilience indicators for management applications and to	This report details a protocol developed by IUCN, identifying 61 metrics that can be used to assess coral reef

	determine how MPA management actions can affect a reef's resilience and resistance. Methods: A rapid assessment of resistance and resilience indicators at individual site levels and to assess past management actions in the maintenance of reef resilience.	resilience, and hence is classified as a resilience study.
Reef Check	Goal: To survey and assess the health of coral reefs globally with a standardised method to allow comparisons of survey results. Methods: Focus on the abundance of specific reef organisms that reflect the condition of reef ecosystem and are easily recognizable to the public. Time period: 1996 – present Reference: Hodgson et al. 2006	Reef check is a global monitoring program designed to allow the public to collect information and document coral reef ecosystem change. It is focused on the abundance and trends of key reef organisms, and hence is classified as a monitoring program.
Rowlands et al. 2012	Goal: To develop a method to use remote sensing data to estimate coral reef resilience and to measure the differences in resilience of different reef sites in the Red Sea. Methods: Indices are used to utilise remote-sensing data to quantify resilience, and are divided between factors that stress, contribute to resistance or promote coral growth and recovery.	This goal of this study is to develop a method to quantify resilience using remote-sensing data, and hence is classified as a resilience study.
Weeks & Jupiter 2013	Goal: To identify critical areas for reef resilience that would be suitable for adaptive co-management by establishing marine protected areas. Data collected in 2005. Methods: Identified site-level indicators for reef resilience based on literature and conducted surveys to collect data that were analysed to produce a single resilience score for individual sites.	Despite being termed as an adaptive co-management study on marine protected areas, one component of this study identified critical areas for reef resilience by using site-level indicators of coral reef resilience and hence is classified as a resilience study.

West & Salm 2003	Goal: Identify factors of resistance and resilience to identify reef areas that most likely to be resilient to climate change. Methods: Proposed indicators that are related to factors that reduce stress and environmental factors that enhance coral resistance and recovery.	This paper identifies metrics that are related to the resistance and recovery of corals, and hence is classified as a resilience study.
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Table S 3.2 Original metrics used in studies and their respective classification the three phases of analyses.

The standard metric, higher-level metric and metric categories were used in Figures 3.1-3.3 respectively.

#	<i>Original metric</i>	<i>Standard metric</i>	<i>Higher-level metric</i>	<i>Metric Categories</i>	<i>Additional information on metric</i>	<i>Reference</i>
1	Latitude and longitude	Latitude/Longitude	Location & Geomorphology	State		AGRRA
2	Reef type	Reef type	Location & Geomorphology	State	Zones of maximum reef development are highly recommended: shallow reef crests (<5m), intermediate depth (5-15m) linear or patch reefs. Other examples are atolls, fringing and barrier reefs, etc.	AGRRA
3	Site exposure (windward or leeward)	Site exposure	Location & Geomorphology	State/Proxy	Location with respect to the normal wind patterns (windward, leeward, seasonally variable) and open ocean	AGRRA
4	Reef zone	Reef zone	Location & Geomorphology	State	Geomorphic zone of a reef on an insular or continental shelf: shore, bay, lagoon, intertidal crest, channel, forereef, etc.	AGRRA
5	Reef subtype	Reef subtype	Location & Geomorphology	State	Thicket, reticulate, coral field, rubble field, sand/mud (not a real reef)	AGRRA
6	Angle relative to horizontal	Slope	Location & Geomorphology	State	Flat, moderate slope, steep slope, wall, etc.	AGRRA
7	Vertical relief	Relief	Location & Geomorphology	State		AGRRA
8	Management	Management	Management Status	State/Proxy		AGRRA
9	Depth	Depth	Location & Geomorphology	State		AGRRA
10	Temperature	Temperature	Physical characteristics	State/Proxy		AGRRA
11	Live coral by species (or genus)	Coral cover (genus)	Coral cover	State	Primary reef constructors, universal reef condition indicator	AGRRA
12	Species diversity	Coral diversity	Coral community	State		AGRRA
13	Bleached coral cover	Bleached coral	Disturbance	State/Proxy	Indicates altered reef conditions (often thermal stress when large	AGRRA

		cover	(Physiological)		scale)	
14	Pale live coral cover	Paling coral cover	Disturbance (Physiological)	State/Proxy	Indicates beginning of bleaching, or beginning of recovery after having bleached	AGRRA
15	Newly dead coral cover	Dead coral cover	Mortality	State/Proxy	Indicates ongoing disease, bleaching, predation, competition, or other perturbations	AGRRA
16	CCA	CCA	Algal cover	State/Proxy	Cement broken corals together to make reef framework, may indicate good conditions for coral recruits to settle	AGRRA
17	Newly dead CCA	CCA Dead	Algal cover	State		AGRRA
18	Calcified worm tubes	Substrate	Substrate	State		AGRRA
19	Microbial and/or microalgal biofilm	Biofilm	Algal cover	State/Proxy	When corals die, skeletons quickly covered with biofilms of bacteria/microalgae, often mistaken as bare space. Coral larvae can settle here.	AGRRA
20	Cyanobacteria cover	Cyanobacteria	Algal cover	State	Photosynthetic organisms that compete with corals for space on reefs, may also shelter pathogens that can kill corals	AGRRA
21	Sparse turf algae	Turf	Algal cover	State	Eaten by many herbivorous fishes and <i>Diadema</i>	AGRRA
22	Turf algal mat (TAM)	Turf algal mat	Herbivory	State/Proxy	Indicates few herbivores, this prevents coral larvae from settling and overgrows corals and CCA. May also shelter pathogens that kills corals	AGRRA
23	Turf algal sediment mat	Turf algal sediment mat	Algal cover	State/Proxy	Not eaten by herbivores, inhibit settlement of coral larvae, overgrow corals and CCA. May shelter pathogens that kill corals.	AGRRA
24	Fleshy/calcareous peyssonnelid	Peyssonnelid	Algal cover	State	Inhibits settlement, unlike other CCA. Some species overgrow corals and CCA.	AGRRA
25	Fleshy macroalgae	Macroalgae	Algal cover	State/Proxy	Eaten by some herbivorous fishes, some overgrow corals and CCA, inhibit coral larvae from settling and shelter pathogens that kill corals	AGRRA
26	Calcareous macroalgae	Coralline algae	Algal cover	State	Eaten by some herbivorous fishes, some overgrow corals and CCA, inhibit coral larvae from settling and shelter pathogens that kill corals	AGRRA
27	Macroalgal height	Algal height	Herbivory	State/Proxy	MA volume = cover x height, proxy for biomass, is inversely related to herbivory	AGRRA

28	Newly dead macroalgae	Macroalgae Dead	Algal cover	State		AGRRA
29	Aggressive invertebrates - <i>Cliona delitrix</i> , zooanthellate <i>Cliona</i>	Harmful organisms	Organisms (Harmful)	State/Proxy	Kill and expand over corals and CCA as they grow	AGRRA
30	Aggressive invertebrates - <i>Chondrilla caribensis</i>	Harmful organisms	Organisms (Harmful)	State/Proxy	Kill and expand over corals and CCA as they grow	AGRRA
31	Aggressive invertebrates - <i>Millepora alcornis</i>	Harmful organisms	Organisms (Harmful)	State/Proxy	Kill and expand over corals and CCA as they grow	AGRRA
32	Aggressive invertebrates - <i>Briarium asbestinum</i> , <i>Erythropodium caribaeorum</i>	Harmful organisms	Organisms (Harmful)	State/Proxy	Kill and expand over corals and CCA as they grow	AGRRA
33	Aggressive invertebrates - <i>Palythoa caribaeorum</i> , <i>Trididemnum solidum</i>	Harmful organisms	Organisms (Harmful)	State/Proxy	Kill and expand over corals and CCA as they grow	AGRRA
34	Sessile invertebrates - Epibenthic sponge	Other Invertebrates (Sessile)	Other invertebrates	State	Usually don't kill and expansively overgrow corals and CCA	AGRRA
35	Sessile invertebrates - Gorgonian	Other Invertebrates (Sessile)	Other invertebrates	State	Usually don't kill and expansively overgrow corals and CCA	AGRRA
36	Non-living - Crevice	Substrate	Substrate	State	Coral larvae can settle here	AGRRA
37	Non-living - Sand, mud, sand-mud mix	Substrate	Substrate	State		AGRRA
38	Substratum - live coral	Substrate	Substrate	State/Proxy	Helps characterise past history of the site	AGRRA
39	Substratum - dead coral	Substrate	Substrate	State/Proxy	Helps characterise past history of the site	AGRRA
40	Substratum - coral rubble, dead coral boulder	Substrate	Substrate	State/Proxy	Helps characterise past history of the site	AGRRA
41	Substratum - carbonate pavement	Substrate	Substrate	State/Proxy	Helps characterise past history of the site	AGRRA
42	Small coral recruits (<2cm), large coral recruits (2-4 cm)	Juvenile corals	Recruitment	State/Proxy	Recruits are counted to learn if reefs might be able to recover when disasters kill adult corals	AGRRA
43	<i>Diadema antillarum</i> (juvenile and adult)	Urchin	Herbivory	State/Proxy	Formerly a key herbivore on many W. Atlantic reefs	AGRRA
44	Spiny lobsters	Motile invertebrates	Other invertebrates	State	Overfished across much of the W. Atlantic	AGRRA
45	Live queen conch	Motile invertebrates	Other invertebrates	State/Proxy	Usually seen only on reefs that have not been overfished	AGRRA
46	Lionfish	Lionfish	Disturbance (Biological)	State/Proxy	Invasive and predatory, preying upon and competing with many native species	AGRRA
47	Trash	Garbage	Disturbance (Anthropogenic)	State/Proxy	Discards reflect human behaviour and activity e.g. boating, fishing, drinking	AGRRA

48	Coral disease	Disease	Disturbance (Physiological)	State/Proxy		AGRRA
49	Coral size	Coral size	Coral community	State/Proxy	Small corals likely to be completely killed by perturbations. A reef without large corals may be recovering from a serious perturbation, one without recruits has no future	AGRRA
50	Fish abundance (Selected functional group)	Fish abundance (key)	Fish abundance	State		AGRRA
51	Fish abundance (Selected species)	Fish abundance (key)	Fish abundance	State		AGRRA
52	Fish size frequency distribution (selected species)	Fish size (key)	Fish size	State		AGRRA
53	Fish diversity	Fish diversity	Fish community	State		AGRRA
54	Herbivorous fish biomass (species)	Herbivore biomass	Herbivory	State/Proxy		AGRRA
55	Fish biomass (estimated)	Fish biomass	Fish biomass	State/Proxy	Total fish biomass gives important information on trophic structure and overall reproductive output of fish	AGRRA
56	Commerical fish biomass (estimated)	Fish biomass	Fish biomass	State/Proxy	Total commercial fish biomass gives indication of stock status, fishing pressure, habitat conditions and recruitment success	AGRRA
57	Crustose coralline algae cover	CCA	Algal cover	State		AIMS LTMP
58	Macroalgae cover	Macroalgae	Algal cover	State		AIMS LTMP
59	Turf algae cover	Turf	Algal cover	State		AIMS LTMP
60	<i>Halimeda</i>	Coralline algae	Algal cover	State		AIMS LTMP
61	Bleached coral cover	Bleached coral cover	Disturbance (Physiological)	State/Proxy		AIMS LTMP
62	Giant clam abundance	Motile invertebrates	Other invertebrates	State		AIMS LTMP
63	Coral cover (Genus)	Coral cover (genus)	Coral cover	State		AIMS LTMP
64	Dead coral cover	Dead coral cover	Coral cover	State		AIMS LTMP
65	Hard coral cover	Coral cover	Coral cover	State		AIMS LTMP
66	COTS abundance	COTS	Disturbance (Biological)	State/Proxy		AIMS LTMP
67	COTS size class distribution	COTS	Disturbance	State/Proxy		AIMS LTMP

			(Biological)			
68	Presence of feeding scars	Feeding scars	Disturbance (Biological)	State/Proxy		AIMS LTMP
69	Coral disease	Disease	Disturbance (Physiological)	State/Proxy		AIMS LTMP
70	Total fish abundance	Total fish abundance	Fish abundance	State		AIMS LTMP
71	Fish diversity	Fish diversity	Fish community	State		AIMS LTMP
72	Fish size frequency distribution (Selected species)	Fish size (key)	Fish size	State		AIMS LTMP
73	Soft coral cover	Other Invertebrates (Sessile)	Other invertebrates	State		AIMS LTMP
74	Sponge cover	Other Invertebrates (Sessile)	Other invertebrates	State		AIMS LTMP
75	Visibility	Turbidity	Physical characteristics	State/Proxy	Water visibility estimates recorded.	AIMS LTMP
76	Tide	Tide	Physical characteristics	State	Tide recorded as low, high, falling or rising, determined from a tide table.	AIMS LTMP
77	Cloud cover	Cloud cover	Physical characteristics	State	Quantified in terms of eighths of the sky area covered by cloud. Unit = okta. One okta means 1/8 of the sky.	AIMS LTMP
78	Wind strength	Wind	Physical characteristics	State/Proxy	5 categories from 0-25 knots.	AIMS LTMP
79	Disease	Disease	Disturbance (Physiological)	State/Proxy	Presence/absence	AIMS LTMP
80	Cyclones	Storm	Disturbance (Physical)	State/Proxy	Presence/absence	AIMS LTMP
81	Abiotic cover	Substrate	Substrate	State		AIMS LTMP
82	Juvenile corals	Juvenile corals	Recruitment	State/Proxy	Up to 5cm are surveyed. Juvenile corals are the net result of processes of larval supply, settlement and post-settlement survivorship.	AIMS LTMP
83	Total Carbon	Carbon	Disturbance (Anthropogenic)	State/Proxy		AIMS LTMP

84	Total Nitrogen	Nitrogen	Disturbance (Anthropogenic)	State/Proxy		AIMS LTMP
85	Temperature	Temperature	Physical characteristics	State/Proxy		AIMS LTMP
86	Suspended solids	Turbidity	Physical characteristics	State/Proxy		AIMS LTMP
87	Salinity	Salinity	Physical characteristics	State		AIMS LTMP
88	Chlorophyll-a	Chlorophyll	Disturbance (Anthropogenic)	State/Proxy		AIMS LTMP
89	Fleshy macroalgae	Macroalgae	Algal cover	State		Bruckner 2012
90	Erect coralline algae	Coralline algae	Algal cover	State		Bruckner 2012
91	Crustose coralline algae	CCA	Algal cover	State		Bruckner 2012
92	Turf algae	Turf	Algal cover	State		Bruckner 2012
93	Cyanobacteria	Cyanobacteria	Algal cover	State		Bruckner 2012
94	Coral cover (species)	Coral cover (species)	Coral cover	State		Bruckner 2012
95	Coral diversity	Coral diversity	Coral community	State		Bruckner 2012
96	Coral size class distribution	Coral size	Coral community	State/Proxy		Bruckner 2012
97	Tunicate	Other Invertebrates (Sessile)	Other invertebrates	State		Bruckner 2012
98	Gorgonian	Other Invertebrates (Sessile)	Other invertebrates	State		Bruckner 2012
99	Anemones	Other Invertebrates (Sessile)	Other invertebrates	State		Bruckner 2012
100	Bioeroding sponges	Other Invertebrates (Sessile)	Other invertebrates	State		Bruckner 2012
101	Hydrozoan coral (<i>Millepora</i>)	Other Invertebrates (Sessile)	Other invertebrates	State		Bruckner 2012
102	Pavement	Substrate	Substrate	State		Bruckner 2012

103	Rubble	Substrate	Substrate	State		Bruckner 2012
104	Sand/Silt	Substrate	Substrate	State		Bruckner 2012
105	Recently dead coral cover (Coral condition)	Dead coral cover	Mortality	State/Proxy	Visual estimates of tissue loss	Bruckner 2012
106	Transitional dead coral cover (Coral condition)	Dead coral cover	Coral cover	State	Visual estimates of tissue loss	Bruckner 2012
107	Old dead coral cover (Coral condition)	Dead coral cover	Coral cover	State	Visual estimates of tissue loss	Bruckner 2012
108	Cause of mortality	Cause of mortality	Mortality	State/Proxy	Assessment of type of disease, extent of bleaching, predation, competition, overgrowth or other cause of mortality	Bruckner 2012
109	Juvenile corals	Juvenile corals	Recruitment	State/Proxy	Sampling for corals smaller than 4cm, divided into 2 classes	Bruckner 2012
110	Settlement location	Settlement location	Recruitment	State/Proxy	Found <i>M. annularis</i> skeletons promoted settlement.	Bruckner 2012
111	Longitude/latitude	Latitude/Longitude	Location & Geomorphology	State		Bruckner 2012
112	Key nuisance invertebrates (Sponge, gorgonian, bioeroding sponge, tunicate)	Harmful organisms	Organisms (Harmful)	State/Proxy	Nuisance species: tunicate (<i>Tredidennum</i>), encrusting gorgonian (<i>Erythropodium</i> , <i>Briareum</i>), colonial anemone (<i>Palythoa</i>), encrusting or bioeroding sponge (<i>Cliona</i>) and hydrozoan coral (<i>Millepora</i>)	Bruckner 2012
113	Disease	Disease	Disturbance (Physiological)	State/Proxy		Bruckner 2012
114	Bleached coral cover	Bleached coral cover	Disturbance (Physiological)	State/Proxy		CARICOMP
115	Algal biomass (Select species)	Algal biomass	Algal biomass	State/Proxy		CARICOMP
116	Calcareous algae	Coralline algae	Algal cover	State		CARICOMP
117	Encrusting calcareous algae	CCA	Algal cover	State		CARICOMP
118	Fleshy Algae	Macroalgae	Algal cover	State		CARICOMP
119	Turf algae	Turf	Algal cover	State		CARICOMP
120	Anemones	Other Invertebrates (Sessile)	Other invertebrates	State		CARICOMP
121	Ascidians	Other Invertebrates (Sessile)	Other invertebrates	State		CARICOMP
122	Branching corals	Coral cover (growth)	Coral community	State/Proxy		CARICOMP

		form)				
123	Massive corals	Coral cover (growth form)	Coral community	State/Proxy		CARICOMP
124	Encrusting corals	Coral cover (growth form)	Coral community	State/Proxy		CARICOMP
125	Foliaceous corals	Coral cover (growth form)	Coral community	State/Proxy		CARICOMP
126	Milleporines	Other Invertebrates (Sessile)	Other invertebrates	State		CARICOMP
127	Recently dead coral	Dead coral cover	Mortality	State/Proxy		CARICOMP
128	Hard coral	Coral cover	Coral cover	State		CARICOMP
129	Coral disease	Disease	Disturbance (Physiological)	State/Proxy		CARICOMP
130	Corallimorpharians	Other Invertebrates (Sessile)	Other invertebrates	State		CARICOMP
131	Fish size frequency distribution by species	Fish size (species)	Fish size	State		CARICOMP
132	Fish abundance (Selected species)	Fish abundance (key)	Fish abundance	State		CARICOMP
133	Fish diversity (Species)	Fish diversity	Fish community	State		CARICOMP
134	Gorgonians (Growth form)	Other Invertebrates (Sessile)	Other invertebrates	State		CARICOMP
135	Encrusting gorgonians	Other Invertebrates (Sessile)	Other invertebrates	State		CARICOMP
136	Bare boulders	Substrate	Substrate	State		CARICOMP
137	Bare rock	Substrate	Substrate	State		CARICOMP
138	Bare rubble	Substrate	Substrate	State		CARICOMP
139	Bare sediment	Substrate	Substrate	State		CARICOMP
140	Holes, gaps, overhangs	Substrate	Substrate	State		CARICOMP
141	Depth	Depth	Location & Geomorphology	State		CARICOMP

142	Latitude and longitude	Latitude/Longitude	Location & Geomorphology	State		CARICOMP
143	Rugosity	Rugosity	Location & Geomorphology	State/Proxy		CARICOMP
144	Erect sponges	Other Invertebrates (Sessile)	Other invertebrates	State		CARICOMP
145	Encrusting sponges	Other Invertebrates (Sessile)	Other invertebrates	State		CARICOMP
146	Sea surface temperature	Temperature	Physical characteristics	State/Proxy		CARICOMP
147	Urchin abundance (Species)	Urchin	Other invertebrates	State/Proxy		CARICOMP
148	Urchin abundance (juvenile)	Urchin	Other invertebrates	State/Proxy		CARICOMP
149	Urchin abundance (adult)	Urchin	Other invertebrates	State/Proxy		CARICOMP
150	Sea urchin density	Urchin	Herbivory	State/Proxy	As a key herbivore, potential of organism to reach high densities will change algal cover.	CARICOMP
151	Sea urchin size class distribution	Urchin	Other invertebrates	State/Proxy		CARICOMP
152	Salinity	Salinity	Physical characteristics	State		CARICOMP
153	Turbidity	Turbidity	Physical characteristics	State/Proxy		CARICOMP
154	Zoanthids	Other Invertebrates (Sessile)	Other invertebrates	State		Cinner et al. 2013
155	Ecological exposure to coral bleaching	Thermal regime	Disturbance (Physiological)	Process	Multivariate model of how variables combine to create environmental conditions that make a site susceptible to coral bleaching impacts including temperature, lights, currents, tidal variation, chlorophyll and water quality	Cinner et al. 2013
156	Temperature	Temperature	Physical characteristics	State/Proxy	Variable included in the multivariate model that produces ecological exposure resilience index	Cinner et al. 2013
157	Light	Light	Physical characteristics	State/Proxy	Variable included in the multivariate model that produces ecological exposure resilience index	Cinner et al. 2013
158	Currents	Current	Physical	Proxy	Variable included in the multivariate model that produces	Cinner et al. 2013

			characteristics		ecological exposure resilience index	
159	Tidal variation	Tide	Physical characteristics	State/Proxy	Variable included in the multivariate model that produces ecological exposure resilience index	Cinner et al. 2013
160	Chlorophyll-a	Chlorophyll	Disturbance (Anthropogenic)	State/Proxy	Variable included in the multivariate model that produces ecological exposure resilience index	Cinner et al. 2013
161	Water quality	Water quality	Disturbance (Anthropogenic)	State/Proxy	Variable included in the multivariate model that produces ecological exposure resilience index	Cinner et al. 2013
162	Susceptibility of the coral community to bleaching	Bleaching	Disturbance (Physiological)	Process		Cinner et al. 2013
163	Susceptibility of the fish community to population declines associated with habitat loss from bleaching	Bleaching	Disturbance (Physiological)	Process		Cinner et al. 2013
164	Hard coral cover	Coral cover	Coral cover	State	Linked to increase resilience and recovery but most studies show no correlation	Cinner et al. 2013
165	Ratio of coral to macroalgal cover	Coral-algal balance	Competition	State/Proxy		Cinner et al. 2013
166	Macroalgae cover	Macroalgae	Algal cover	State/Proxy	Limit coral recovery via competition for benthic substrate, allelopathy and trapping sediment that smothers coral recruits	Cinner et al. 2013
167	Coral size distribution	Coral size	Coral community	State/Proxy	Evidence that evenness across size classes increases recovery. Lack of large adult colonies may limit spawning stock.	Cinner et al. 2013
168	Coral richness	Coral diversity	Coral community	State	Expected to promote recovery, but limited evidence.	Cinner et al. 2013
169	Fish biomass (estimated)	Fish biomass	Fish biomass	State/Proxy	Indicates status of fish stock, it's potential growth and a proxy for ecological metabolism	Cinner et al. 2013
170	Fish species richness	Fish diversity	Fish community	State/Proxy	Often used as proxy for functional redundancy, expected to promote ecological recovery by avoiding undesired ecological states	Cinner et al. 2013
171	Fish size distribution	Fish size	Fish size	State/Proxy	Large individuals can increase fecundity to promote recovery of fish communities	Cinner et al. 2013
172	Substrate complexity	Rugosity	Location & Geomorphology	State/Proxy		Cinner et al. 2013
173	Herbivore diversity	Herbivore diversity	Fish community	State/Proxy		Cinner et al. 2013
174	Index of herbivore grazing relative to algal	Grazing/Algal	Herbivory	Proxy		Cinner et al. 2013

	production	Production				
175	Latitude and longitude	Latitude/Longitude	Location & Geomorphology	State		Cinner et al. 2013
176	Depth	Depth	Location & Geomorphology	State		Cinner et al. 2013
177	Calcifying to non-calcifying cover	Substrate availability	Substrate	State/Proxy	Calcifying organisms important for reef framework e.g. settlement, recruitment and cementation of reef structure, expect to increase recovery following disturbance	Cinner et al. 2013
178	CCA cover	CCA	Algal cover	State		CRAMP
179	Cyanobacteria cover	Cyanobacteria	Algal cover	State		CRAMP
180	Fleshy macroalgae	Macroalgae	Algal cover	State		CRAMP
181	Macroalgae	Macroalgae	Algal cover	State		CRAMP
182	Turf cover	Turf	Algal cover	State		CRAMP
183	Coral cover (Species)	Coral cover (species)	Coral cover	State		CRAMP
184	Coral mortality	Coral mortality	Mortality	Process		CRAMP
185	Coral richness	Coral diversity	Coral community	State		CRAMP
186	Total fish abundance	Total fish abundance	Fish abundance	State		CRAMP
187	Total fish biomass	Fish biomass	Fish biomass	State/Proxy		CRAMP
188	Fish size class distribution	Fish size	Fish size	State		CRAMP
189	Sediment size	Sediment size	Physical characteristics	State/Proxy	Used as an indicator of the environment and provide a characterisation of the benthos, suppling information about benthic structure	CRAMP
190	Coral recruitment	Juvenile corals	Recruitment	State/Proxy		CRAMP
191	Depth	Depth	Location & Geomorphology	State		CRAMP
192	Latitude and longitude	Latitude/Longitude	Location & Geomorphology	State		CRAMP
193	Rugosity	Rugosity	Location & Geomorphology	State/Proxy	More habitat for coral reef organisms, and proxy for fish abundance	CRAMP

194	Nutrients	Nutrients	Disturbance (Anthropogenic)	State/Proxy		CRAMP
195	Percent Carbon	Carbon	Disturbance (Anthropogenic)	State/Proxy		CRAMP
196	Percent Nitrogen	Nitrogen	Disturbance (Anthropogenic)	State/Proxy		CRAMP
197	Wave exposure	Wave exposure	Physical characteristics	Proxy		CRAMP
198	Conservation status	Management	Management Status	State/Proxy		CRAMP
199	Habitat	Habitat	Location & Geomorphology	State		CRAMP
200	Sand/Silt/Bare/Rock	Substrate	Substrate	State		CRAMP
201	Habitat type	Habitat	Location & Geomorphology	State	3 types: carbonate fringing, granitic rocky and patch reef. Habitats differ in coral recruitment success/likelihood of ecosystem collapse	Graham et al. 2015
202	Pre-disturbance branching coral cover	Coral cover (branching)	Coral cover	State/Proxy	Branching vulnerable to bleaching, and once dead erodes quickly. More branching vulnerable to coral loss and reduction in organisms	Graham et al. 2015
203	Juvenile coral density	Juvenile corals	Recruitment	State/Proxy	Proxy for successful recruitment, survival and growth of new corals, assumed to be key to coral recovery dynamics	Graham et al. 2015
204	Depth	Depth	Location & Geomorphology	State/Proxy	Threats on reefs are mostly in shallow water, light penetration also favour rapid growth of macroalgae	Graham et al. 2015
205	Herbivorous fish biomass	Herbivore biomass	Herbivory	State/Proxy	Good proxy for function as the area of reef grazed by fish to mediate competition for space among coral and algae	Graham et al. 2015
206	Herbivorous fish diversity	Herbivore diversity	Fish community	State/Proxy	Many types of algae have defences against herbivores, proxy for effective control of macroalgae	Graham et al. 2015
207	Marine reserve status	Management	Management Status	State/Proxy	No take reserves expect to reduce fishing and enhance ecosystem processes	Graham et al. 2015
208	Nutrient regime	Nutrients	Disturbance (Anthropogenic)	State/Proxy	High nutrient loads enhance growth of algae, resulting in algae outcompeting corals	Graham et al. 2015
209	Pre-disturbance structural complexity	Rugosity	Location &	State/Proxy	Provide refuge, and space for coral settlement and larvae. Prior	Graham et al. 2015

			Geomorphology		to a disturbance, expect to maintain ecosystem processes through a disturbance	
210	Sea urchin density	Urchin	Herbivory	State/Proxy	Sea urchins important herbivores to control algal growth, promote successful recruitment and recovery	Graham et al. 2015
211	Proximity to upwelling or exposure to strong currents	Upwelling	Physical characteristics	State/Proxy	Wave exposure influence distribution patterns, growth forms and colony sizes. Also enhance algal growth rates, and dislodge algae where wave exposure is strong	Graham et al. 2015
212	Coral cover (species)	Coral cover (species)	Coral cover	State		CREMP
213	Coral richness	Coral diversity	Coral community	State		CREMP
214	Octocoral cover (Gorgonian and soft coral)	Other Invertebrates (Sessile)	Other invertebrates	State		CREMP
215	Zoanthid cover	Other Invertebrates (Sessile)	Other invertebrates	State		CREMP
216	Sponge cover	Other Invertebrates (Sessile)	Other invertebrates	State		CREMP
217	Seagrass cover	Seagrass	Seagrass	State		CREMP
218	Macroalgae cover	Macroalgae	Algal cover	State		CREMP
219	Cyanobacteria cover	Cyanobacteria	Algal cover	State	Monitored in datasheets.	CREMP
220	Clionid sponge cover	Harmful organisms	Organisms (Harmful)	State/Proxy		CREMP
221	Bleached coral cover	Bleached coral cover	Disturbance (Physiological)	State/Proxy		CREMP
222	Disease	Disease	Disturbance (Physiological)	State/Proxy		CREMP
223	Habitat	Habitat	Location & Geomorphology	State	Four main habitat types: nearshore hardbottom, patch reefs, offshore shallow reefs and offshore deep reefs	CREMP
224	Temperature	Temperature	Physical characteristics	State/Proxy		CREMP
225	Diadema abundance/density	Urchin	Other invertebrates	State/Proxy		CREMP
226	Grazer biomass	Herbivore biomass	Herbivory	State/Proxy	Grazer crop on algal turf, prevent the establishment and growth	Jouffray et al. 2015

					of macroalgae	
227	Scraper biomass	Herbivore biomass	Herbivory	State/Proxy	Scrapers also feed on turf but remove some component of the reef substratum, providing bare areas for coral recruitment	Jouffray et al. 2015
228	Browser biomass	Herbivore biomass	Herbivory	State/Proxy	Browsers consistently feed on macroalgae, may play a crucial role for reversing macroalgae-dominated states	Jouffray et al. 2015
229	Latitude	Latitude/Longitude	Location & Geomorphology	State		Jouffray et al. 2015
230	Depth	Depth	Location & Geomorphology	State		Jouffray et al. 2015
231	Distance from coast	Distance from coast	Disturbance (Anthropogenic)	Proxy		Jouffray et al. 2015
232	Distance from stream	Distance from stream	Disturbance (Anthropogenic)	Proxy		Jouffray et al. 2015
233	Effluent	Effluent	Disturbance (Anthropogenic)	Proxy		Jouffray et al. 2015
234	Human population density	Human population	Disturbance (Anthropogenic)	Proxy		Jouffray et al. 2015
235	Urban index	Urban disturbance	Disturbance (Anthropogenic)	Proxy	Representation of urban disturbance within a catchment	Jouffray et al. 2015
236	Point pollution index	Pollution	Disturbance (Anthropogenic)	State/Proxy	Representation of the density of sources of point pollution within a catchment (6 point sources of pollution)	Jouffray et al. 2015
237	Fragmentation index	Stream fragmentation	Disturbance (Anthropogenic)	Proxy	Representation of stream fragmentation, which may indicate migration limitations and disruption of the natural flow regime	Jouffray et al. 2015
238	Former pineapple/sugarcane plantation index	Landuse	Disturbance (Anthropogenic)	Proxy	Representation of lands that were formerly pineapple/sugarcane plantations that may contribute to disturbance through legacy effects	Jouffray et al. 2015
239	Ditch index	Ditch infrastructure	Disturbance (Anthropogenic)	Proxy	Relative density of ditch infrastructure.	Jouffray et al. 2015
240	Agricultural index	Agricultural disturbance	Disturbance (Anthropogenic)	Proxy	Representation of agricultural disturbance within a catchment.	Jouffray et al. 2015
241	Reef zone	Reef zone	Location &	State		Jouffray et al. 2015

			Geomorphology			
242	Hard coral cover	Coral cover	Coral cover	State	Used in PCA to cluster into 3 regimes	Jouffray et al. 2015
243	Macroalgae cover	Macroalgae	Algal cover	State	Used in PCA to cluster into 3 regimes	Jouffray et al. 2015
244	Turf algae cover	Turf	Algal cover	State	Used in PCA to cluster into 3 regimes	Jouffray et al. 2015
245	CCA cover	CCA	Algal cover	State	Used in PCA to cluster into 3 regimes	Jouffray et al. 2015
246	Structural complexity	Rugosity	Location & Geomorphology	State/Proxy	Used in PCA to cluster into 3 regimes, and a key aspect of reef habitat quality	Jouffray et al. 2015
247	Sand cover	Substrate	Substrate	State	Used in PCA to cluster into 3 regimes	Jouffray et al. 2015
248	Connectivity	Connectivity	Connectivity	Process	Reef recovery depends on nearby and upstream reefs to provide recruits	Maynard et al. 2010
249	Free from water pollution	Pollution	Disturbance (Anthropogenic)	State/Proxy	Pesticides, nutrients and pathogens increase susceptibility of corals to disease and bleaching, increase algal growth rates	Maynard et al. 2010
250	Previous exposure to thermal stress events	Thermal regime	Physical characteristics	State/Proxy	Previous exposure, tolerance/quick recovery from thermal stress events suggests same can occur in future	Maynard et al. 2010
251	Coral cover	Coral cover	Coral cover	State/Proxy	Recruitment and intensifies grazing in areas available for algal colonisation	Maynard et al. 2010
252	Abundance of resistant/tolerant species	Resistant corals	Coral community	State/Proxy	Massive corals more tolerant of thermal and physical stress	Maynard et al. 2010
253	Water mixing	Mixing	Physical characteristics	Process	Mixing keeps water temperatures constant and reduces chances of corals in shallow water from heating	Maynard et al. 2010
254	Free from physical impacts	Physical impact	Disturbance (Physical)	State/Proxy	Wave action produced by storms can cause breakage of colonies, increase susceptibility to disease and bleaching	Maynard et al. 2010
255	Abundance of mature coral colonies	Mature coral colonies	Coral community	State/Proxy	Large colonies survived long and withstood range of stressors, also likely to produce more recruits	Maynard et al. 2010
256	Substrate availability	Substrate availability	Substrate	State/Proxy	Recruits need suitable substrate to settle on and grow	Maynard et al. 2010
257	Free from anthropogenic physical impacts	Human impact	Disturbance (Anthropogenic)	Proxy	Anchors, fins of snorkelers and divers can damage corals and increase susceptibility to disease and bleaching	Maynard et al. 2010
258	Herbivore abundance	Herbivore abundance	Herbivory	State/Proxy	Reduce cover of algae that compete with corals for space	Maynard et al. 2010
259	Exposure to upwelling	Upwelling	Physical characteristics	Process	Cool water reduces temperature stress and alleviate reefs from mass bleaching events	Maynard et al. 2010

260	Light reduction	Shading	Physical characteristics	Proxy	Reduce thermal stress to coral communities	Maynard et al. 2010
261	Free from fishing pressure	Fishing pressure	Disturbance (Anthropogenic)	Proxy	Fish important for grazing, particularly post-disturbance to free up space for coral recruits	Maynard et al. 2010
262	Topographic complexity	Rugosity	Location & Geomorphology	State/Proxy	Self-shading can reduce light stress that can cause bleaching	Maynard et al. 2010
263	Coral submersion	Reef exposure at low tide	Location & Geomorphology	Proxy	Stress to corals exposed to air for long periods can cause mortality	Maynard et al. 2010
264	Free from sedimentation	Sedimentation	Disturbance (Anthropogenic)	State/Proxy	Tolerating sediment requires physiological resources increasing susceptibility to corals to other stressors	Maynard et al. 2010
265	Absence of bioeroders	Bioeroder abundance	Disturbance (Biological)	State/Proxy	At high abundances can reduce integrity of reef framework, increases susceptibility to physical stresses such as waves caused by storms	Maynard et al. 2010
266	Absence of coral disease	Disease	Disturbance (Physiological)	State/Proxy	Disease can quickly and kill colonies, and increase susceptibility of corals to other stressors	Maynard et al. 2010
267	Resistant coral species	Resistant corals	Coral community	State/Proxy	Confers resistance	McClanahan et al. 2012
268	Temperature variability	Thermal regime	Physical characteristics	State/Proxy	Previous exposure of corals to different thermal regimes, increase resistance to bleaching	McClanahan et al. 2012
269	Nutrients (Pollution)	Nutrients	Disturbance (Anthropogenic)	State/Proxy	Nutrient pollution can reduce coral reef resistance to stress, but depends on species.	McClanahan et al. 2012
270	Sedimentation	Sedimentation	Disturbance (Anthropogenic)	State/Proxy	Increased sediment linked to decrease in thermal tolerance of corals.	McClanahan et al. 2012
271	Coral diversity	Coral diversity	Coral community	State	Diversity increases resistance but likely depend on species composition. Association unclear.	McClanahan et al. 2012
272	Herbivore biomass	Herbivore biomass	Herbivory	State/Proxy	Reduce algal competition	McClanahan et al. 2012
273	Physical human impacts	Human impact	Disturbance (Anthropogenic)	Proxy	Strong negative relationship between human impacts and corals' ability to resist stressors	McClanahan et al. 2012
274	Coral disease	Disease	Disturbance (Physiological)	State/Proxy	Corals more susceptible to bleaching after disease	McClanahan et al. 2012
275	Macroalgae cover	Macroalgae	Algal cover	State/Proxy	Macroalgae reduce coral growth rates	McClanahan et al. 2012
276	Recruitment	Recruitment	Recruitment	Process	Coral recruits and small size classes more resistant to bleaching	McClanahan et al. 2012

					and mortality	
277	Fishing pressure	Fishing pressure	Disturbance (Anthropogenic)	Proxy	Indirect impact of fishing pressure	McClanahan et al. 2012
278	Sea surface temperature	Temperature	Physical characteristics	State/Proxy		Mumby et al. 2014
279	Live coral cover	Coral cover	Coral cover	State		Mumby et al. 2014
280	Spawning coral cover	Coral cover (repro group)	Coral community	State/Proxy		Mumby et al. 2014
281	Brooding coral cover	Coral cover (repro group)	Coral community	State/Proxy		Mumby et al. 2014
282	Parrotfish biomass	Herbivore biomass	Herbivory	State/Proxy		Mumby et al. 2014
283	Wave exposure index	Wave exposure	Physical characteristics	Proxy		Mumby et al. 2014
284	Hurricane occurrence	Storm	Disturbance (Physical)	State/Proxy		Mumby et al. 2014
285	Hurricane intensity	Storm intensity	Disturbance (Physical)	State/Proxy		Mumby et al. 2014
286	Coral recruitment	Recruitment	Recruitment	Process		Mumby et al. 2014
287	Coral growth	Coral growth	Growth	Process		Mumby et al. 2014
288	Coral reproduction	Coral reproduction	Reproduction	Process		Mumby et al. 2014
289	Cropped algae	Substrate availability	Substrate	State/Proxy	Grazing results in cropped algae - corals can recruit to cropped algae includes filamentous, coralline red algae and short turfs <5mm. Proxy for substrate availability.	Mumby et al. 2014
290	Site exposure (windward or leeward)	Site exposure	Location & Geomorphology	State/Proxy		Mumby et al. 2014
291	Season	Season	Physical characteristics	State		Mumby et al. 2014
292	<i>Dictyota</i> growth	Algal growth	Growth	Process		Mumby et al. 2014
293	<i>Lobophora</i> growth	Algal growth	Growth	Process		Mumby et al. 2014
294	Competition (corals)	Competition	Competition	Process		Mumby et al. 2014

295	Competition (corals and cropped algae)	Competition	Competition	Process		Mumby et al. 2014
296	Competition (corals and macroalgae): effect of macroalgae on corals	Competition	Competition	Process		Mumby et al. 2014
297	Competition (corals and macroalgae): effect of corals on macroalgae	Competition	Competition	Process		Mumby et al. 2014
298	Grazing by fishes and impact of fishing	Herbivory	Herbivory	Process		Mumby et al. 2014
299	Partial-colony mortality of corals	Coral mortality	Mortality	Process		Mumby et al. 2014
300	Whole-colony mortality of juvenile and adult corals	Coral mortality	Mortality	Process		Mumby et al. 2014
301	Parrotfish predation on coral recruits	Corallivory	Disturbance (Biological)	Process		Mumby et al. 2014
302	Hurricane impact on juvenile & mature corals (>60 cm ²): whole-colony mortality	Coral mortality	Mortality	Process		Mumby et al. 2014
303	Hurricane impact on mature corals (>250 cm ²): partial-colony mortality	Coral mortality	Mortality	Process		Mumby et al. 2014
304	Hurricane impact on juvenile corals (1-60 cm ²)	Coral mortality	Mortality	Process		Mumby et al. 2014
305	Hurricane impact on macroalgae	Algal mortality	Mortality	Process		Mumby et al. 2014
306	Bleaching impact on corals: whole-colony mortality	Coral mortality	Mortality	Process		Mumby et al. 2014
307	Bleaching impact on corals: partial-colony mortality	Coral mortality	Mortality	Process		Mumby et al. 2014
308	Bleaching frequency	Bleaching	Disturbance (Physiological)	State/Proxy		Mumby et al. 2014
309	Degree heating weeks	Thermal regime	Physical characteristics	State/Proxy		Mumby et al. 2014
310	Ungrazable substratum	Substrate	Herbivory	Proxy		Mumby et al. 2014
311	Macroalgae cover	Macroalgae	Algal cover	State/Proxy	Used to indicate coral-algal balance.	Mumby et al. 2014
312	Turf cover	Turf	Algal cover	State		Mumby et al. 2014
313	Wind direction	Wind	Physical characteristics	State/Proxy	Used to derive wind exposure	Mumby et al. 2014

314	Wind strength	Wind	Physical characteristics	State/Proxy	Used to derive wind exposure	Mumby et al. 2014
315	Fetch	Fetch	Physical characteristics	State/Proxy	Used to derive wind exposure	Mumby et al. 2014
316	Rhodolith algae	CCA	Algal cover	State	Rhodolith belongs under CCA category	NOAA CCMA-BB
317	Crustose coralline algae	CCA	Algal cover	State		NOAA CCMA-BB
318	Cyanobacteria	Cyanobacteria	Algal cover	State		NOAA CCMA-BB
319	Filamentous algae	Turf	Algal cover	State	Categorized as turf	NOAA CCMA-BB
320	Macroalgae	Macroalgae	Algal cover	State		NOAA CCMA-BB
321	Turf algae	Turf	Algal cover	State		NOAA CCMA-BB
322	Macroalgal canopy height	Algal height	Algal height	State/Proxy		NOAA CCMA-BB
323	Abiotic - Hard bottom	Substrate	Substrate	State		NOAA CCMA-BB
324	Abiotic - Sand	Substrate	Substrate	State		NOAA CCMA-BB
325	Abiotic - Rubble	Substrate	Substrate	State		NOAA CCMA-BB
326	Abiotic - Fine sediment	Substrate	Substrate	State		NOAA CCMA-BB
327	Abiotic - Rugosity	Rugosity	Location & Geomorphology	State/Proxy		NOAA CCMA-BB
328	Abiotic - Water Depth	Depth	Location & Geomorphology	State		NOAA CCMA-BB
329	Coral cover (Species)	Coral cover (species)	Coral cover	State		NOAA CCMA-BB
330	Coral diversity	Coral diversity	Coral community	State		NOAA CCMA-BB
331	Bleached coral cover	Bleached coral cover	Disturbance (Physiological)	State/Proxy		NOAA CCMA-BB
332	Recently dead coral cover	Dead coral cover	Mortality	State/Proxy		NOAA CCMA-BB
333	Seagrass cover	Seagrass	Seagrass	State		NOAA CCMA-BB
334	Seagrass height	Seagrass	Seagrass	State		NOAA CCMA-BB
335	Gorgonian cover	Other Invertebrates (Sessile)	Other invertebrates	State		NOAA CCMA-BB
336	Gorgonian height	Other Invertebrates	Other invertebrates	State		NOAA CCMA-BB

		(Sessile)				
337	Gorgonian abundance	Other Invertebrates (Sessile)	Other invertebrates	State		NOAA CCMA-BB
338	Sponge abundance	Other Invertebrates (Sessile)	Other invertebrates	State		NOAA CCMA-BB
339	Sponge cover	Other Invertebrates (Sessile)	Other invertebrates	State		NOAA CCMA-BB
340	Sponge canopy height	Other Invertebrates (Sessile)	Other invertebrates	State		NOAA CCMA-BB
341	Other benthic - Anemonies & hydroids cover	Other Invertebrates (Sessile)	Other invertebrates	State		NOAA CCMA-BB
342	Other benthic - Anemonies & hydroids abundance	Other Invertebrates (Sessile)	Other invertebrates	State		NOAA CCMA-BB
343	Other benthic - Tunicates & zoanthids	Other Invertebrates (Sessile)	Other invertebrates	State		NOAA CCMA-BB
344	Macro-invertebrates - queen conch abundance & maturity	Motile invertebrates	Other invertebrates	State		NOAA CCMA-BB
345	Macro-invertebrates - spiny lobster abundance	Motile invertebrates	Other invertebrates	State		NOAA CCMA-BB
346	Macro-invertebrates - long-spined sea urchin	Urchin	Other invertebrates	State/Proxy		NOAA CCMA-BB
347	Marine debris	Garbage	Disturbance (Anthropogenic)	State/Proxy	E.g. cloth, champagne bottle, plastic cylinder, rectangular frame and glass bottles etc.	NOAA CCMA-BB
348	Fish abundance (species)	Fish abundance (species)	Fish abundance	State		NOAA CCMA-BB
349	Fish diversity	Fish diversity	Fish community	State		NOAA CCMA-BB
350	Fish size class	Fish size	Fish size	State		NOAA CCMA-BB
351	Fish biomass (estimated)	Fish biomass	Fish biomass	State/Proxy		NOAA CCMA-BB
352	Habitat	Habitat	Location & Geomorphology	State	Hard/soft or mangrove	NOAA CCMA-BB
353	Season	Season	Physical characteristics	State		NOAA CCMA-BB
354	Herbivore biomass	Herbivore biomass	Herbivory	State/Proxy		NOAA CCMA-BB

355	Parrotfish biomass	Herbivore biomass	Herbivory	State/Proxy		NOAA CCMA-BB
356	Temperature	Temperature	Physical characteristics	State/Proxy		NOAA CCMA-BB
357	Conductivity	Conductivity	Physical characteristics	State		NOAA CCMA-BB
358	Turbidity	Turbidity	Physical characteristics	State/Proxy		NOAA CCMA-BB
359	Chlorophyll-a	Chlorophyll	Disturbance (Anthropogenic)	State/Proxy		NOAA CCMA-BB
360	Rugosity	Rugosity	Location & Geomorphology	State/Proxy		NOAA CCMA-BB
361	Hard coral cover	Coral cover	Coral cover	State/Proxy	Primary indicator of reef health	IUCN
362	Soft coral cover	Other Invertebrates (Sessile)	Other invertebrates	State/Proxy	Competitor, indicate nutrient and wave energy conditions	IUCN
363	Macroalgal Cover	Macroalgae	Algal cover	State/Proxy	Competitor, indicate nutrient/bottom-up/herbivory/top-down processes	IUCN
364	Turf Algae Cover	Turf	Algal cover	State/Proxy	Competitor, indicate nutrient/bottom-up/herbivory/top-down processes	IUCN
365	CCA Cover	CCA	Algal cover	State/Proxy	Indicator for suitable habitat for coral recruitment, consolidation of reef framework	IUCN
366	Rubble	Substrate	Substrate	State/Proxy	Indicator of substratum integrity, suitability for coral recruitment and growth	IUCN
367	Substrate & Morphology (Topographic complexity - micro)	Rugosity	Location & Geomorphology	State/Proxy	Relevant to the recruitment of corals.	IUCN
368	Substrate & Morphology (Topographic complexity - macro)	Rugosity	Location & Geomorphology	State/Proxy	Relevant as habitat for bigger organisms	IUCN
369	Substrate & Morphology (Sediment texture)	Sediment size	Physical characteristics	State/Proxy	Sediment grain size and sorting affects benthic organisms	IUCN
370	Substrate & Morphology (Sediment layer)	Sediment abundance	Physical characteristics	State/Proxy	Depth of sediment layer on hard substrata, particularly in association with algal filaments/turf	IUCN
371	Cooling & Flushing (Temperature)	Temperature	Physical	State/Proxy	Primary stressor for bleaching related to climate change	IUCN

			characteristics			
372	Cooling & Flushing (Currents)	Current	Physical characteristics	Proxy	Currents cause vertical mixing that may reduce surface temperature	IUCN
373	Cooling & Flushing (Wave energy/exposure)	Wave exposure	Physical characteristics	Proxy	Wave energy causes vertical mixing, also represents exposure to weather events	IUCN
374	Cooling & Flushing (Proximity to deep water (30-50m))	Upwelling	Physical characteristics	State/Proxy	Proximity to deep water enables mixing with cold water by upwelling and waves, currents and exposure. Changed from deep water to upwelling since meant for it to be a proxy of upwelling.	IUCN
375	Cooling & Flushing (Depth of reef base)	Mixing	Physical characteristics	State/Proxy	Depth of base of reef slope affects potential mixing of deep cool waters. Changed from depth of reef base to mixing because proxy for mixing	IUCN
376	Shade & Screen (Depth)	Depth	Location & Geomorphology	State/Proxy	Zonation for reef and community structure, attenuation of temp, light and other variables	IUCN
377	Shade & Screen (Visibility (m))	Turbidity	Physical characteristics	State/Proxy	Proxy for turbidity and attenuation of light levels	IUCN
378	Shade & Screen (Compass direction/aspect)	Aspect	Physical characteristics	State/Proxy	Aspect of a reef slope affects the angle of incidence of the sun of reef surface (radiation per area of reef)	IUCN
379	Shade & Screen (Slope (degrees))	Slope	Location & Geomorphology	State/Proxy	Angle of reef slope affects the angle of incidence of the sun	IUCN
380	Shade & Screen (Physical shading)	Shading	Physical characteristics	Proxy	Shading can protect corals from stress	IUCN
381	Shade & Screen (Canopy corals)	Coral cover (growth form)	Coral community	State/Proxy	Shading of understory corals by canopy corals (table, staghorn, plates) can protect them from stress	IUCN
382	Extremes & Acclimatization (Temperature variability)	Thermal regime	Physical characteristics	State/Proxy	Variability promotes acclimatization over time, but only up to a certain point, suggests to interpret with local knowledge	IUCN
383	Extremes & Acclimatization (Exposed low tide)	Reef exposure at low tide	Location & Geomorphology	Proxy	Corals exposed to air experience frequent stress and may be more resistant to thermal stress	IUCN
384	Extremes & Acclimatization (Ponding/pooling)	Ponding/pooling	Physical characteristics	State/Proxy	Restricted bodies of water heat up more and are more stressed	IUCN
385	Extremes & Acclimatization (Survival of past bleaching events)	Thermal regime	Physical characteristics	State/Proxy	Evidence of corals been bleached and survived, survival indicates acclimatization	IUCN

386	Bleaching	Bleaching	Disturbance (Physiological)	State/Proxy	Current levels of bleaching	IUCN
387	Mortality-recent	Dead coral cover	Mortality	State/Proxy	Current levels of mortality - partial/full mortality	IUCN
388	Coral disease	Disease	Disturbance (Physiological)	State/Proxy	Percent corals showing disease conditions	IUCN
389	Mortality-old	Dead coral cover	Coral cover	State		IUCN
390	Recovery-old	Dead coral cover	Coral cover	State		IUCN
391	Coral population structure	Coral population structure	Coral community	Proxy	Represents succession of coral community as documented by the next 4 variables.	IUCN
392	Population Biology (Recruitment)	Juvenile corals	Recruitment	State/Proxy	Estimated number of recruits <2-3cm per square meter	IUCN
393	Population Biology (Fragmentation)	Fragmentation	Reproduction	State/Proxy	Estimated contribution of fragmentation in producing new colonies from 5-20cm	IUCN
394	Population Biology (Dominant size class)	Coral size	Coral community	State/Proxy	Estimate dominance in coral community by size class, indicating successional stage of community	IUCN
395	Population Biology (Largest corals)	Coral size	Coral community	State/Proxy	Largest corals at a site indicate suitability of site and degree of env. Stability/community persistence	IUCN
396	Positive coral associates (Obligate feeders)	Coral-dependent organisms	Organisms (Unharmful)	State/Proxy	Abundance and diversity of obligate coral feeders indicative of health of coral colonies and complexity of interactions	IUCN
397	Positive coral associates (Branching residents (Abundance and diversity of fish/crustacean residents in corals))	Coral-dependent organisms	Organisms (Unharmful)	State/Proxy	Abundance and diversity of fish and invertebrate residents are indicative of health and complexity of interactions	IUCN
398	Negative coral associates (Competitors)	Competitor abundance	Competition	State/Proxy	Abundance and diversity of coral competitors indicative of inhibiting factors to coral growth and recovery	IUCN
399	Negative coral associates (Bioeroders (internal))	Bioeroder abundance	Disturbance (Biological)	State/Proxy	Urchins, nonfish - inhibiting factors to coral growth and recovery	IUCN
400	Negative coral associates (Bioeroders (external))	Bioeroder abundance	Disturbance (Biological)	State/Proxy	Sponges, worms - inhibiting factors to coral growth and recovery	IUCN
401	Negative coral associates (Corallivores (negative))	Corallivores	Disturbance (Biological)	State/Proxy	Indicative to additional mortality to coral colonies	IUCN
402	Herbivore diversity	Herbivore diversity	Fish community	State/Proxy	Overall critical for suppressing algal growth and inhibiting effects on corals	IUCN

403	Herbivore abundance (Excavators)	Herbivore abundance	Herbivory	State/Proxy	Control on algal growth	IUCN
404	Herbivore abundance (Scrapers)	Herbivore abundance	Herbivory	State/Proxy	Control on macroalgal fronds	IUCN
405	Herbivore abundance (Grazers/browsers)	Herbivore abundance	Herbivory	State/Proxy	Control on epilithic turf algae	IUCN
406	Top Predators (Piscivores)	Fish abundance (key)	Fish abundance	State		IUCN
407	Dispersal (self-seeding)	Larval supply	Connectivity	Process	Recruitment of new corals driven more by self-seeding	IUCN
408	Dispersal (local-seeding)	Larval supply	Connectivity	Process	Larval density decreases with distance from source	IUCN
409	Dispersal (distant-seeding)	Larval supply	Connectivity	Process	Larval density decreases with distance from source	IUCN
410	Transport (Currents)	Current	Connectivity	Proxy		IUCN
411	Transport (Dispersal barrier)	Dispersal barrier	Location & Geomorphology	State/Proxy	Barriers reduce larvae flow	IUCN
412	Water (Nutrient input)	Nutrients	Disturbance (Anthropogenic)	State/Proxy	Nutrient enhancement alter reef processes	IUCN
413	Water (Pollution (Chemical))	Pollution	Disturbance (Anthropogenic)	State/Proxy	Reduce ability to withstand other stresses	IUCN
414	Substrate (Pollution (Solid))	Garbage	Disturbance (Anthropogenic)	State/Proxy	Unsuitable for coral growth and recruitment	IUCN
415	Turbidity/sedimentation	Turbidity	Physical characteristics	State/Proxy	Anthropogenic enhanced turbidity and sedimentation negatively affects corals	IUCN
416	Anthropogenic (Physical damage)	Human impact	Disturbance (Anthropogenic)	Proxy	Mortality/inhibits recovery	IUCN
417	Fishing pressure	Fishing pressure	Disturbance (Anthropogenic)	Proxy	Overfishing causes reef degradation	IUCN
418	Destructive fishing	Destructive fishing	Disturbance (Physical)	State/Proxy	Physical damage to site, alters balance of fish dynamics	IUCN
419	Connectivity (Dispersal barrier) Anthropogenic	Dispersal barrier	Disturbance (Anthropogenic)	State/Proxy	Construction that affects connectivity	IUCN
420	Management (Biodiversity)	Management	Management Status	State/Proxy	Protection of biodiversity	IUCN

421	Management (Environmental quality)	Management	Management Status	State/Proxy	Protection from extraction of resources by fishing or other activities	IUCN
422	Management (Resources)	Management	Management Status	State/Proxy	Limitation of human activities that degrade the environment, e.g. pollution	IUCN
423	Depth	Depth	Location & Geomorphology	State		Reef Check
424	Latitude and longitude	Latitude/Longitude	Location & Geomorphology	State		Reef Check
425	Site exposure (windward or leeward)	Site exposure	Location & Geomorphology	State/Proxy		Reef Check
426	Impacts - Blast/poison/net aquarium fishing/collecting invertebrates for food/curio sales/tourists	Human impact	Disturbance (Anthropogenic)	Proxy		Reef Check
427	Impacts - Sewage/industrial pollution	Pollution	Disturbance (Anthropogenic)	State/Proxy		Reef Check
428	Impacts - Commercial fishing	Fishing pressure	Disturbance (Anthropogenic)	Proxy		Reef Check
429	Number of yachts/motorboats	Human impact	Disturbance (Anthropogenic)	Proxy		Reef Check
430	Management	Management	Management Status	State/Proxy		Reef Check
431	Fish abundance (Selected species)	Fish abundance (key)	Fish abundance	State		Reef Check
432	Fish size class distribution (Selected species)	Fish size (key)	Fish size	State		Reef Check
433	Urchin	Urchin	Herbivory	State/Proxy	Important algae grazers	Reef Check
434	COTS abundance	COTS	Disturbance (Biological)	State/Proxy	Coral damage	Reef Check
435	Triton abundance	Motile invertebrates	Other invertebrates	State		Reef Check
436	Banded coral shrimp	Motile invertebrates	Other invertebrates	State		Reef Check
437	Lobster abundance	Motile invertebrates	Other invertebrates	State/Proxy	Usually seen only on reefs that have not been overfished	Reef Check
438	Giant clam abundance	Motile invertebrates	Other invertebrates	State/Proxy	Usually seen only on reefs that have not been overfished	Reef Check

439	Triton abundance	Motile invertebrates	Other invertebrates	State/Proxy	Usually seen only on reefs that have not been overfished	Reef Check
440	Gorgonian	Other Invertebrates (Sessile)	Other invertebrates	State		Reef Check
441	Cowries abundance	Motile invertebrates	Other invertebrates	State		Reef Check
442	Coral disease	Disease	Disturbance (Physiological)	State/Proxy		Reef Check
443	Bleached coral cover	Bleached coral cover	Disturbance (Physiological)	State/Proxy		Reef Check
444	Coral cover (species)	Coral cover (species)	Coral cover	State		Reef Check
445	Coral diversity	Coral diversity	Coral community	State		Reef Check
446	Soft coral cover	Other Invertebrates (Sessile)	Other invertebrates	State		Reef Check
447	Recently killed coral	Dead coral cover	Mortality	State/Proxy		Reef Check
448	Nutrient indicator algae	Macroalgae	Algal cover	State/Proxy	Macroalgae that indicates nutrient presence. All algae except coralline, calcareous (<i>Halimeda</i>) and turf	Reef Check
449	Turf algae	Turf	Algal cover	State		Reef Check
450	CCA algae	CCA	Algal cover	State		Reef Check
451	Sponge	Other Invertebrates (Sessile)	Other invertebrates	State		Reef Check
452	Rock	Substrate	Substrate	State		Reef Check
453	Rubble	Substrate	Substrate	State		Reef Check
454	Sand	Substrate	Substrate	State		Reef Check
455	Silt/Clay	Substrate	Substrate	State		Reef Check
456	Other organisms (sea anemones, tunicates, gorgonians or non-living substrate)	Other Invertebrates (Sessile)	Other invertebrates	State		Reef Check
457	Physical damage	Physical impact	Disturbance (Physical)	State/Proxy		Reef Check
458	Reef zone	Reef zone	Location & Geomorphology	State		Reef Check

459	Habitat	Habitat	Location & Geomorphology	State		Reef Check
460	Live coral abundance	Coral cover	Coral cover	State/Proxy	Indicative of past stress tolerance; more corals will produce more gametes. Used total coral cover, not coral size, coral genus in S2 because it is only used to prove that depth should be included in the RSRI.	Rowlands et al. 2012
461	Habitat	Habitat	Location & Geomorphology	State		Rowlands et al. 2012
462	Framework abundance index	Substrate availability	Substrate	Proxy	Proportion of grid cell occupied by coral framework (alive/dead) suitable for coral recruitment. When reef framework is abundant close to source patch, more likely to be colonized.	Rowlands et al. 2012
463	Sand, rubble, sediment	Substrate	Substrate	State		Rowlands et al. 2012
464	Macroalgae	Macroalgae	Algal cover	State		Rowlands et al. 2012
465	Water depth variability	Depth variability	Physical characteristics	State/Proxy	Species show different stress tolerance, cooler regime found in deeper areas yielding a thermal stress refuge. Ratio of SD of water depth at site to maximum SD of water depth for 5 study sites	Rowlands et al. 2012
466	Water depth	Depth	Location & Geomorphology	State		Rowlands et al. 2012
467	Fishing intensity	Fishing pressure	Disturbance (Anthropogenic)	Proxy	Removal of herbivorous fish affects coral-algal balance; removal of predators alters dynamics and food web structure. Combine industrial and traditional fishing pressure	Rowlands et al. 2012
468	Industry and development	Development index	Disturbance (Anthropogenic)	Proxy	Light proximity index, with assumption that reefs are more impacted if close to light source at night. Nutrient enrichment, pollution, desalination outflow, oil cause stress, reduced productivity or death. Development (industrial and residential) have harmful impacts to corals across range of distances from source, typically most harmful to close proximity	Rowlands et al. 2012
469	Thermal stress index	Thermal regime	Disturbance (Physiological)	Proxy	Warming waters cause stress, reduced productivity and ultimately death through coral bleaching	Rowlands et al. 2012
470	Sea surface temperature	Temperature	Physical	State/Proxy	To calculate thermal stress index	Rowlands et al. 2012

			characteristics			
471	Degree heating days	Thermal regime	Physical characteristics	State/Proxy	To calculate thermal stress index, considered a measure of chronic thermal stress, the slow exposure of corals to abnormally high temperature	Rowlands et al. 2012
472	Heating rate	Heating rate	Physical characteristics	Process	To calculate thermal stress index	Rowlands et al. 2012
473	High recovery rate from past disturbances	Recovery rate	Coral community	Process	Past recovery an indicator of future recovery	Weeks & Jupiter 2013
474	Coral population structure	Coral population structure	Coral community	State/Proxy	Proxy (juvenile coral density). High abundance of mature colonies + strong recruitment an indicator of strong future recovery	Weeks & Jupiter 2013
475	Juvenile coral density	Juvenile corals	Recruitment	State/Proxy	Evidence of strong coral recruitment are likely to demonstrate high potential to withstand and recover from disturbance	Weeks & Jupiter 2013
476	Connectivity	Connectivity	Connectivity	Process	Proxy: Juvenile coral density. Protected sites well connected to each other may provide larvae to promote recovery	Weeks & Jupiter 2013
477	Substrate availability	Substrate availability	Substrate	State/Proxy	High availability of suitable substrate on which coral recruits can settle likely to promote recovery	Weeks & Jupiter 2013
478	Herbivore abundance	Herbivore abundance	Herbivory	State/Proxy	Proxy: Herbivore biomass. High abundance of herbivores likely to reduce harmful coral-algal interactions and provide substrate for coral recruits to settle	Weeks & Jupiter 2013
479	Herbivore functional diversity	Herbivore diversity	Fish community	State/Proxy	Measure: Pielou's evenness of herbivore functional groups present. High functional diversity of herbivores likely to reduce harmful coral-algal interactions and provide substrate for coral recruits to settle	Weeks & Jupiter 2013
480	Abundance of bioeroders	Bioeroder abundance	Disturbance (Biological)	State/Proxy	Reefs with low abundance of bioeroders are more resistant to other forms of disturbance	Weeks & Jupiter 2013
481	Absence of coral disease	Disease	Disturbance (Physiological)	State/Proxy	Low disease likely to be more resistant to other forms of disturbance	Weeks & Jupiter 2013
482	Fish diversity	Fish diversity	Fish community	State/Proxy	High fish diversity & functional diversity likely to demonstrate higher resilience	Weeks & Jupiter 2013
483	Fish size	Fish size	Fish size	State		Weeks & Jupiter 2013
484	Fish abundance	Total fish abundance	Fish abundance	State		Weeks & Jupiter 2013

485	Fish biomass (estimated)	Fish biomass	Fish biomass	State/Proxy		Weeks & Jupiter 2013
486	Coral diversity	Coral diversity	Coral community	State	High coral diversity likely to demonstrate higher resilience	Weeks & Jupiter 2013
487	Coral cover	Coral cover	Coral cover	State		Weeks & Jupiter 2013
488	Coral community dominated by resistant/tolerant taxa	Resistant corals	Coral community	State/Proxy	More resistant to disturbance	Weeks & Jupiter 2013
489	Fishing pressure	Fishing pressure	Disturbance (Anthropogenic)	Proxy	Low fishing pressure/not targetting herbivores likely to show higher resilience	Weeks & Jupiter 2013
490	Anthropogenic physical impacts	Human impact	Disturbance (Anthropogenic)	Proxy	Reefs not subjective to pressure are likely to have higher resilience	Weeks & Jupiter 2013
491	Water quality	Water quality	Disturbance (Anthropogenic)	State/Proxy	Water pollution and unnatural levels of nutrients impact resistance and recovery	Weeks & Jupiter 2013
492	Reef aspect	Aspect	Physical characteristics	State/Proxy	Sites angled away from sunlight may be less exposed to thermal stress	Weeks & Jupiter 2013
493	Depth	Depth	Location & Geomorphology	State/Proxy	Deeper sites cooler, but shallow sites more acclimated to hot temperatures	Weeks & Jupiter 2013
494	Reef exposure at low tide	Reef exposure at low tide	Location & Geomorphology	Proxy	Proxy: Reef exposure at low tide. Reefs routinely exposed are better adapted to thermal stress, but extremely low tides with high noon irradiances may result in bleaching mortality	Weeks & Jupiter 2013
495	Proximity to upwelling or exposure to strong currents	Upwelling	Physical characteristics	State/Proxy	Sites influenced by upwelling may not experience as severe positive temperature anomalies	Weeks & Jupiter 2013
496	Shading from high, steep sided islands or reef topography	Shading	Physical characteristics	Proxy	Shaded sites may not experience as severe positive temperature anomalies	Weeks & Jupiter 2013
497	Turbid water	Turbidity	Physical characteristics	State/Proxy		Weeks & Jupiter 2013
498	Natural physical impacts	Physical impact	Disturbance (Physical)	State/Proxy	Sites not frequently physically disturbed likely to show higher resilience	Weeks & Jupiter 2013
499	Resistance (physical factors that reduce temp. stress) - Exchange	Exchange	Physical characteristics	Process	Warm water replaced with cooler oceanic water	West & Salm 2003
500	Resistance (physical factors that reduce temp. stress) - Upwelling	Upwelling	Physical characteristics	Process		West & Salm 2003
501	Resistance (physical factors that reduce temp. stress) - Deep water	Deep water	Physical	State/Proxy		West & Salm 2003

	stress) - Areas adjacent to deep water		characteristics			
502	Resistance (physical factors that reduce temp. stress) - Wind-driven mixing	Mixing	Physical characteristics	Process		West & Salm 2003
503	Resistance (physical factors that enhance water movement and flush toxins) - Fast currents	Current	Physical characteristics	Proxy	Eddies, tidal and ocean currents, gyres	West & Salm 2003
504	Resistance (physical factors that enhance water movement and flush toxins) - Topography	Topography	Location & Geomorphology	State/Proxy	Does not refer to rugosity, but of geological structures promoting water flow	West & Salm 2003
505	Resistance (physical factors that enhance water movement and flush toxins) - High wave energy	Wave exposure	Physical characteristics	Proxy		West & Salm 2003
506	Resistance (physical factors that enhance water movement and flush toxins) - Tidal range	Tide	Physical characteristics	State/Proxy		West & Salm 2003
507	Resistance (physical factors that enhance water movement and flush toxins) - Wind	Wind	Physical characteristics	State/Proxy		West & Salm 2003
508	Resistance (physical factors that decrease light stress) - Shade	Shading	Physical characteristics	Proxy		West & Salm 2003
509	Resistance (physical factors that decrease light stress) - Aspect relative to the sun	Aspect	Physical characteristics	State/Proxy		West & Salm 2003
510	Resistance (physical factors that decrease light stress) - Slope	Slope	Location & Geomorphology	State/Proxy		West & Salm 2003
511	Resistance (physical factors that decrease light stress) - Turbidity	Turbidity	Physical characteristics	State/Proxy		West & Salm 2003
512	Resistance (physical factors that decrease light stress) - Absorption/CDOM	CDOM	Disturbance (Anthropogenic)	State/Proxy		West & Salm 2003
513	Resistance (physical factors that decrease light stress) - Cloud cover	Cloud cover	Physical characteristics	State/Proxy		West & Salm 2003
514	Resistance (factors that correlate with bleaching tolerance) - Temperature variability	Thermal regime	Physical characteristics	State/Proxy		West & Salm 2003

515	Resistance (factors that correlate with bleaching tolerance) - Emergence at low tide	Reef exposure at low tide	Location & Geomorphology	Proxy		West & Salm 2003
516	Resistance (indirect indicators of bleaching tolerance) - Broad size and species distributions	Coral size	Coral community	State/Proxy		West & Salm 2003
517	Resistance (indirect indicators of bleaching tolerance) - Areas of greatest remaining coral cover	Coral cover	Coral cover	State/Proxy		West & Salm 2003
518	Resistance (indirect indicators of bleaching tolerance) - History of corals surviving bleaching events	Thermal regime	Physical characteristics	State/Proxy		West & Salm 2003
519	Resilience (Intrinsic) - Availability and abundance of local larvae	Reproduction	Reproduction	Process		West & Salm 2003
520	Resilience (Intrinsic) - Recruitment success	Recruitment	Recruitment	Process		West & Salm 2003
521	Resilience (Intrinsic) - Low abundance of bioeroders, corallivores, diseases	Harmful organisms	Organisms (Harmful)	State/Proxy		West & Salm 2003
522	Resilience (Intrinsic) - Diverse well-balanced community to prepare substratum for coral settlement	Substrate availability	Substrate	State/Proxy		West & Salm 2003
523	Resilience (Extrinsic) - Good potential for recovery because of effective management regime	Management	Management Status	State/Proxy		West & Salm 2003
524	Resilience (Extrinsic) - Connectivity by currents	Current	Connectivity	Proxy		West & Salm 2003
525	Resilience (Extrinsic) - Concentration of larval supply	Larval supply	Connectivity	Process		West & Salm 2003

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Table S 3.3 Results of two-way permutational MANOVA testing for differences between metrics used by study groups and location (A) and PERMDISP test of homogeneity of dispersions in the metrics used by monitoring and resilience assessments (B).

(A) Fixed factor: group and locations. (B) Fixed factor: group.

Source of variation	df	SS	MS	Pseudo-F	P(perm)
Group	1	6324.8	6324.8	1.8631	0.001
Location	3	11637	3879.1	1.1427	0.184
Goal x Location	2	6560.9	3280.4	0.96635	0.534
Residual	16	37341	3394.7		

S3B Table. Results from PERMDISP test of homogeneity of dispersions in the metrics used by monitoring and resilience assessments. Fixed factor: group.

Group	n	Average	SE	Pseudo-F	P(perm)
Monitoring	6	47.12	2.1289	33.529	0.0007
Resilience	12	59.121	1.026		

Table S 3.4 Results of SIMPER analysis for studies in the monitoring group (A), resilience group (B) and a comparison between the two groups (C).

(A) Monitoring metrics	Average abundance	Average similarity	Sim/SD	Contribution (%)	Cumulative (%)
Macroalgae	1	4.49	5.87	10.69	10.69
Bleached coral cover	0.83	2.98	1.31	7.09	17.78
Other Invertebrates (Sessile)	0.83	2.98	1.31	7.09	24.88
CCA	0.83	2.68	1.36	6.38	31.25
Substrate	0.83	2.68	1.36	6.38	37.63
Turf	0.83	2.68	1.36	6.38	44.01
Coral cover (species)	0.67	1.89	0.77	4.5	48.51
Coral diversity	0.67	1.89	0.77	4.5	53
Disease	0.67	1.89	0.77	4.5	57.5
Habitat	0.67	1.89	0.77	4.5	62
Urchin	0.67	1.89	0.77	4.5	66.49
Temperature	0.67	1.83	0.77	4.36	70.85
Depth	0.67	1.66	0.79	3.94	74.79
Dead coral cover	0.67	1.56	0.79	3.71	78.51
Cyanobacteria	0.5	0.99	0.48	2.36	80.87
Latitude/Longitude	0.5	0.87	0.48	2.07	82.94
Rugosity	0.5	0.84	0.48	1.99	84.93
Fish diversity	0.5	0.77	0.48	1.84	86.77
Turbidity	0.5	0.77	0.48	1.84	88.61
Motile invertebrates	0.5	0.74	0.48	1.77	90.37

(B) Resilience metrics	Average abundance	Average similarity	Sim/SD	Contribution (%)	Cumulative (%)
Macroalgae	0.67	1.92	0.77	8.7	8.7
Coral cover	0.67	1.82	0.81	8.26	16.96
Thermal regime	0.58	1.51	0.64	6.83	23.79
Depth	0.58	1.38	0.62	6.26	30.05
Substrate availability	0.5	1.07	0.53	4.83	34.88
Fishing pressure	0.5	0.99	0.49	4.49	39.37
Disease	0.5	0.94	0.5	4.24	43.61
Substrate	0.5	0.92	0.5	4.16	47.77
Herbivore biomass	0.42	0.77	0.39	3.48	51.25
Rugosity	0.42	0.7	0.4	3.16	54.41
Coral diversity	0.42	0.68	0.4	3.1	57.51
Upwelling	0.42	0.65	0.4	2.93	60.44
Juvenile corals	0.42	0.59	0.39	2.67	63.11
Temperature	0.42	0.55	0.4	2.47	65.58
Turf	0.42	0.53	0.4	2.41	67.99
Coral size	0.42	0.52	0.4	2.36	70.35
Human impact	0.33	0.39	0.3	1.78	72.12
Latitude/Longitude	0.33	0.37	0.3	1.69	73.81
Herbivore diversity	0.33	0.37	0.3	1.69	75.5
Reef exposure at low tide	0.33	0.33	0.31	1.48	76.98
Shading	0.33	0.33	0.31	1.48	78.46
Management	0.33	0.31	0.3	1.43	79.89
CCA	0.33	0.31	0.3	1.4	81.29
Other Invertebrates (Sessile)	0.33	0.3	0.3	1.35	82.64
Resistant corals	0.25	0.25	0.21	1.13	83.77
Nutrients	0.25	0.24	0.19	1.11	84.88
Recruitment	0.25	0.23	0.21	1.02	85.9
Pollution	0.25	0.17	0.21	0.77	86.67
Harmful organisms	0.25	0.17	0.21	0.76	87.43
Mixing	0.25	0.16	0.21	0.72	88.15
Bioeroder abundance	0.25	0.16	0.21	0.71	88.86
Herbivore abundance	0.25	0.16	0.21	0.71	89.56
Fish biomass	0.25	0.15	0.21	0.69	90.25

(C) Monitoring & resilience metrics	Avg. abund. (M)	Avg. abund. (R)	Avg. dissimilarity	Diss/SD	Contribution (%)	Cumulative (%)
Bleached coral cover	0.83	0.08	1.86	1.61	2.47	2.47
Coral cover (species)	0.67	0.08	1.52	1.19	2.02	4.49
Other Invertebrates (Sessile)	0.83	0.33	1.51	1.15	2.01	6.5
Urchin	0.67	0.17	1.46	1.14	1.94	8.44
CCA	0.83	0.33	1.43	1.19	1.91	10.35
Habitat	0.67	0.17	1.41	1.15	1.87	12.22
Thermal regime	0	0.58	1.36	1.08	1.81	14.03
Turf	0.83	0.42	1.33	1.07	1.77	15.8
Dead coral cover	0.67	0.25	1.31	1.13	1.75	17.55
Temperature	0.67	0.42	1.28	0.97	1.7	19.25
Coral cover	0.33	0.67	1.28	1.04	1.7	20.95
Coral diversity	0.67	0.42	1.24	0.97	1.66	22.6
Cyanobacteria	0.5	0.17	1.22	0.91	1.62	24.23
Substrate	0.83	0.5	1.2	0.95	1.6	25.83
Disease	0.67	0.5	1.19	0.93	1.59	27.41
Substrate availability	0	0.5	1.16	0.95	1.54	28.95
Rugosity	0.5	0.42	1.15	0.93	1.54	30.49
Latitude/Longitude	0.5	0.33	1.15	0.94	1.53	32.02
Fishing pressure	0.17	0.5	1.14	0.91	1.51	33.54
Depth	0.67	0.58	1.12	0.88	1.5	35.03
Fish diversity	0.5	0.25	1.1	0.95	1.46	36.49
Turbidity	0.5	0.25	1.1	0.96	1.46	37.95
Juvenile corals	0.33	0.42	1.06	0.88	1.41	39.36
Herbivore biomass	0.17	0.42	1.06	0.82	1.4	40.76
Motile invertebrates	0.5	0.08	1.05	0.96	1.39	42.16
Management	0.33	0.33	0.99	0.83	1.32	43.47
Upwelling	0	0.42	0.93	0.79	1.24	44.71
Fish biomass	0.33	0.25	0.9	0.81	1.2	45.91
Human impact	0.17	0.33	0.88	0.74	1.17	47.09
Fish size	0.33	0.17	0.86	0.77	1.14	48.23
Coralline algae	0.33	0.17	0.85	0.76	1.13	49.36
Seagrass	0.33	0	0.85	0.65	1.13	50.5
Fish abundance (key)	0.33	0.17	0.83	0.76	1.11	51.61
Coral size	0	0.42	0.82	0.8	1.1	52.71
Harmful organisms	0.17	0.25	0.81	0.64	1.08	53.79
Nutrients	0.17	0.25	0.81	0.65	1.08	54.86
Macroalgae	1	0.67	0.81	0.68	1.07	55.94
Total fish abundance	0.33	0.08	0.79	0.72	1.05	56.99
Chlorophyll	0.33	0.08	0.75	0.73	1	57.99

Fish size (key)	0.33	0.08	0.75	0.72	0.99	58.98
Herbivore diversity	0	0.33	0.73	0.66	0.98	59.96
Carbon	0.33	0	0.73	0.68	0.97	60.93
Nitrogen	0.33	0	0.73	0.68	0.97	61.89
Salinity	0.33	0	0.73	0.68	0.97	62.86
Pollution	0.17	0.25	0.72	0.67	0.96	63.82
Wave exposure	0.17	0.25	0.7	0.67	0.93	64.75
COTS	0.33	0	0.7	0.68	0.93	65.68
Reef exposure at low tide	0	0.33	0.68	0.68	0.9	66.58
Shading	0	0.33	0.68	0.68	0.9	67.48
Resistant corals	0	0.25	0.63	0.55	0.84	68.32
Physical impact	0.17	0.17	0.62	0.6	0.83	69.14
Recruitment	0	0.25	0.6	0.55	0.8	69.95
Tide	0.17	0.17	0.59	0.6	0.79	70.74
Reef zone	0.17	0.17	0.58	0.59	0.78	71.52
Wind	0.17	0.17	0.58	0.6	0.78	72.29
Site exposure	0.17	0.17	0.57	0.6	0.75	73.05
Garbage	0.17	0.17	0.51	0.6	0.68	73.73
Coral mortality	0.17	0.08	0.5	0.52	0.67	74.4
Mixing	0	0.25	0.5	0.55	0.67	75.07
Bioeroder abundance	0	0.25	0.5	0.55	0.66	75.73
Herbivore abundance	0	0.25	0.5	0.55	0.66	76.39
Current	0	0.25	0.48	0.56	0.64	77.03
Bleaching	0	0.25	0.48	0.56	0.64	77.67
Aspect	0	0.25	0.47	0.56	0.63	78.3
Coral cover (growth form)	0.17	0.08	0.47	0.51	0.62	78.92
Sediment size	0.17	0.08	0.47	0.51	0.62	79.55
Cloud cover	0.17	0.08	0.46	0.52	0.62	80.16
Season	0.17	0.08	0.46	0.52	0.61	80.78
Storm	0.17	0.08	0.46	0.52	0.61	81.39
Sedimentation	0	0.17	0.46	0.43	0.61	82
Algal height	0.17	0.08	0.43	0.52	0.57	82.57
Coral cover (genus)	0.17	0.08	0.43	0.52	0.57	83.13
Slope	0	0.25	0.43	0.56	0.57	83.7
Algal biomass	0.17	0	0.39	0.43	0.52	84.22
Fish size (species)	0.17	0	0.39	0.43	0.52	84.73
Connectivity	0	0.17	0.38	0.44	0.5	85.23
Water quality	0	0.17	0.36	0.44	0.48	85.71
Conductivity	0.17	0	0.34	0.43	0.45	86.16
Feeding scars	0.17	0	0.34	0.43	0.45	86.61
Fish abundance (species)	0.17	0	0.34	0.43	0.45	87.06
Larval supply	0	0.17	0.3	0.43	0.4	87.46

Coral population structure	0	0.17	0.29	0.43	0.39	87.85
Coral cover (branching)	0	0.08	0.25	0.29	0.34	88.19
Depth variability	0	0.08	0.25	0.29	0.33	88.52
Development index	0	0.08	0.25	0.29	0.33	88.85
Heating rate	0	0.08	0.25	0.29	0.33	89.17
Cause of mortality	0	0.08	0.21	0.3	0.28	89.46
Settlement location	0	0.08	0.21	0.3	0.28	89.74
Mature coral colonies	0	0.08	0.2	0.3	0.27	90.01

4. ACUTE DISTURBANCES MASK CHRONIC WATER QUALITY IMPACTS ON INSHORE CORAL REEFS OF THE GREAT BARRIER REEF

Abstract

Tropical cyclones, coral predation by crown-of-thorns starfish (COTS) and coral bleaching are recognised as the major drivers of coral loss at clear water mid- and off-shore reefs along the Great Barrier Reef (GBR). In comparison, little is known about what drives temporal trends in coral cover at inshore reefs closer to major anthropogenic stress. We assess the spatial and temporal dynamics of coral cover using a multivariate state-space modelling approach that accounts for observation error and identify potential drivers within the six major catchments of the inshore GBR. Based on ten years of data from 2005 to 2014, there was an overall decline of coral cover in nearly half (46%) of the 15 reefs examined, while the rest exhibited fluctuating (23%), static (17%) or positive (13%) trends. We found that inshore reefs respond similarly to offshore counterparts in that coral trends were predominantly influenced by acute disturbance events, yet the disturbances themselves generally differ. Storms and floods emerged as the major drivers affecting the northern and southern inshore GBR respectively, with other drivers such as disease, juvenile coral density, macroalgal and turf cover varying from one catchment to another. Flooding was strongly associated with coral dynamics in southern regions but the response could not be tied to the more specific water quality metrics available. Thus, while water quality is undoubtedly impacting the dynamics of inshore reefs, unpacking causality is exceptionally challenging even with a decadal dataset. A clearer identification of mechanism will likely require further experimental work together with a diversification of intensive field monitoring along appropriate gradients.

Introduction

Coral reefs are dynamic ecosystems typically exhibiting periods of recovery between successive disturbances such as cyclones (Connell 1978). While many reefs still exhibit prolific recovery (Connell 1997; Adjerooud *et al.* 2009; Roff & Mumby 2012; Mumby *et al.* 2015), combinations of chronic stressors and frequent disturbances have reduced the average reef health of ecosystems as far afield as the Caribbean and the Great Barrier Reef (Pandolfi *et al.* 2003; Gardner *et al.* 2005; Bruno & Selig 2007; De'ath *et al.* 2012). Yet, unpacking the relative importance of different stressors is challenging and undoubtedly varies among physical environments and community structures (Tomascik & Sander 1987; Doropoulos *et al.* 2015; Graham *et al.* 2015). The majority of research into coral reef ecosystems has focused on relatively clear-water ecosystems, generally located in areas of high water quality but extensive reefs also occur in areas that are either naturally or unnaturally turbid (Perry & Larcombe 2003). On the Great Barrier Reef (GBR) – which includes more than 2900 reefs, spanning an area of 350,000 km² along 2000 km of the Queensland coast (Colette 2007). Most investigations have focused on mid- and off-shore sites (Bruno & Selig 2007; Sweatman, Delean & Syms 2011), where episodic events such as cyclones, bleaching and crown-of-thorns starfish (COTS) appear to be primary impacts on corals (Osborne *et al.* 2011; De'ath *et al.* 2012; Johns, Osborne & Logan 2014). In inshore areas, the GBR reefs are exposed routinely to vastly different physical conditions resulting from higher turbidity and nutrient levels potentially exposing coral communities to additional impacts associated with poor water quality (Fabricius 2005).

Inshore reef development was historically believed to be limited by unsuitable conditions such as high turbidity and nutrient concentrations, and low light levels (Roy & Smith 1970; Rogers 1990; Baldwin 1992). Yet, later studies demonstrate inshore reefs have surprisingly high coral cover and diversity (Anthony & Larcombe 2000; DeVantier *et al.* 2006; Smithers, Hopley & Parnell 2006; Done *et al.* 2007; Côté & Darling 2010; Morgan *et al.* 2016). These reefs offer a chance to understand how adjacent anthropogenic disturbances affect corals and how reefs respond to land-based pollution sources such as sediment and nutrient loading. Despite extensive research on the biological properties of inshore reefs, such as effects of individual stressors on coral cover (Fabricius *et al.* 2008; Thompson & Dolman 2010; Browne 2012; Guest *et al.* 2016a), community structure (Wismer, Hoey & Bellwood 2009;

Browne, Smithers & Perry 2010; Cleary *et al.* 2014), response mechanisms (Stafford-Smith 1993; Thompson *et al.* 2014), water quality gradients (Fabricius *et al.* 2005; De'ath & Fabricius 2010; Fabricius *et al.* 2014; Wenger *et al.* 2016) and palaeoecological reconstructions (Smithers, Hopley & Parnell 2006; Perry *et al.* 2008; Roff *et al.* 2013), studies of overall community dynamics are in their infancy. Inshore environments may alter fundamental ecological mechanisms such as coral-algal interactions, and studies have hypothesised that increased suspended sediments and nutrients result in the competitive advantage of turf and macroalgae over coral growth (Birrell, McCook & Willis 2005; Vermeij *et al.* 2010; Barott *et al.* 2012; Gordon, Goatley & Bellwood 2016). Yet, it is currently unclear how characteristics unique to inshore environments (e.g. high sedimentation, high nutrients, low light) interact with ecological processes to affect coral dynamics.

Analysis of long-term monitoring data to investigate population trends has occasionally been hampered by limitations in sampling strategies, data coverage, missing values and irregular data points (Nakagawa & Freckleton 2008; Humbert *et al.* 2009; Nakagawa & Freckleton 2011; Dennis & Ponciano 2014). Here, we use a Multivariate Autoregressive State Space (MARSS) model based on a density-dependent Gompertz population model (MARSS: R Package) (Holmes, Ward & Scheuerell 2014) to identify key drivers of variability in coral cover trends in the inshore GBR. State space models are routinely used in fisheries research (Jorgensen *et al.* 2016; Ohlberger, Scheuerell & Schindler 2016; Siple & Francis 2016), and increasingly in ecological studies (Nguyen *et al.* 2015; Walsh, Carpenter & Vander Zanden 2016; Erickson, Gray & Eager 2017). MARSS can be used to produce realistic estimates of coral cover trends by estimating true underlying population trends, accounting separately for natural variability in biological data (process error) and observation error inherent in all surveys. Additionally, this modelling approach allows the influence of covariates on both the process and observed time series to explain changes in population trends.

Specifically, we analyse a 10-year time series of inshore benthic community structure with environmental and disturbance data to examine trends and potential drivers of coral dynamics across the region. A suite of 33 potential drivers were explored including ecological variables such as turf, macroalgae (Mumby *et al.* 2007; Bozec *et al.* 2016) and coral recruitment (Doropoulos *et al.* 2015), stochastic abiotic stressors such as storms (Connell 1997) and floods (Devlin *et al.* 2001), as well as chronic anthropogenic influences from land-based

runoff such as sedimentation (Rogers 1990; Fabricius 2005) (Table S 4.1). Through an investigation of driver combinations on coral cover, we attempt to address the following questions for the inshore GBR: (i) What are the true underlying reef trends? (ii) What are the key biotic and abiotic drivers of inshore reefs? (iii) Is water quality a key driver of inshore coral reef dynamics? (iv) Does the modelling of observation covariates (water clarity) significantly improve predictions of reef dynamics in turbid environments?

Methods

Data

Time-series data included benthic community structure and environmental variables collected from 15 inshore reefs (Figure 4.1, Table S 4.1). Benthic community data was sourced from the Marine Monitoring Programme (MMP) managed by the Great Barrier Reef Marine Park Authority on behalf of the Australian Government Reef Programme. Surveys spanned an area from S 16°18' to S 23°15' along the GBR and were carried out between 2005 and 2014.

Reefs were surveyed annually during the austral winter. Two sites were sampled at each reef stratified by depth at 2 m and 5 m. Each site and depth was sampled using five 20 m permanent transects along the appropriate depth contour. Percent cover of benthos categories was estimated using the photo point-intercept method (Jonker, Johns & Osborne 2008).

Images capturing 0.1 m² substrate were taken at 50 cm intervals along each transect. A subset of 32 images was selected from each transect and the substrata falling below five evenly spaced points on each image identified. Juvenile corals (0-5 cm) were counted within a 34cm-wide belt along each transect. Transects of 2 m wide centered on each 20m transect were used to document causes of coral mortality at the time of survey such as bleaching, crown-of-thorns starfish, disease, flooding and cyclones as described by Miller, Jonker and Coleman (2009), temperature records, flood mapping and cyclone tracks also informed attribution of disturbances that occurred between consecutive surveys. To account for environmental history, a literature search was conducted to include known disturbances at each reef ten years prior to the start of the surveys. Additionally, sediment samples were collected for the analysis of grain size (proportion of clay and silt sized particles) and to quantify the amount of inorganic carbon, organic carbon and total nitrogen. Refer to Thompson *et al.* (2016) for full sampling design and operational procedures. Additional environmental data, including annual averaged chlorophyll *a*, Secchi depth, coloured

dissolved organic matter (CDOM), non-algal particulates (Nap) and a light attenuation coefficient (K_d) estimates based on daily MODIS-Aqua satellite observations were sourced from the Bureau of Meteorology (BOM). Multivariate ENSO Index (MEI), an index used to represent the intensity of an El Niño Southern Oscillation Event (ENSO) and Extended Reconstructed Sea Surface Temperature (ERSST) were also extracted to represent regional temperature effects (Wolter & Timlin 1993; Wolter & Timlin 1998; Huang *et al.* 2015; Liu *et al.* 2015; Huang *et al.* 2016).

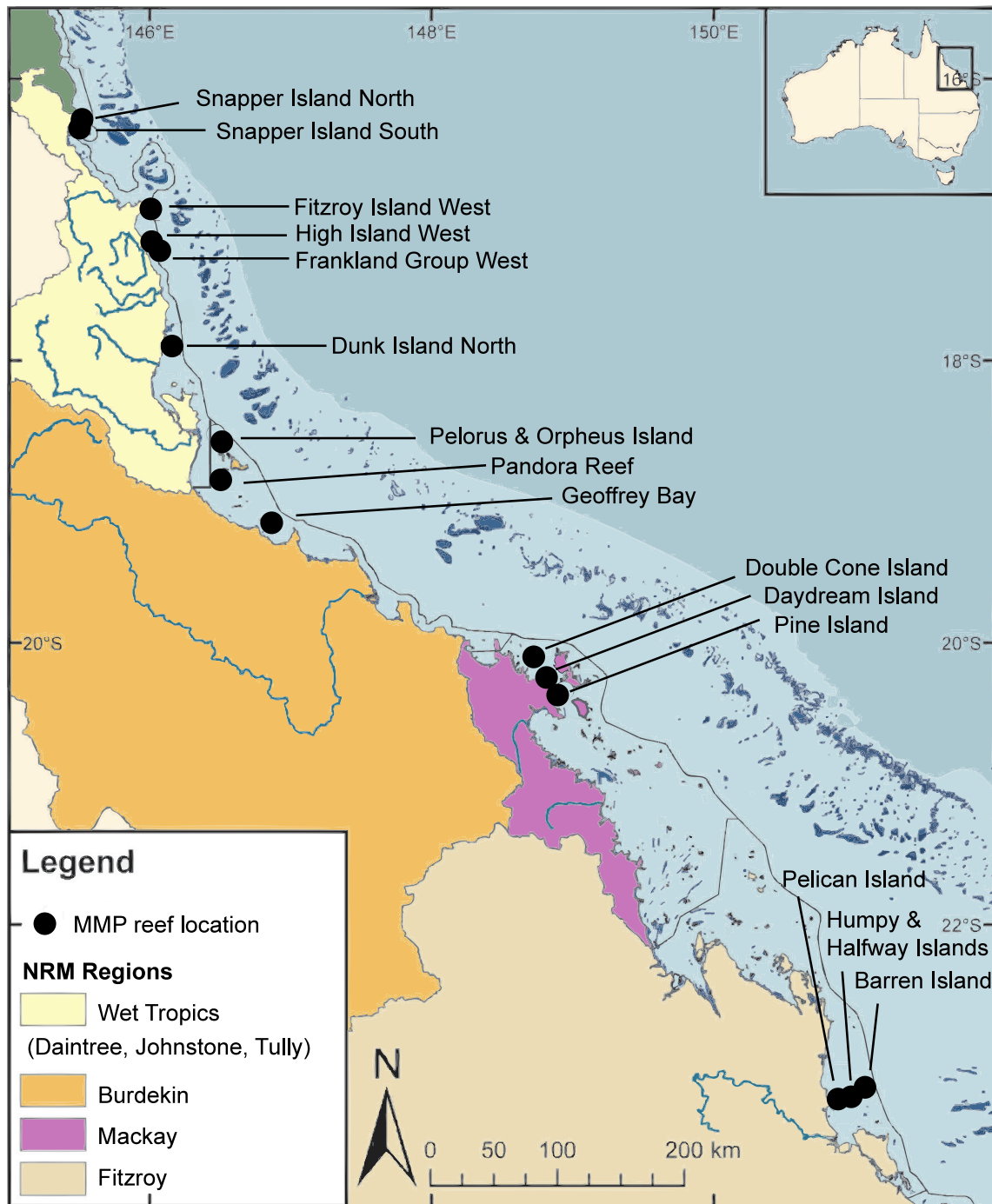


Figure 4.1 Map of the 15 Marine Monitoring Program (MMP) reef sites and adjacent catchment-based natural resource management (NRM) regions.

The Wet Tropics NRM includes three catchments: Daintree, Johnstone and Tully.

MARSS modelling approach

We used a multivariate autoregressive state-space approach (Hinrichsen & Holmes 2009; Holmes, Ward & Wills 2012; Holmes, Ward & Scheuerell 2014) to explore the spatial

structure, estimate hidden population trends and identify key drivers of coral trends. The MARSS approach accounts for both process variability and observation error with a basic form characterised by two equations: a state process that describes the latent (true) underlying dynamics (1), and an observation process based on survey data (2).

$$(1) \mathbf{x}_t = \mathbf{B}_t \mathbf{x}_{t-1} + \mathbf{u} + \mathbf{C}_t \mathbf{c}_t + \mathbf{w}_t, \text{ where } \mathbf{w}_t \sim \text{MVN}(0, \mathbf{Q})$$

$$(2) \mathbf{y}_t = \mathbf{Z}_t \mathbf{x}_t + \mathbf{a} + \mathbf{D}_t \mathbf{d}_t + \mathbf{v}_t, \text{ where } \mathbf{v}_t \sim \text{MVN}(0, \mathbf{R})$$

In the above equations, $\mathbf{x}$ represents the true hidden states (i.e. estimated coral cover at each reef) at time t . Coral cover data enter the model as $\mathbf{y}$ at the site within reef level, forming the observation equation. The parameter $\mathbf{w}_t$ is the process error (variability) with a mean of 0 and covariance matrix of $\mathbf{Q}_t$, whereas $\mathbf{v}_t$ is the observation error with a mean of 0 and covariance matrix of $\mathbf{R}_t$ following a multivariate normal distribution (MVN) at time t . Various options for $\mathbf{Q}$ ('unconstrained', 'diagonal and equal', 'equalvarcov' and 'diagonal and unequal') were tested to find an adequate parameterisation for each MARSS model. For the observation model, we assumed that the observation errors were uncorrelated and equal across sampling sites (i.e. $\mathbf{R}$ fixed as 'diagonal and equal') since all data were collected using the same methodology. The parameter $\mathbf{u}$ can be interpreted as an estimated trend of the hidden states, and $\mathbf{a}$ is the trend of the observed data. An identity matrix was used for $\mathbf{B}$ to represent independent reefs. $\mathbf{Z}$ is a matrix used to specify the spatial structure (the number of hidden states) to which the observed data belong. $\mathbf{C}$ and $\mathbf{D}$ represent the process and observation covariate effects respectively, whereas $\mathbf{c}$ and $\mathbf{d}$ are the values of the process covariates. All covariates were centered and scaled to allow a standardised comparison of the effects of different drivers (Gelman 2008). The final best-fit model was selected using a derivative of Akaike Information Criterion (AICc), which corrects for small sample size (Burnham & Anderson 2002; Johnson & Omland 2004). Models with a ΔAICc of <2 were considered to have similar support from the data (Burnham & Anderson 2004). Where competing models exist, the model with the lowest AICc was chosen and the alternative model also reported in Table S 4.2. All analysis were performed using the MARSS package in R (Holmes, Ward & Wills 2012).

Modelling strategy

Models used the spatial structure of the MMP in which reef sites are replicated adjacent to major catchments draining to the GBR (Thompson *et al.* 2016; Figure 4.1). A total of twelve models were constructed for the six inshore catchments at two depths (2m and 5m), including Daintree, Johnstone, Tully, Burdekin, Mackay and Fitzroy respectively.

An initial number of 33 benthic, environmental and disturbance variables were considered (Table S 4.1), but were analytically eliminated to refine the modelling strategy. First, correlation matrices were created for the overall models (Figure S 4.3, Figure S 4.4) and variables correlated (>0.6) with one another and redundant for the analyses were discarded. Second, variables unlikely to be key drivers that had little fluctuation and low abundance throughout the time-series were also excluded as they affected model convergence.

Ultimately, a total of twelve variables were chosen to represent different aspects of ecological, disturbance, environmental drivers and observation covariates (Table 4.1). Macroalgae and turf cover were lagged for 1-year, whereas juvenile coral densities, sea surface temperature (SST) and multivariate ENSO index (MEI) were lagged by zero, one and two years based on previous study outcomes (Bramanti & Edmunds 2016) and potential thermal inertia (Gill *et al.* 2006). Only relevant variables were chosen for the individual catchment models: for example, COTS were not found on reefs in the Mackay catchment so were excluded from that model. Also, disturbances that never occurred on an individual reef were blocked through the configuration of the C matrix (e.g. disease in Snapper Island South). In any single model, a maximum of two covariates was allowed (Table S 4.2), following the modelling strategy of Ohlberger, Scheuerell and Schindler (2016) to minimise the number of model combinations and to ensure model convergence. After the best-fit model had been selected, regional (SST and MEI) and observation covariates (Secchi depth and proportion of clay and silt sized particles, hereafter known as clay/silt) were added to see if best-fit models were improved. The residuals of the best-fit models were examined for normality.

Table 4.1 Rationale for covariates used in the study

<i>Predictor</i>	<i>Rationale</i>	<i>References</i>
<i>Biological</i>		
Macroalgae	A direct competitor for space and an increase in macroalgae also inhibits recruitment of corals. <u>Hypothesis</u> : an increase in macroalgae will lead to a decrease in coral cover, caused by negative feedback mechanisms.	Done 1992, Birrell et al. 2005, Mumby et al. 2007
Turf	Studies have proposed that turf interacts with sediment and nutrients, leading to a competitive advantage of turf over coral growth. <u>Hypothesis</u> : an increase in turf will have a negative impact on coral cover.	Vermeij et al. 2010, Barott et al. 2012, Gordon et al. 2016
Juvenile coral density	Juvenile corals are crucial for the recovery of coral reef systems after disturbances, but effects on coral cover may be lagged depending on genus. <u>Hypothesis</u> : an increase in juvenile density will lead to an increase in coral cover.	Pearson 1981; Bramanti & Edmunds 2016
<i>Water Quality</i>		
Secchi depth	Secchi depth is a proxy for water clarity and found to be correlated with all satellite-derived water quality variables. Reduced water clarity may affect coral growth through light availability mechanisms. Studies have shown that areas of low secchi depth have lower coral biodiversity and increased macroalgae. <u>Hypothesis</u> : an increase in secchi depth (better water quality) will lead to an increase in coral cover.	De'ath and Fabricius 2010
<i>Disturbances</i>		
Bleaching	Climate-induced ocean warming causes mortality in corals.	Glynn 1993
COTS	Crown-of-thorns starfish predation causes mortality in corals.	
Disease	Disease is found to be a cause of coral mortality, especially in areas with high nutrient concentrations such as the inshore reefs.	Häapkyä et al. 2011; 2013
Flooding	Flood-induced coral mortality occurs during periods of high rainfall and river discharge, and can be related to either direct exposure to freshwater or reduced water caused by terrestrial runoff.	Devlin et al. 2001
Storm	Widely known to be a major cause of coral cover decline through mechanical damage. <u>Overall hypothesis (disturbances)</u> : an increase in the years since a disturbance will lead to an increase in coral cover.	Connell 1983, Harmelin-Vivien 1994

<i>Regional</i>		
MEI	An increase in multivariate ENSO index (El Niño/Southern Oscillation) suggests abnormal warming of the ocean surface, which is known to cause mortality in corals. <u>Hypothesis</u> : an increase in MEI will lead to a decrease in coral cover.	Wolter & Timlin 2011 (DeCarlo <i>et al.</i> 2017)
SST	Increase in sea surface temperature causes mortality in corals. <u>Hypothesis</u> : an increase in SST will lead to a decrease in coral cover.	Ateweberhan & McClanahan 2010
<i>Observation</i>		
Clay/silt	An increase in proportion in claysilt signals increased sedimentation. <u>Hypothesis</u> : Relatively high rates of sediment accumulation may result in potential burial of live coral and a reduction in cover estimate.	Rogers 1990

Results

Of the 15 reefs at two depths (i.e., 30 combinations), almost half (14) exhibited a declining trend, seven exhibited fluctuating dynamics with no overall long-term change in coral cover, five reefs remained static and four showed a trend of coral recovery (Figure 4.2, Figure 4.3). Acute environmental drivers were found to be strongly associated with declining coral trends, whereas the effects of biological drivers were generally relatively weakly associated in both shallow and deeper reefs (Table S 4.2). The importance of drivers were ordered from storm (strongest) > flood and disease > clay/silt, macroalgae, turf and juvenile coral density (Table 4.2, Figure 4.2, Figure 4.3). Shallow reefs of the Burdekin were the only systems where no clear drivers were identified (i.e. the best-fit model was the base model with no covariates, Table S 4.2). In the case of deeper reefs (5m) in the Fitzroy, the model with floods and the base model are both presented due to the small difference in AICc (0.75).

Table 4.2 Key drivers of coral reef dynamics from 2005-2014 in inshore GBR.

Key drivers identified are based on model AICc values in Table S 4.2. Drivers in parentheses represent alternative competing models of similar fit. Base represents models with no covariates and observation indicates the variable was used as a covariate that affects the observation process (observation covariate). Disease, storm and flood drivers all represent years since the previous disturbance. Macroalgae and turf represent algal cover the previous year. Clay/silt and JuvHC is the proportion of clay and silt sized particles collected from sediment samples and juvenile coral density at the time of survey.

	<i>Daintree</i>	<i>Johnstone</i>	<i>Tully</i>	<i>Burdekin</i>	<i>Mackay</i>	<i>Fitzroy</i>
2m	Storm (Base)	Disease & storm (Disease)	Turf & storm	Base	Base + Observation: Clay/silt	Flood (Base)
5m	Macroalgae & disease	Disease & storm	Storm (Turf & Storm)	Storm (Base)	Juvenile coral density & flood	Base/ Flood

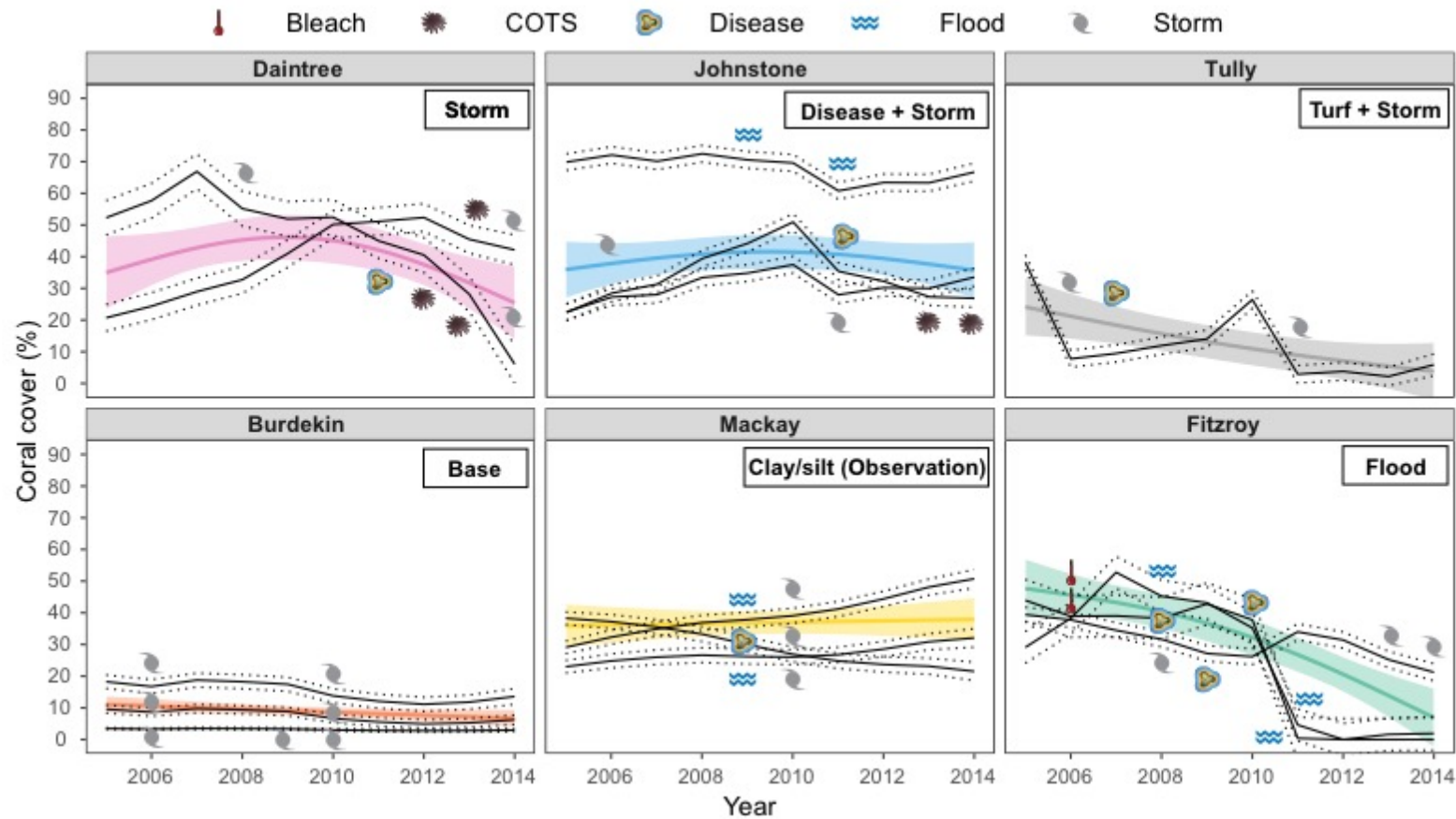


Figure 4.2 MARSS predictions for 15 reefs across 6 catchments at 2m depth illustrated with disturbance occurrence from 2005-2014.

Catchments are ordered from north to south (top left to bottom right). Averaged catchment trends based on observed monitoring data are shown in colour, with coloured bands representing 95% CIs. Reef predictions are based on best-fit catchment models (in black), with dotted lines representing 95% CIs. Symbols represent disturbance events during sampling period. Text in upper right-corner shows key drivers of each catchment.

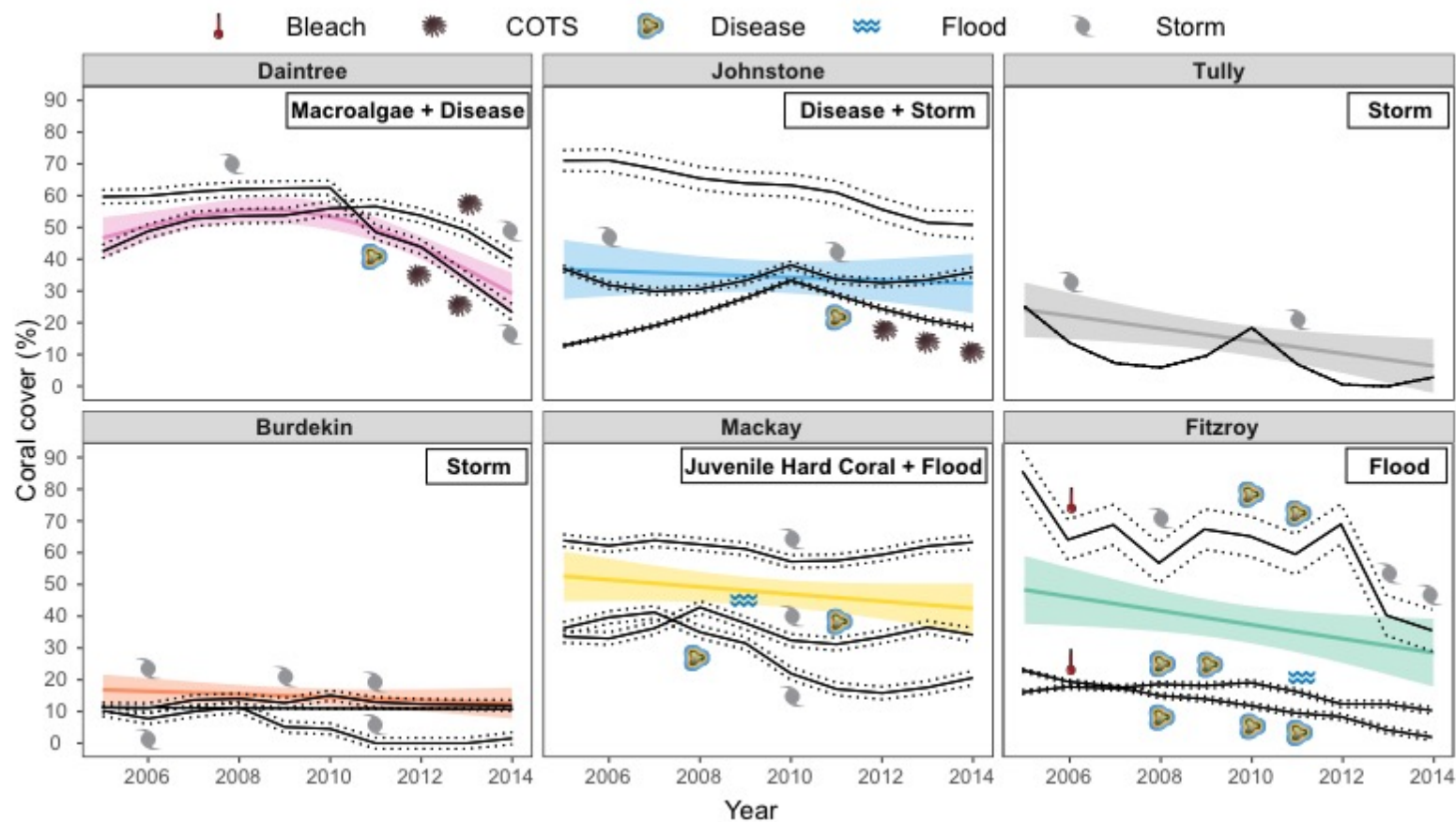


Figure 4.3 MARSS predictions for 15 reefs across 6 catchments at 5m depth illustrated with disturbance occurrence from 2005-2014.

Catchments are ordered from north to south (top left to bottom right). Averaged catchment trends based on coral cover monitoring data are shown in colour, with coloured bands representing 95% CIs. Reef predictions are based on best-fit catchment models (in black), with dotted lines representing 95% CIs. Symbols represent disturbance events during sampling period. Text in upper right-corner shows key drivers of each catchment.

Two drivers repeatedly emerged from best-fit models; storms in the north and floods in the south (Table 4.2). Water quality, represented by Secchi depth, was not found to be associated with trends in coral cover. However, adding the proportion of clay/silt as an observation covariate significantly improved model fits in the Mackay region (2m). A catchment-level SST and a regional ENSO index (MEI) did not improve model fits. Hence, local episodic events were predominantly found to be more important than regional and chronic factors in driving coral dynamics along the inshore GBR for the past ten years. Further investigation of the coral community also shows that substantial increases and decreases in coral cover in shallow reefs (2m) were almost always driven by changes associated with species of *Acropora* (Figure S 4.1), though the role of this genus was less pronounced at 5m other than in the Fitzroy catchment (Figure S 4.2).

Although drivers of coral cover differed among models and were often specific to individual reefs (Figure 4.2, Figure 4.3, Table 4.2, Table S 4.2), the directionality of each driver tended to remain consistent wherever it was found to be associated with coral cover (Table 4.3). The only exception was the effect of juvenile coral density in the Mackay model at 5m, where juvenile coral had a positive effect on one reef and a slight negative effect on another (Table 4.3). In general, coral cover was higher as the passage of time since storms, diseases, and flood increased. Where significant, an increase in macroalgal cover in the previous year was associated with less coral in the following year. Corals clearly outgrew algal turfs since the cover of turf in the previous year had a slight positive association with coral cover in the following year.

Table 4.3 Estimates of driver impacts on coral cover from best-fit models with 95% confidence intervals.

Positive and negative estimates (C) imply a positive and negative effect on coral cover respectively. The CIs of significant estimates do not straddle zero and are presented in bold. Disease, storm and flood drivers all represent years since the previous disturbance. Macroalgae and turf represent algal cover the previous year. Clay/silt and JuvHC is the proportion of clay and silt sized particles collected from sediment samples and juvenile hard coral density at the time of survey. Each driver estimate is presented for individual reefs within each catchment and corresponding reef names are found in Figures S5-S10.

<i>Drivers (2m)</i>	<i>Estimates (C)</i>	<i>Low CI</i>	<i>Upper CI</i>	<i>Drivers (5m)</i>	<i>Estimates (C)</i>	<i>Low CI</i>	<i>Upper CI</i>
<i>Daintree</i>							
Storm (SIN)	0.070	0.028	0.111	Macroalgae (SIN)	0.022	-0.010	0.051
Storm (SIS)	-0.005	-0.041	0.027	Macroalgae (SIS)	-0.039	-0.059	-0.021
				Disease (SIN)	0.066	0.038	0.092
<i>Johnstone</i>							
Disease (FIW)	0.057	0.041	0.074	Disease (FIW)	0.039	0.024	0.054
Storm (FGW)	0.017	0.001	0.033	Storm (FGW)	0.075	0.050	0.102
<i>Tully</i>							
Turf (DIN)	0.073	0.042	0.102	Storm (DIN)	0.151	0.079	0.212
Storm (DIN)	0.222	0.173	0.267				
<i>Burdekin</i>							
Base		NA		Storm (PAN)	0.038	0.019	0.060
				Storm (GEO)	0.012	-0.006	0.027
<i>Mackay</i>							
Clay/silt (Observation)	-0.025	-0.040	-0.011	Flood (PIN)	0.044	0.022	0.065
				JuvHC (DCI)	0.017	-0.008	0.041
				JuvHC (DAY)	0.054	0.031	0.077
				JuvHC (PIN)	-0.032	-0.061	-0.004
<i>Fitzroy</i>							
Flood (HHI)	0.028	-0.004	0.404	Flood (PEL)	0.016	-0.002	0.033
Flood (PEL)	0.084	0.050	0.119				

Discussion

Overall, storms and floods were identified as likely drivers of the true underlying trends of coral dynamics across hundreds of kilometres of the inshore GBR. Our findings suggest that inshore reefs share similarities with offshore reefs, in that episodic events can exert striking

impacts on their state (De'ath *et al.* 2012). Yet, with the exception of storms, the nature of the acute disturbances varies in that inshore reefs are predominantly affected by storms, floods and disease, whereas mid- and off-shore reefs are mostly impacted by storms (also), COTS, and bleaching.

Although chronic water quality metrics were not found to be strongly associated with trends in coral cover, acute flooding appears to be a major driver of southern catchments, where exposure to low salinity flood waters caused a substantial loss of coral cover at 2m depths in the Fitzroy catchment and smothering of corals with fine sediment at 5m depths in the Mackay region. Additionally, we revealed the value in accounting for factors that may affect the observation in ecological surveys, an advantage of the MARSS model, such that the inclusion of the proportion of clay and silt significantly improved model fits of reefs in Mackay, which is a particularly turbid catchment (Brodie *et al.* 2010).

Reefs of the inshore GBR can be separated into dynamic and non-dynamic systems post 2005. Stable reefs exhibited flat coral trends, although absolute levels of coral varied among reefs and catchments. Reefs in the Burdekin catchment generally resemble a degraded state with low cover and limited recovery, likely due to historical disturbance regime and conceivably a lack of recovery capacity brought about by low resilience (Mumby & Steneck 2008; Nyström *et al.* 2012). Paleontological studies found that some reefs in the Burdekin may have suffered early declines between 1920-50s and have not recovered since, following the collapse of *Acropora* assemblages (Roff *et al.* 2013). Others may have experienced relatively recent declines in the mid-1990s including some of the Palm Islands such as Havannah and Pandora reefs (Done *et al.* 2007; Sweatman *et al.* 2007; Cheal *et al.* 2013). Cover in the Mackay region has also been fairly but unlike the Burdekin, cover was relatively high at around 40-50 percent. A likely cause of the lack of dynamism was the paucity of acute disturbances throughout the survey period, the exception being Cyclone Ului in 2010 where coral loss was highly variable owing to sheltered survey locations (Thompson *et al.* 2014). Identifying drivers of coral cover in these relatively non-dynamic systems was challenging and resulted in several best-fit models that either lacked covariates or had little difference between the base model and those with covariates. A major cause of this statistical difficulty or ambiguity is that analyses are predicated on detecting associations between the changes in response and covariates yet the response was almost constant.

Dynamic reefs are mainly driven by changes in *Acropora*, consistent with examples documented in both the offshore (Osborne *et al.* 2011; Johns, Osborne & Logan 2014) and inshore reefs such as the Keppel Islands (Diaz-Pulido *et al.* 2009). The dynamic nature of *Acropora*-dominated reefs can be attributed to the rapid growth of corals in this genus and high recruitment rates (Wallace 1985; Halford *et al.* 2004; Doropoulos *et al.* 2015), as well as high sensitivity to disturbances (Baird & Marshall 2002). Dynamic reefs were found in the catchments of Daintree, Johnstone, Tully and Fitzroy. Many reefs in Daintree and Johnstone catchments exhibited stable or recovering cover trends until 2010/2011, after which the impacts of disease, COTS, flooding and cyclones drove a decline from 2011-2014. The recovery of Dunk Island North, in the Tully catchment, is evident between the occurrence of two major cyclones in 2006 and 2011, whereas Fitzroy was affected by a multitude of disturbances throughout the time-series, causing considerable fluctuation of coral cover. Unlike stable reefs with flat cover trends, the difficulty in identifying drivers at the deeper Fitzroy reefs had two causes. First, multiple disturbances impacted the region simultaneously and second, reefs exhibited variable responses to the same stressor. For instance, in 2006 bleaching caused extensive coral decline at Barren Island but not at Humpy and Halfway Islands, whereas coral cover remained constant at Pelican Island but declined at Barren, Humpy and Halfway Island sites when levels of coral disease were regionally high. These examples also highlight the high spatio-temporal variability amongst reefs and that drivers often have site-specific impacts that are dependent on many factors such as geomorphology and individual reef histories (Perry *et al.* 2014).

Surprisingly, no significant relationships were found between coral dynamics and direct water quality metrics. The negative effect of sedimentation, nutrient enrichment and turbidity leading to the degradation of coral reefs has been well documented at local (Fabricius 2005) and regional scales (De'ath & Fabricius 2010). Long-term exposure to high turbidity and nutrient concentrations is associated with increased macroalgal cover and reduced coral biodiversity (De'ath & Fabricius 2010; Brodie *et al.* 2012; Fabricius *et al.* 2012). Although the results of the study might appear to be inconsistent with the wider literature on inshore reefs, our findings do not imply that water quality is unimportant. First, flood was strongly associated with coral losses in southern catchments and while none of the water quality metrics could provide better statistical fits, the mechanism responsible very likely involves

water quality. A study of ten catchments along the inshore GBR found that Fitzroy is one of the two catchments that contribute the highest sediment and nutrient exports (Joo *et al.* 2012); and another study pointed out reefs in the Mackay region are highly degraded by elevated sediment and nutrient discharge from rivers due to sugarcane cultivation and beef grazing (van Woesik, Tomascik & Blake 1999; Mitchell, Brodie & White 2005), the same southern catchments that showed flood effects in our study. Second, the inability to detect specific water quality impacts on inshore reefs highlights the likely complexity of mechanisms involved, which almost certainly vary over time and space. Third, a feasible scenario is that chronic water quality stress already impacted reefs decades ago, and are not discernible over and above the short-term and punctuated severe events over the recent decadal study reported here.

Compelling evidence from several studies suggests that anthropogenic sediment and nutrient pollution on the GBR are linked to early European settlement circa 1850 A.D. (McCulloch *et al.* 2003; Perry *et al.* 2008; Kroon *et al.* 2012). In addition, models by Moss *et al.* (1992) concluded a three- to five-fold increase in sediments and nutrient exports from Queensland catchments since European settlement. If the deterioration of water quality occurred more than 100 years ago, chronic impacts will be hard to capture as reefs may already have responded to antecedent impacts, and unlikely to show detectable changes in the past ten years. This phenomenon is particularly likely in the Burdekin. To note, critical levels of water quality are likely to be site specific and are especially difficult to capture by temporal aggregation as used in our study which likely limits the detection of significant results.

Storms are a major driver of coral dynamics and vary in their frequency and temporal clustering along the GBR (Done, Ayling & van Woesik 1991; Wolff *et al.* 2016). Indeed, those catchments identified as having a strong association between inshore coral dynamics and storms all fall within the cyclone belt (i.e., Daintree, Johnstone, Tully and Burdekin). Daintree was impacted by Cyclone Ita in 2014 and has a history of major storm disturbance, such as Cyclone Rona in 1999 where average coral cover declined from 66% to 17% in Snapper Island North (Ayling & Ayling 2005). Johnstone and Tully were impacted by Cyclones Larry in 2006 (Thompson & Dolman 2010) and Yasi in 2011 (Perry *et al.* 2014; Beeden *et al.* 2015). Located in the central GBR, Burdekin falls within the region of highest cyclone activity (Wolff *et al.* 2016).

Flooding was found to be a major driver in the southern-most catchments of Fitzroy, and at 5 m depth in Mackay. In Mackay, the O'Connell and Proserpine Rivers transport substantial amounts of sediments and nutrients to nearby reefs, documented in the 2009 flooding event (Joo *et al.* 2012). In Fitzroy, the best-fit model captures the marked impacts of the Fitzroy floods in 2011 which caused extensive mortality of corals due to freshwater inundation (Jones & Berkelmans 2014). Fitzroy River floods have previously impacted reefs in the Keppel Islands, such as low salinity plumes from Cyclone Joy in 1991 which caused up to 90% coral mortality in fringing reefs (Byron & O'Neill 1992; van Woesik, De Vantier & Glazebrook 1995). The strong flood signal in the two southern catchments replicates the findings in geochemical studies, where inshore reefs were found to be greatly influenced by variable freshwater delivery with evidence from highly periodic Ba/Ca ratios corresponding to the onset of monsoonal rains and terrigenous sediment caused by floods (Walther, Kingsford & McCulloch 2013). Moreover, the impact of floods may be more pronounced than years prior to the start of the dataset owing to a contrast between extreme wet and dry years with a period of high river flows (2007-2013) following dry years from 2002 to 2006 (Fabricius *et al.* 2016).

The other drivers that emerged include disease, juvenile hard coral density, macroalgal and turf cover, and the proportion of clay/silt as an observation covariate. Disease impacts corals by causing either partial or total mortality and lowered reproductive output (Harvell *et al.* 1999; Weil 2004). Indeed, diseases are increasingly recognised as a threat to turbid inshore reefs of the GBR (Willis, Page & Dinsdale 2004; Paley *et al.* 2013). Finding an association of disease and coral in Johnstone, a catchment with long established sugarcane cultivation (Furnas, Mitchell & Skuza 1997; Devlin & Brodie 2005), is consistent with other studies (Haapkylä *et al.* 2013) though whether disease has been a persistent long-term problem or relatively recent phenomenon – perhaps stimulated by higher sea temperatures – remains unclear. Short-term studies suggest an increase in rainfall and subsequent runoff, as well as exposure to sediment plumes, is linked to higher coral disease prevalence (Haapkylä *et al.* 2011; Pollock *et al.* 2014).

The association between juvenile coral density and coral cover in Mackay corresponds to the unsurprising importance of recruitment on reef recovery demonstrated by Jones and

Berkelmans (2014) in Keppel Bay, Doropoulos *et al.* (2015) at Heron Reef, Gilmour *et al.* (2013) at Scott Reef, and Graham *et al.* (2015) in the Seychelles. The density of juvenile hard corals was found to have both positive and negative effects on corals in Daydream and Pine Island respectively. The differing effects of juvenile density on coral cover may be attributed to differences in juvenile composition. Water quality extremes can cause reductions of juvenile density without affecting coral cover (Thompson *et al.* 2014), which may help explain the divergent associations of juvenile coral density detected on different reefs.

Macroalgae were associated with coral decline in the Daintree which fits the general expectations of a negative relationship between macroalgae and corals through a variety of mechanisms including competition for space, interference with recruitment, localised coral mortality and its key role in negative feedbacks that tips the resilience of systems (McCook, Jompa & Diaz-Pulido 2001; Birrell *et al.* 2008; Mumby & Steneck 2008). Finally, the positive relationship between turf cover and coral recovery at shallow Tully reefs is of interest because the finding suggests that there is no evidence for the postulated negative effect of turf in inshore habitats through sediment trapping and inhibition of herbivory thus impeding coral recruitment (Birrell, McCook & Willis 2005; Arnold, Steneck & Mumby 2010). Rather, the weak positive relationship with coral cover found implies that corals were overgrowing turfs as they often do in offshore environments.

There are several limitations to our study which should be noted. First, our assessment of water quality was based on annual averages of satellite-derived photic depth (Secchi depth), as the most complete water quality variable available for the duration of the analysis. Several water quality metrics can be used but recent studies have focused on derived photic depth owing to its association with nutrients, suspended particles, and reductions in light availability (Weeks *et al.* 2012; Fabricius *et al.* 2016). Second, the disturbance data used were limited to presence/absence and lacked information on intensity. For example, differences in storm intensity and hydrodynamics contribute to varied responses in coral mortality (Madin & Connolly 2006; Edwards *et al.* 2011; Puotinen *et al.* 2016). However, to capture historical and legacy effects, disturbance data were modified to ‘years since disturbance’ and those ten years prior to the start of the survey were included. Thirdly, insights from certain drivers would likely be clearer if we had more years of data, especially given the static trends of catchments like Burdekin where much of the system transformation

pre-dated monitoring surveys. Although we had a 10-year dataset with a spatial coverage of 30 sites which is considered comprehensive for a coral reef system, MARSS models are still the most effective with longer time-series (Ward *et al.* 2010; Siple & Francis 2016).

Our results clearly imply that factors associated with water quality impact upon inshore coral reef dynamics but postulating specific mechanisms was impossible because of the lack of strong statistical association with individual water quality metrics. The functional absence of corals on reefs within the Burdekin catchment is evidence that reef dynamics is cannot simply be explained by acute disturbances and contemporary chronic water quality. Indeed, it is feasible that the persistent lack of recovery indicates that reefs have contravened a critical threshold and undergone a regime shift with ecological feedbacks preventing recovery. Since most regime shifts involve hysteresis it is important to identify the nature of such feedbacks, (if they exist) and then evaluate whether water quality contributes to the resilience of the coral-depleted state. If it does, then theory predicts that water quality might have to be improved to extraordinarily high levels (for this region) to allow recovery. What remains to be explored is how the detection of chronic water quality effects can be improved across a large spatial scale. A combination of experimental study of mechanism, combined with in situ monitoring of appropriate metrics will likely prove fruitful, particularly if field components can be stratified with respect to acute stressors. Further insights into the resilience of such reefs could be drawn by explicitly disaggregating and measuring processes of recovery (including somatic growth rates) in addition to those of disturbance.

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Supporting Information

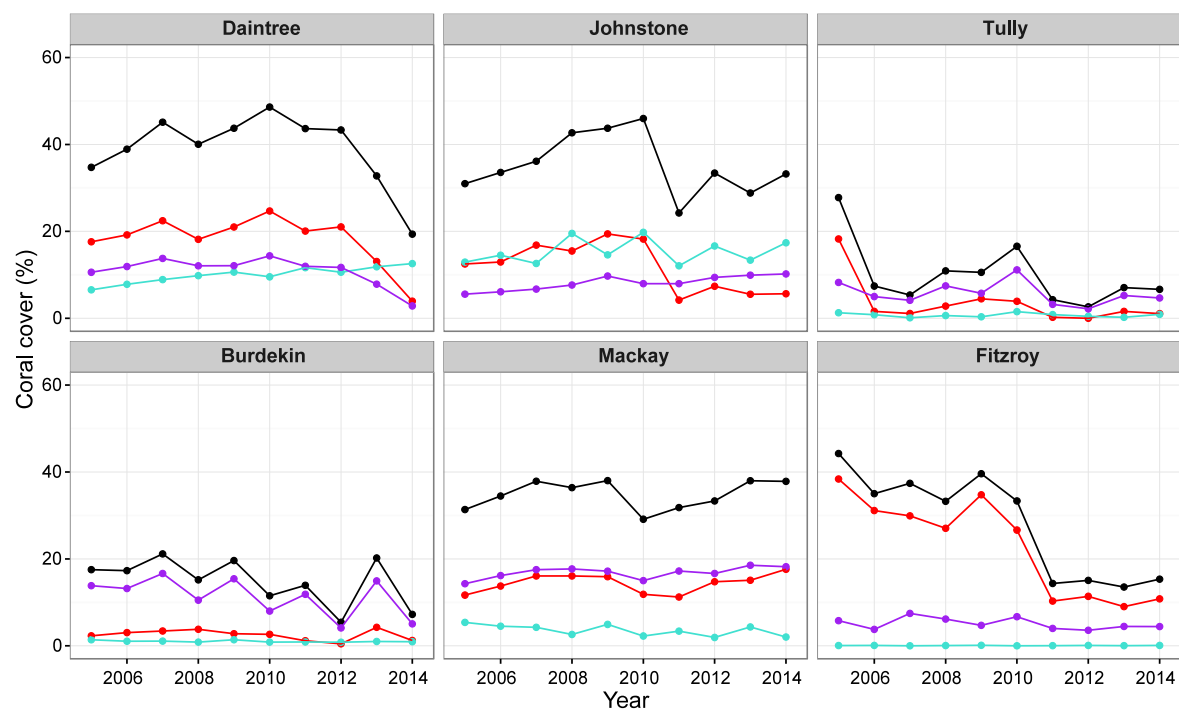


Figure S 4.1 Average coral cover of 2m reefs in 6 GBR catchments from 2005-2014.

Total coral cover (black), *Acropora* (red), *Porites* (turquoise) and other corals (purple):
Montipora (27.5%), *Goniopora* (13.5%), *Galaxea* (12%), *Pachyseris* (4.4%) and
Pocillipora (4%).

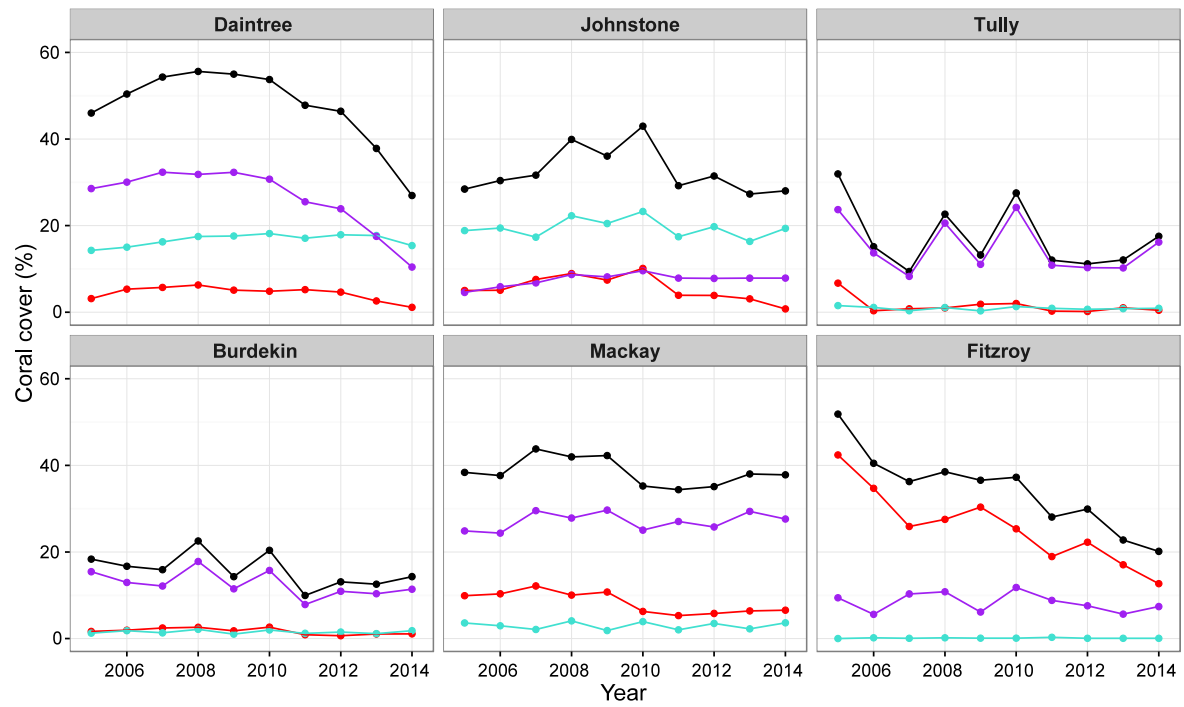


Figure S 4.2 Average coral cover of 5m reefs in 6 GBR catchments from 2005-2014.

Total coral cover (black), *Acropora* (red), *Porites* (turquoise) and other corals (purple): *Goniopora* (22.6%), *Montipora* (10.2%), *Pachyseris* (7.3%), *Galaxea* (6.6%) and *Turbinaria* (4.7%).

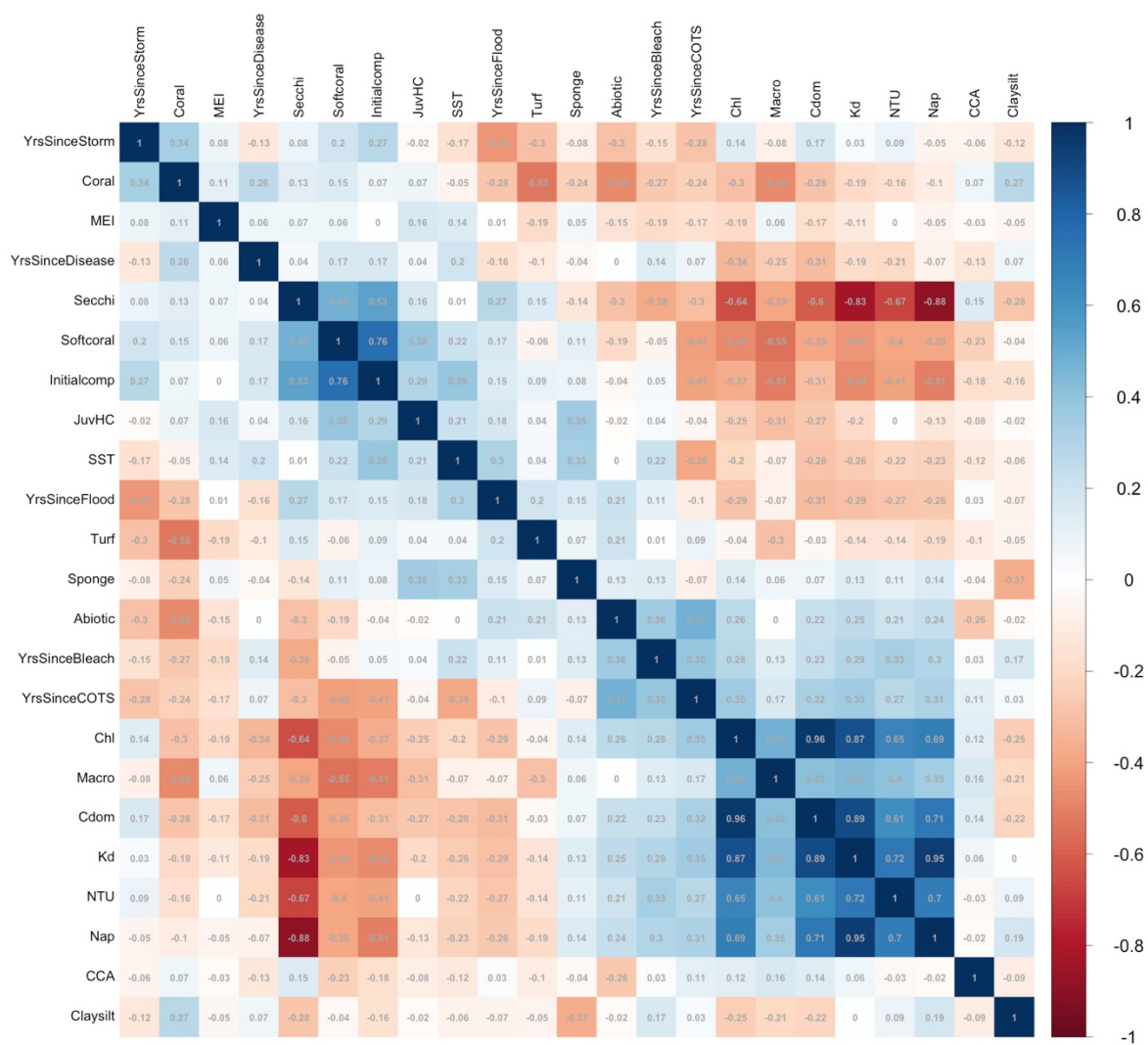


Figure S 4.3 Correlation matrix of the predictor variables at 2m shallow reefs.

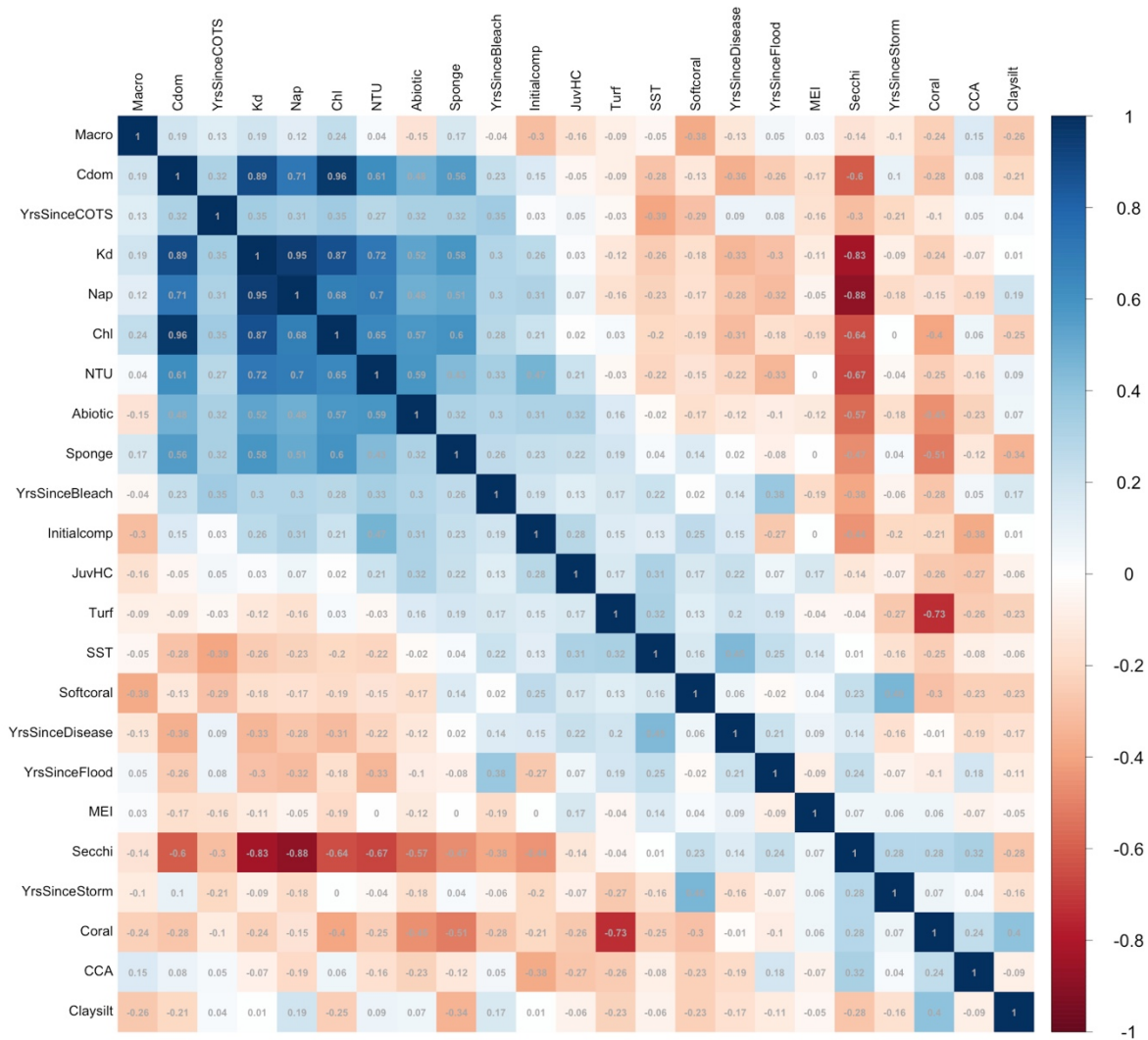


Figure S 4.4 Correlation matrix of the predictor variables at 5m deeper reefs.

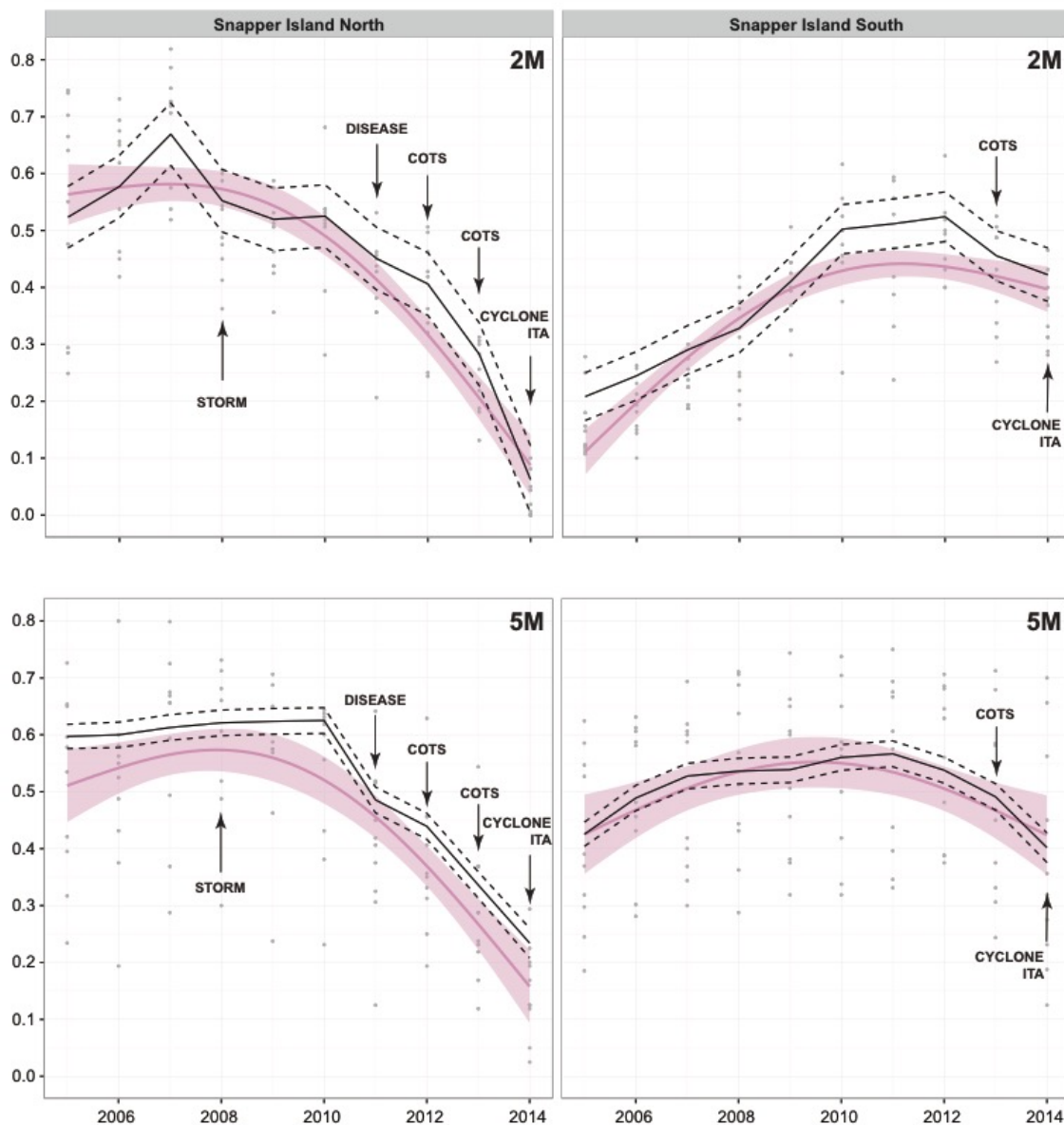


Figure S 4.5 MARSS predicted versus observed coral reef trajectories in Daintree. Observed trends based on monitoring of coral cover at Snapper Island North (SIN) and Snapper Island South (SIS) at 2m and 5m depths are shown in colour, with shaded area representing 95% CIs. Points are the averaged observed coral cover at each reef in each year. MARSS predicted trends based on best-fit model are shown in black, with dashed lines representing 95% CIs.

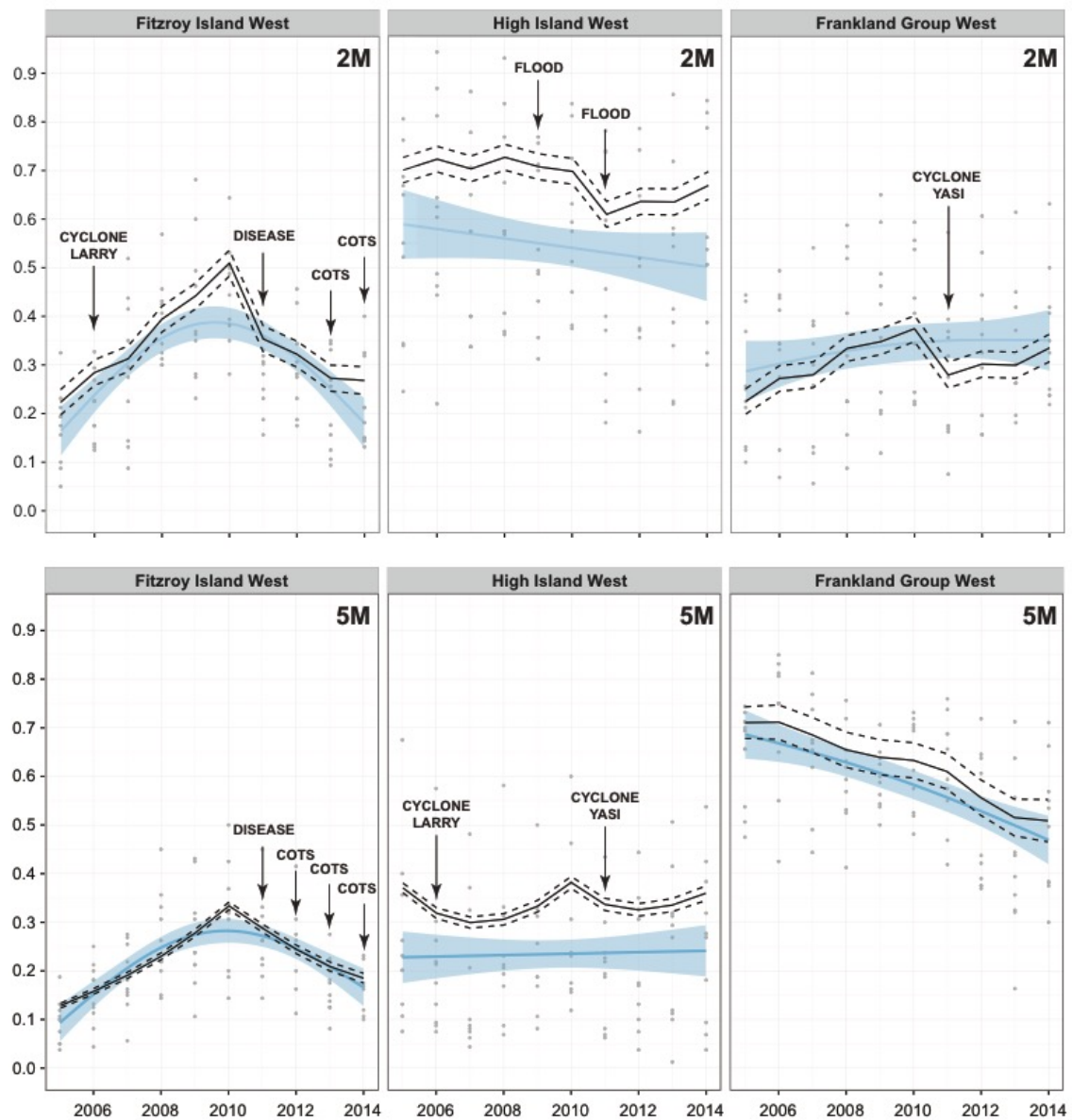


Figure S 4.6 MARSS predicted versus observed coral reef trajectories in Johnstone. Observed trends based on monitoring of coral cover at Fitzroy Island West (FIW), High Island West (HIW) and Frankland Group West (FGW) at 2m and 5m depths are shown in colour, with shaded area representing 95% CIs. Points are the averaged observed coral cover at each reef in each year. MARSS predicted trends based on best-fit model are shown in black, with dashed lines representing 95% CIs.

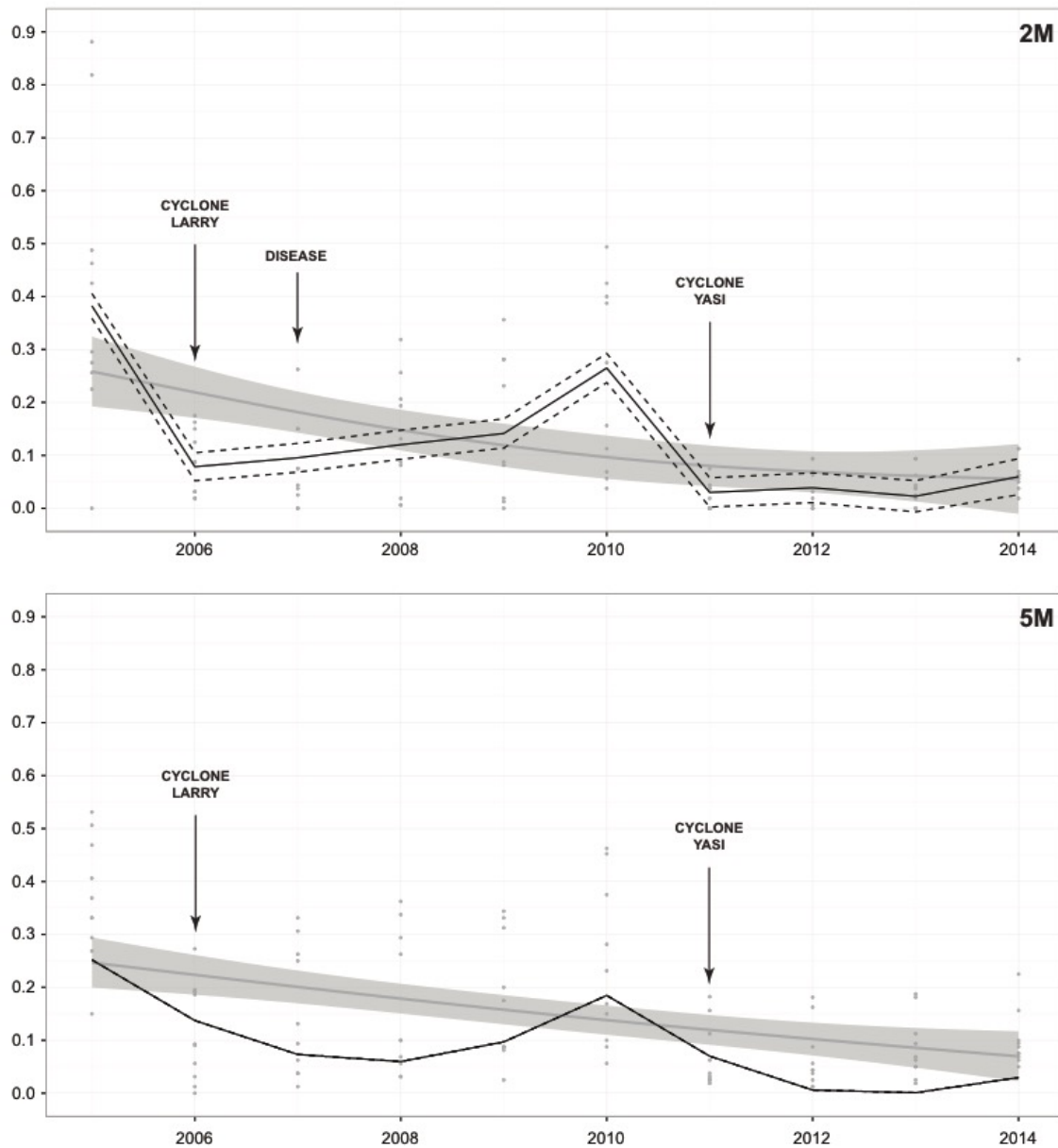


Figure S 4.7 MARSS predicted versus observed coral reef trajectories in Tully.

Observed trends based on monitoring of coral cover at Dunk Island North (DIN) at 2m and 5m depths are shown in colour, with shaded area representing 95% CIs. Points are the averaged observed coral cover at each reef in each year. MARSS predicted trends based on best-fit model are shown in black, with dashed lines representing 95% CIs.

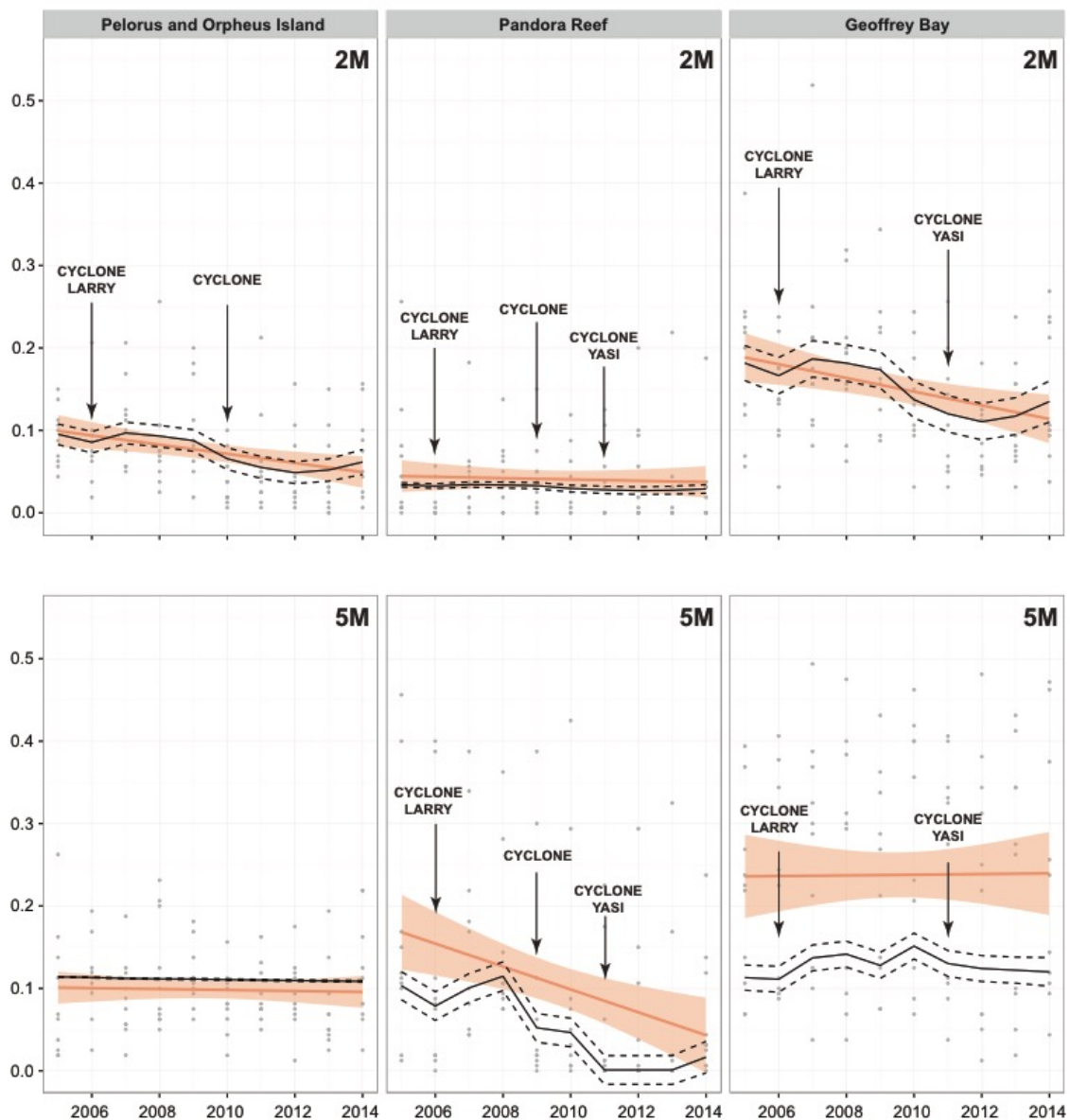


Figure S 4.8 MARSS predicted versus observed coral reef trajectories in Burdekin.

Observed trends based on monitoring of coral cover at Pelorus and Orpheus Island (POI), Pandora Reef (PAN) and Geoffrey Bay (GEO) at 2m and 5m depths are shown in colour, with shaded area representing 95% CIs. Points are the averaged observed coral cover at each reef in each year. MARSS predicted trends based on best-fit model are shown in black, with dashed lines representing 95% CIs.

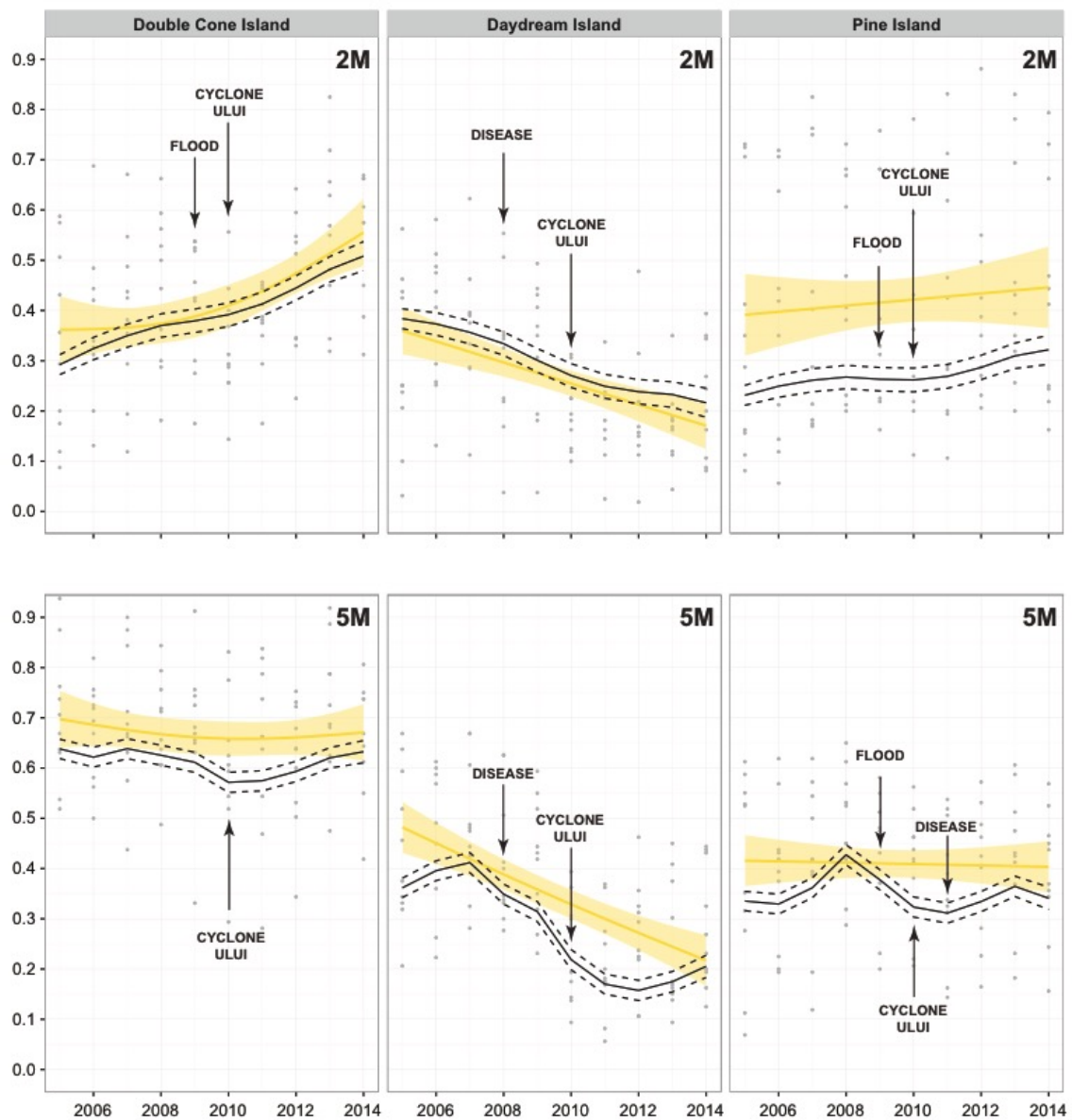


Figure S 4.9 MARSS predicted versus observed coral reef trajectories in Mackay.

Observed trends based on monitoring of coral cover at Double Cone Island (DCI), Daydream Island (DAY) and Pine Island (PIN) at 2m and 5m depths are shown in colour, with shaded area representing 95% CIs. Points are the averaged observed coral cover at each reef in each year. MARSS predicted trends based on best-fit model are shown in black, with dashed lines representing 95% CIs.

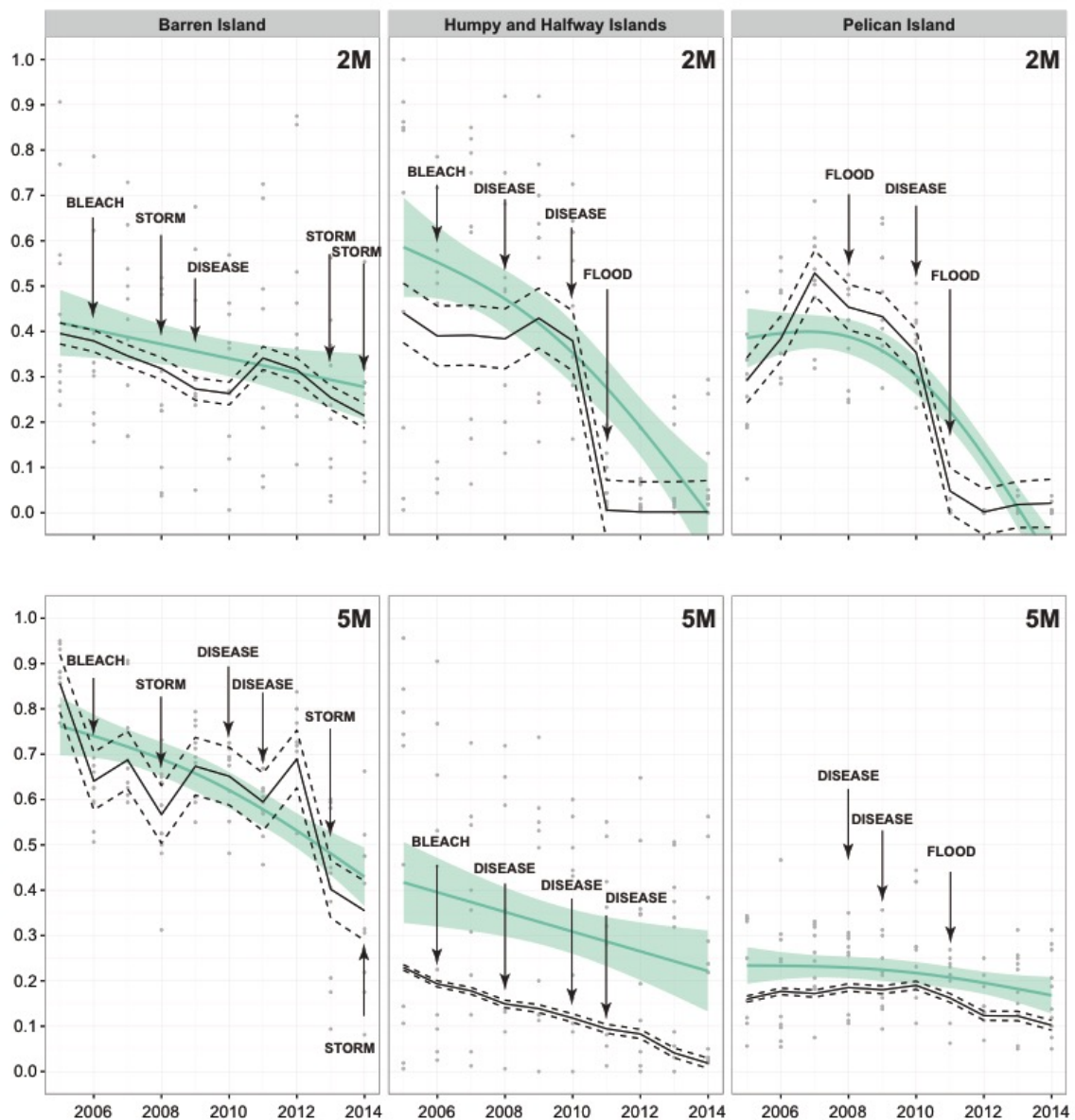


Figure S 4.10 MARSS predicted versus observed coral reef trajectories in Fitzroy. Observed trends based on monitoring of coral cover at Barren Island (BAR), Humpy and Halfway Islands (HHI) and Pelican Island (PEL) at 2m and 5m depths are shown in colour, with shaded area representing 95% CIs. Points are the averaged observed coral cover at each reef in each year. MARSS predicted trends based on best-fit model are shown in black, with dashed lines representing 95% CIs.

Table S 4.1 Variables considered in the MARSS analysis.

Variables in bold are the final variables incorporated in the MARSS models.

Variables	Unit	Reef	Depth	Site	Transect	Method	Notes
<u>Biological Variables</u>							
Benthic data	%	X	X	X	X	Photo point intercept	Includes coral (total coral , <i>Acropora</i> , <i>Porites</i> , other coral), turf , macroalgae , CCA, other algae, soft coral, sponge, abiotic, others
Initial Composition	NA	X	X				Cluster analysis of reefs, split into 5 community groups based on 2005 benthic community composition data
Juvenile Density	m ²	X	X	X		Belt transects	
NTU	NTU	X				Water quality logger	In situ CTD, deployed at 5m.
Disturbance	#	X	X			Scuba search	Includes presence/absence data on bleaching, crown-of-thorns starfish (COTS), cyclone, disease, flood and multiple disturbances
<u>Environmental Variables</u>							
Nitrogen	%	X		X		Sediment sampling	Monitored every year at core reefs
Carbon	%	X		X		Sediment sampling	Monitored every year at core reefs
Organic Carbon	%	X		X		Sediment sampling	Monitored every year at core reefs
Clay/silt	%	X		X		Sediment sampling	Monitored every year at core reefs. Syringe tubes used to collect sediment at 5m and correlated with all sediment samples.
Chlorophyll	µg/L	X				Satellite Modis-AQUA	Yearly average of daily estimates.
Secchi depth	m	X				Satellite Modis-AQUA	Estimation of water clarity from satellite data, calibrated against in-situ measured secchi depth (Weeks et al. 2012). Satellite-derived photic depth. Correlated with all other satellite data. Yearly average of daily estimates.
CDOM	/m	X				Satellite Modis-AQUA	Coloured dissolved organic matter. Yearly average of daily estimates.
Nap	Mg/L	X				Satellite Modis-AQUA	Non-algal particulates. Yearly average of daily estimates.
Kd	/m	X				Satellite Modis-AQUA	Light attenuation coefficient. Yearly average of daily

SST	°C	X		Satellite	estimates. Retrieved from ERSST dataset, averaged catchment value. Also lag-1, lag-2.
MEI	NA	X		Index	Regional value for inshore GBR, multivariate ENSO index. Also lag-1, lag-2.
<u>Disturbance variables</u>					
Bleaching	NA	X	X	Presence/absence	Converted into years since disturbance, accounting for 10 years prior to 2005.
COTS	NA	X	X	Presence/absence	Converted into years since disturbance, accounting for 10 years prior to 2005.
Disease	NA	X	X	Presence/absence	Converted into years since disturbance, accounting for 10 years prior to 2005.
Flood	NA	X	X	Presence/absence	Converted into years since disturbance, accounting for 10 years prior to 2005.
Storm	NA	X	X	Presence/absence	Converted into years since disturbance, accounting for 10 years prior to 2005.
Multiple	NA	X	X	Presence/absence	Converted into years since disturbance, accounting for 10 years prior to 2005.

Table S 4.2 Model selection results for six catchments of the inshore GBR at 2m and 5m based on AICc.

The best-fit model identified for each of the catchments of Daintree, Johnstone, Tully, Burdekin, Mackay and Fitzroy is in bold.

Number	Model	AICc	Number	Model	AICc
<u>Daintree 2m</u>			<u>Daintree 5m</u>		
1	Storm	-73.85	1	Macro + Disease	-116.38
2	Base	-73.06	2	JuvHC(Lag2) + COTS	-114.15
3	Disease + Storm	-73.01	3	JuvHC	-113.39
4	Bleach + Storm	-72.42	4	JuvHC(Lag2)	-113.07
5	JuvHC	-71.70	5	COTS +Disease	-112.64
6	JuvHC(Lag2) + Storm	-71.33	6	Macro + Disease + Secchi (Obs)	-112.02
7	Storm + Claysilt	-70.34	7	Macro + Disease + Claysilt (Obs)	-112.00
8	Base + Secchi	-70.30	8	Macro + JuvHC	-111.90
9	COTS	-70.27	9	JuvHC + COTS	-111.75
10	Storm + SST	-70.23	10	Turf + JuvHC(Lag2)	-110.82
11	Storm + Secchi	-70.00	11	Disease	-110.37
12	MEI (Lag2)	-69.74	12	Secchi	-109.87
13	Disease	-69.66	13	Turf + JuvHC	-109.59
14	Base + Claysilt	-69.61	14	Secchi + JuvHC	-109.56
15	JuvHC (Lag1)	-69.22	15	JuvHC(Lag2) + Disease	-109.42
16	SST	-69.17	16	JuvHC + Disease	-109.28
17	COTS + Disease	-68.74	17	Secchi + COTS	-109.10
18	JuvHC + Storm	-68.28	18	Secchi + Disease	-109.10
19	JuvHC + Disease	-68.17	19	Turf + Disease	-107.86
20	Turf + COTS	-68.16	20	COTS	-107.44
<u>Johnstone 2m</u>			<u>Johnstone 5m</u>		

1	Disease + Storm	-167.04
2	Disease	-166.25
3	Disease + MEI(Lag2)	-164.79
4	Disease + Storm + Secchi (Obs)	-164.06
5	Disease + Flood	-163.81
6	Disease + Storm + Claysilt (Obs)	-163.65
7	Bleach	-163.14
8	Disease + Claysilt	-163.00
9	Disease + Secchi	-162.92
10	COTS + Disease	-162.88
11	Disease + Storm + MEI(Lag2)	-162.48
12	Bleach + Flood	-161.33
13	JuvHC(Lag1) + Disease	-161.26
14	Bleach + Disease	-161.04
15	Disease + Storm + SST	-160.91
16	Disease + SST	-160.90
17	Turf + Bleach	-160.76
18	Secchi + Disease	-160.36
19	Bleach + Storm	-159.74
20	JuvHC	-159.68

Tully 2m

1	Turf + Storm	-47.23
2	Turf + Storm + Claysilt (Obs)	-44.46
3	Turf + Storm + SST(Lag1)	-43.77
4	Turf + Storm + MEI	-43.38
5	Turf + Macro	-43.36
6	JuvHC + Disease	-42.52

1	Disease + Storm	-144.25
2	Disease + Storm + Secchi (Obs)	-141.52
3	Storm	-138.73
4	Base	-138.2
5	COTS + Storm	-136.69
6	COTS	-136.4
7	Macro	-136.27
8	Storm + Secchi	-136.19
9	Macro + Storm	-135.87
10	Storm + Claysilt (Obs)	-135.51
11	Base + Claysilt (Obs)	-135.38
12	Base + Secchi	-135.09
13	Disease + Storm + SST(Lag1)	-134.74
14	Disease + Storm + SST	-134.12
15	JuvHC(Lag2) + Storm	-134.05
16	JuvHC(Lag2)	-133.71
17	Secchi + Storm	-133.66
18	Turf + Storm	-133.08
19	Macro + Disease	-132.97
20	Macro + COTS	-132.35

Tully 5m

1	Storm	-38.28
2	Turf + Storm	-36.65
3	Storm + SST(Lag1)	-36.01
4	Storm + MEI(Lag1)	-35.45
5	JuvHC(Lag1) + Storm	-34.84
6	Secchi + Storm	-34.72

7	Turf + Storm + SST	-41.7	7	Storm + Secchi (Obs)	-34.36
8	Turf + Storm + Secchi (Obs)	-41.53	8	Turf + JuvHC	-34.35
9	Secchi + Storm	-36.9	9	Storm + SST	-34.28
10	Storm	-35.27	10	JuvHC + Storm	-33.86
11	Bleach + Storm	-34.93	11	Turf + Storm + Secchi (Obs)	-33.85
12	Storm + Claysilt (Obs)	-34.52	12	Bleach + Storm	-33.75
13	Disease + Storm	-34.05	13	Storm + SST(Lag2)	-33.72
14	Macro + Storm	-33.44	14	Macro + Storm	-33.5
15	JuvHC(Lag1) + Storm	-32.05	15	Storm + MEI	-33.5
16	Storm + Secchi	-31.58	16	JuvHC(Lag2) + Storm	-33.46
17	JuvHC(Lag2) + Storm	-31.2	17	Storm + Claysilt (Obs)	-33.41
18	Turf + JuvHC(Lag2)	-31.01	18	Storm + MEI(Lag2)	-33.37
19	JuvHC + Storm	-30.44	19	Turf + Macro	-33.25
20	Turf + JuvHC	-30.14	20	Turf	-32.72
<u>Burdekin 2m</u>			<u>Burdekin 5m</u>		
1	Base	-217.88	1	Storm	-225.34
2	JuvHC(Lag2)	-208.03	2	Base	-223.81
3	JuvHC(Lag)	-207.32	3	JuvHC + Storm	-222.88
4	Storm	-206.51	4	Storm + Secchi (Obs)	-222.17
5	Secchi	-206.44	5	Storm + Claysilt (Obs)	-220.9
6	Bleach	-205.85	6	Base + Secchi (Obs)	-220.46
7	Disease	-205.84	7	Base + Claysilt (Obs)	-219.9
8	JuvHC	-205.75	8	Storm + MEI	-219.22
9	Secchi + JuvHC	-193.29	9	Macro	-217.95
10	JuvHC + Bleach	-192.89	10	JuvHC(Lag2)	-216.85
11	JuvHC + Disease	-192.86	11	Disease	-216.76
12	Secchi + Disease	-192.4	12	Bleach	-216.74

13	Secchi + Storm	-192.38
14	Secchi + Bleach	-192.3
15	Bleach + Storm	-191.51
16	Disease + Storm	-190.41

13	Storm + SST	-216.2
14	Secchi	-215.78
15	Turf	-215.77
16	JuvHC(Lag2) + Storm	-215.23
17	JuvHC(Lag1) + Storm	-215.21
18	JuvHC	-214.67
19	Storm + SST(Lag2)	-214.36
20	Storm + MEI(Lag1)	-214.33

Mackay 2m

1	Base + Claysilt(Obs)	-149.85
2	Base	-144.57
3	Disease	-144.35
4	Base + Secchi (Obs)	-143.92
5	JuvHC	-142.09
6	JuvHC(Lag1)	-139.82
7	Disease + Flood	-139.68
8	Bleach	-139.31
9	Flood	-138.87
10	Bleach + Disease	-138.77
11	Secchi	-138.54
12	JuvHC(Lag2) + Disease	-138.32
13	SST(Lag2)	-138.3
14	Storm	-137.87
15	Disease + SST(Lag2)	-137.84
16	JuvHC(Lag2)	-137.76
17	MEI(Lag2)	-136.76
18	Turf	-136.65

Mackay 5m

1	JuvHC + Flood	-188.85
2	JuvHC	-185.17
3	JuvHC + Flood + Claysilt (Obs)	-184.94
4	JuvHC + Flood + Secchi (Obs)	-184.79
5	JuvHC + Flood + SST(Lag2)	-183.16
6	Disease + Storm	-183.06
7	JuvHC + Flood + MEI	-182.83
8	Macro + Storm	-182.73
9	Macro + Bleach	-182.65
10	Macro + LagJuv	-181.62
11	Macro + JuvHC	-181.59
12	JuvHC + Claysilt (Obs)	-181.59
13	JuvHC + Secchi (Obs)	-181.54
14	Disease	-181.45
15	Bleach + Disease	-181.3
16	Macro + JuvHC(Lag2)	-181.19
17	JuvHC + Flood + MEI(Lag1)	-181.17
18	JuvHC(Lag2) + Disease	-181.05

19	Disease + Storm	-136.56	19	JuvHC + Disease	-180.96
20	Secchi + Disease	-136.53	20	Macro	-180.8
<u>Fitzroy 2m</u>			<u>Fitzroy 5m</u>		
1	Flood	-75.96	1	Base	-115.85
2	SST(Lag1)	-75.25	2	Flood	-115.1
3	Base	-74.13	3	Base + Secchi (Obs)	-113.57
4	Flood + Secchi (Obs)	-72.98	4	Storm	-113.22
5	Flood + Claysilt (Obs)	-71.85	5	Macro	-113.04
6	Base + Secchi	-71.69	6	Base + Claysilt (Obs)	-112.09
7	Flood + Storm	-71.67	7	Flood + Secchi (Obs)	-111.53
8	JuvHC(Lag1)	-71.3	8	Secchi	-111.31
9	Base + Claysilt (Obs)	-71.24	9	MEI(Lag2)	-111.27
10	Storm	-70.63	10	Flood + MEI(Lag2)	-111.15
11	Macro	-69.83	11	Flood + Claysilt (Obs)	-110.93
12	Flood + MEI(Lag1)	-69.72	12	MEI(Lag1)	-110.7
13	Macro + Flood	-69.36	13	Bleach	-110.3
14	MEI	-68.65	14	Flood + MEI(Lag1)	-110.09
15	Bleach + Flood	-68.31	15	JuvHC(Lag1)	-109.83
16	Secchi	-67.72	16	Flood + Storm	-109.58
17	MEI(Lag2)	-67.61	17	Bleach + Flood	-109.37
18	Flood + MEI	-67.34	18	Macro + Storm	-109.35
19	Bleach	-67.3	19	Macro + Flood	-108.51
20	SST(Lag2)	-67.19	20	MEI	-108.51

5. SPATIAL, TEMPORAL AND MORPHOLOGY-SPECIFIC CORAL DYNAMICS ON THE GREAT BARRIER REEF

Abstract

The use of existing long-term monitoring data to disentangle drivers of reef coral dynamics is a challenge given the high spatial and temporal variability inherent in reef systems world-wide. Using a Bayesian geosadditive mixed Beta regression modelling approach, we assess the dynamics of 1) total coral cover, 2) total *Acropora* cover, and 3) acroporids by growth forms along the world's largest coral reef system – The Great Barrier Reef (GBR). With Bayesian regression models, we were able to account for structured spatial effects, nonlinear covariate functional forms, in addition to using an appropriate Beta likelihood model for coral cover. Model fit was evaluated using a range of graphical posterior prediction check metrics. GBR-wide total coral and *Acropora* cover displayed similar regional-specific long-term temporal trends since 1992: stable in the north, declining in the central region, and with fluctuating temporal trends in the south. Crown-of-thorns starfish (COTS) density and storms were the key drivers of declining coral and *Acropora* cover in the GBR. Additional associations of bleaching and water quality were also detected when *Acropora* morphologies were incorporated. While all acroporid growth forms displayed similar negative responses to COTS density, effects of other drivers (storms, degree heating weeks and plume frequency) were morphology-specific with a range of responses apparent, such as nonlinear threshold effects of elevated seawater temperatures. Our results show that a more nuanced monitoring approach accounting for species traits (e.g. morphology) is needed to develop a better understanding of reef coral dynamics at regional scales.

Introduction

The most comprehensive analysis on the drivers of the Great Barrier Reef (GBR), arguably one of the most well-known coral reef ecosystem in the world, concluded that episodic impacts of storms, bleaching and crown-of-thorns starfish (COTS) were the three key drivers of coral cover decline from 1985-2012. Moreover, it was suggested that storms, COTS and bleaching accounted for 48%, 42% and 10% of total cover decline in the GBR respectively De'ath *et al.* (2012). Unquestionably, the three drivers exert significant local impacts on coral cover through mechanical damage from storms (Harmelin-Vivien 1994), physiological stress from bleaching (Glynn 1993) and direct predation from COTS (Endean & Stablum 1973b; Moran *et al.* 1992). Furthermore, water quality is also acknowledged as a key driver of coral populations (Fabricius *et al.* 2005; De'ath & Fabricius 2010; De'ath *et al.* 2012). However, spatial variability in the relative importance of drivers on coral dynamics have been difficult to disentangle (Vercelloni *et al.* 2017).

Species display diverse life-history traits that strongly influence organism function and fitness (McGill *et al.* 2006). Traits relevant to physiology, morphology, phylogeny and biogeography govern how species perform and survive as a function of environmental factors (Nock, Vogt & Beisner 2016). In recent years, there is strong support for the application of trait-based approaches to reef research but is often hampered by data unavailability and the difficulty of integration with large-scale analyses (Madin *et al.* 2016a; Madin *et al.* 2016b). Important traits ('supertraits') significantly influence species' responses to disturbances and one simple example is growth form in coral species. Coral morphology can infer life-history strategies (Jackson 1991; Darling *et al.* 2012; Pratchett *et al.* 2015), so quantifying how life forms react differently to drivers can provide a nuanced understanding of coral population dynamics. Some aspects are well understood. For example, massive corals are found to be more resistant to bleaching than branching corals (Marshall & Baird 2000; Loya *et al.* 2001) and tabulate *Acropora* are more susceptible to mechanical damage by storms than branching forms (Madin, Donnell & Connolly 2008). To elucidate how morphology influences the susceptibility of corals to disturbances, studies have examined areas affected by acute disturbance events in isolation from other drivers. For example, Muko *et al.* (2013) documented the different effects of storms and bleaching on four acroporid growth forms (arborescent, tabular, corymbose, and digitate) from two reef sites in Japan over a three-year

period. Yet, there is in general a lack of analysis of long-term empirical data to discern the relative impacts of disturbance on different growth forms.

The coral genus *Acropora* is characterised by fast growth rates and therefore an ability to cause large fluctuations in reef dynamics (Mayor 1918; Buddemeier & Kinzie 1976; Wallace 1985), as well as sensitivity to disturbances (Woodley *et al.* 1981; Brown 1997; Loya *et al.* 2001). Studies on coral decline and recovery globally have acknowledged the importance of *Acropora*, such as in the Caribbean (Jeremy 1992; Hughes 1994; Greenstein, Curran & Pandolfi 1998), Chagos (Sheppard, Harris & Sheppard 2008), Maldives (McClanahan 2000), Seychelles (Graham *et al.* 2015), western Australia (Gilmour *et al.* 2013) and GBR (Done 1982; Emslie *et al.* 2008). On the GBR, *Acropora* alone was found to account for 68% of total coral cover changes from 1995-2009 (Osborne *et al.* 2011). A study by Johns, Osborne and Logan (2014) also found that reefs with substantial coral loss recovered and reassembled faster with a higher abundance of tabulate *Acropora*. However, there are substantial differences in coral responses to external pressures within the same taxa because of the interactions between growth form characteristics and factors such as mechanical vulnerability (Madin *et al.* 2014) and intrinsic growth rates (Gladfelter, Monahan & Gladfelter 1978) affect survival and recovery. Moreover, life forms can also affect the capacity of corals to adapt to changing environments. For example, although tabulate *Acropora* are particularly vulnerable to bleaching, cyclone and COTS, they are fast-growing and play an important role in recovery after disturbances on the GBR (Halford *et al.* 2004). Understanding how different life forms respond to and recover from different impacts can shed light on likely future reef trajectories under different disturbance and environmental regimes. Hence a major focus of this study is to investigate the relationship between drivers and different *Acropora* life forms because of its importance in driving reef dynamics.

Using a Bayesian regression modelling approach, we assess the dynamics of coral cover of the GBR with a 23-year time series. A Bayesian regression allows the use of the appropriate Beta likelihood for proportional data bounded by 0 and 1 (i.e. proportional coral cover in our study). Our study aims are three-fold. First, we determine the importance of potential drivers on total coral and *Acropora* cover accounting for the effects of bleaching, COTS predation, storms and water quality. Second, moving beyond coral cover, we evaluate how various drivers affect the abundance of different growth forms of the *Acropora* genus. Third, our

results identify areas where the understanding of drivers is weakest and further studies might be prioritised.

Methods

Benthic community data

The benthic community data are collected by the Australian Institute of Marine Science (AIMS) on the GBR from 1992 to 2014 as part of the Long-Term Monitoring Program (LTMP). The whole dataset includes 93 reefs monitored using permanent transects distributed across the north, central and southern sections of the GBR (Figure 5.1, Table 5.1). Originally, 47 sites were monitored annually but in 2003, 46 reefs were added to the program and all reefs were surveyed in alternate years onwards. Each reef has three sites with five 50m-long permanent transects located along a depth contour between six to nine meters. A photo-point intercept method was used to determine the percent cover of benthic community data from photos. At each transect, 50 photos were taken whereby 40 images were selected at random to determine benthic community under five fixed points and converted into percentage cover. Refer to Jonker, Johns and Osborne (2008) for details on the standard operational procedures.

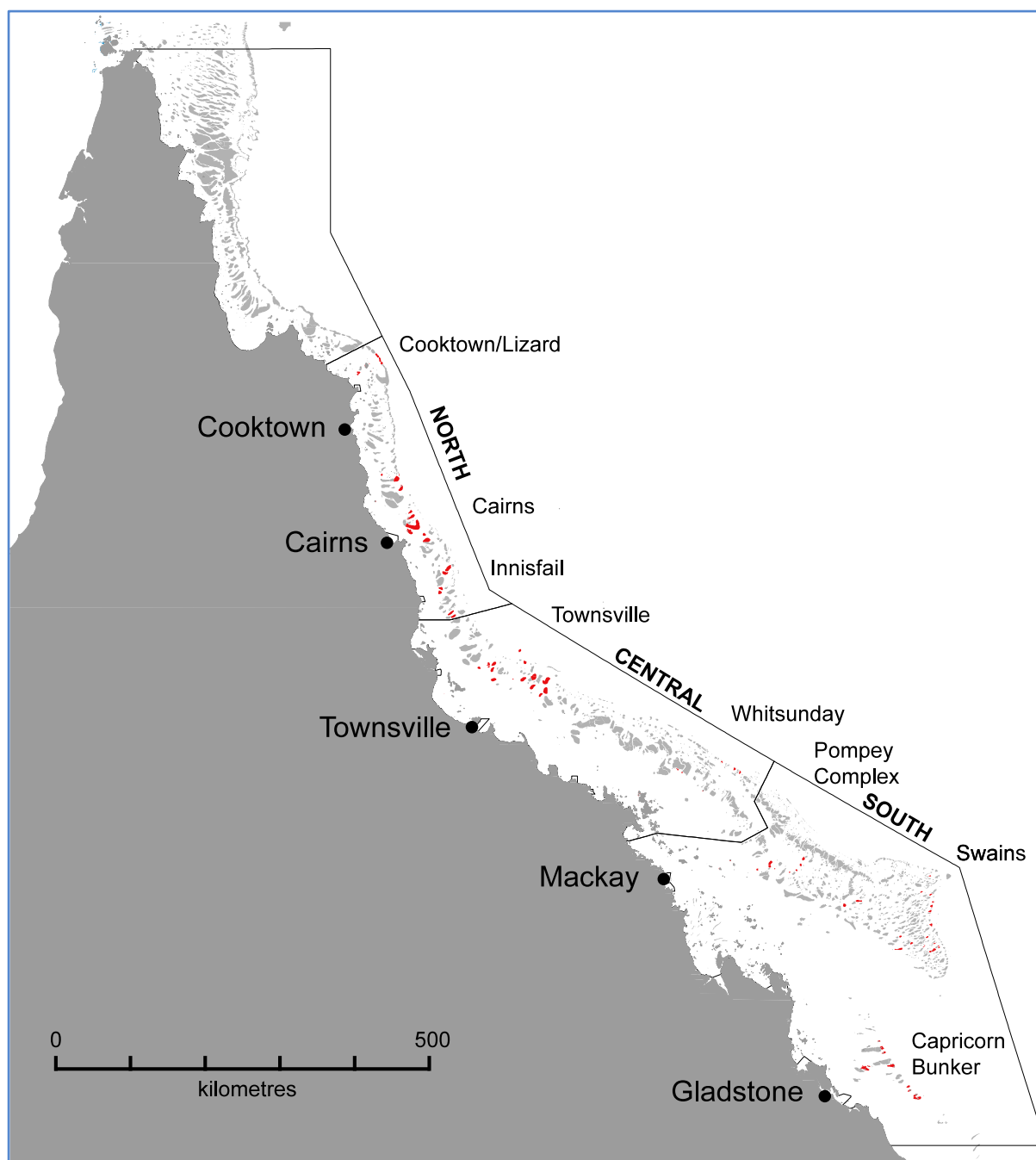


Figure 5.1 Map of 93 reef sites surveyed by the Australian Institute of Marine Science Long-Term Monitoring Program highlighted in red.

Table 5.1 The distribution of reefs in the north, central and southern GBR regions.

<i>Region/Shelf habitat</i>	<i>Inner</i>	<i>Middle</i>	<i>Outer</i>
North	5	14	7
Central	6	14	8
South	0	24	15

Predictor variables

Density of Crown-of-Thorns Starfish (COTS). The maximum number of COTS per manta tow detected was recorded to obtain visual estimates of COTS densities at each reef. COTS data entered the model as the maximum number of COTS per manta tow detected on each reef. As per Moran and De'Ath (1992), densities of >0.22 and >1 indicate an incipient and active outbreak respectively. COTS density metric was $\log(x+1)$ transformed for analysis since it spanned a wide range of values including zero.

Maximum wind stress. Data on cyclone tracks were downloaded from the Australia Bureau of Meteorology (BOM) and included the location of cyclone eye and maximum winds every six hours. Maximum winds were calculated based on the BoM cyclone intensity scale from one to five. The spatial extent of winds was estimated using asymmetric buffers following Wolff *et al.* (2016) and the maximum wind stress in pascals that each reef experienced was extracted in GIS. Maximum wind stress is used as a proxy of wave damage caused by cyclonic activity.

Maximum degree heating weeks (DHW). Data on annual maximum degree heating weeks were downloaded from NOAA Coral Reef Watch at a spatial resolution of 50km. The DHW metric detects any hot spots higher than 1°C over a 12-week window for each reef site, and is commonly used as a proxy for coral reef bleaching (Liu *et al.* 2013).

Total plume frequency. The proportion of total wet season weeks that each reef was exposed to primary, secondary or tertiary plumes from 2003 to 2014. River plumes transport nutrients, sediments and land-based pollution and is a suitable proxy for chronic water quality at each reef (Petus *et al.* 2014; Devlin *et al.* 2015).

Spatial coordinates. The geolocation of each reef (latitude and longitude) was used to construct a structured 2D spatial effect to account for spatial correlation between reefs (Fahrmeir & Lang 2001).

Morphology. Only present in the *Acropora* growth form model. Coral cover data were grouped into the three most dominant life forms of branching, tabulate and other *Acropora* (digitate, encrusting and submassives).

Region. Due to the large geographical coverage of the LTMP, the 93 reefs surveyed were assigned to regions. Different subregional groupings were explored, including the commonly used eight sectors (Cooktown/Lizard Island, Cairns, Innisfail, Townsville, Whitsunday, Pompey Complex, Swain and Capricorn Bunker) and three habitats (inner, middle and outershelf). Finally, the 93 reefs were classified into 3 regions: north (14–18°S), central (18–20°S) and south (20–24°S) following (De'ath *et al.* 2012) (Figure 5.1).

All continuous predictors were standardised by centring and scaling using the procedure proposed by Gelman (2008). Standardised predictors supported model convergence and enabled the comparison of the relative importance of each predictor in the fitted model.

Statistical modelling approach

To explore the potential impact of drivers on reef-averaged total coral cover, total *Acropora* cover and *Acropora* growth forms in the GBR, we developed three Generalised Additive Mixed Models (GAMM) within a Bayesian framework using geoaddivitive coefficients. Interaction terms were implemented in the GAMMs using a varying coefficient approach where the covariate is nested within each level of a factor (Hastie & Tibshirani 1993). From here on, the term coral cover will be used for total coral cover, *Acropora* for total *Acropora* cover and acroporid growth forms will be specifically defined where relevant.

Coral cover was modelled as a function of potentially informative predictors. A Beta likelihood was used for the total coral cover regression model as the response is percentage data that is soft interval bound (0,1). For the analysis of *Acropora* and *Acropora* growth forms, a zero-inflated Beta likelihood was used owing to the presence of zeros where the data interval is [0,1) bound (Liu & Eugenio 2016).

For all model runs, we used the potential scale reduction factor or Gelman-Rubin statistic (Rhat) to evaluate model convergence and only accepted models when Rhat is close to one for all variables (Gelman, Lee & Guo 2015). Models were selected using leave-one-out cross-validation (LOO-cv) via the *loo* package for R (Vehtari, Gelman & Gabry 2016). The geoaddivitive GAMMs were implemented in a Bayesian framework using weakly informative regularising normal priors (Gelman 2006; Gelman *et al.* 2008), with posterior samples

sourced from 5 chains and 50,000 iterations after a warm-up of 2,000 iterations. All geoadditive GAMMs were then implemented with the Stan computation engine (Stan Development Team 2016) with NUTS sampling (Carpenter *et al.* 2017) via the brms package for R (Bürkner 2017).

Modelling strategy

All variables used in the models were first reviewed for collinearity using a matrix of correlation coefficients. Models had one response variable (coral cover) and eight potential covariates (six fixed and two random effects). Out of the six fixed effects, subregion is the only categorical factor and the other five are continuous. The *Acropora* growth form model has an additional fixed covariate morphology (factor). All models were fitted with a two-dimensional structured spatial effect for the georeferenced reef specific data, making this a spatially explicit or geoadditive GAMM model (Kammann & Wand 2003). The structured spatial effect was based on a tensor product of cubic regression splines (Wood 2006). Moreover, we included random effects for each reef and for each sampling year to account for reef-specific heterogeneity and year-specific effects not accounted for by the fixed covariates. All random effects were significant and improved fits in all three models.

To determine the best fit models, we explored a wide range of potentially informative covariates and factors, as well as some interactions with fixed effects such as subregions. For example, whether the effect of maximum COTS density on coral cover was different in the north, central and southern subregions. Since ecological functional relationships are unlikely to be linear (Barbier *et al.* 2008), cubic regression splines were used to model any nonlinear functional form between coral cover and potential informative covariates such as maximum COTS density, maximum wind stress, DHW and plume frequency (Wood 2006). All smoothing terms were significant and improved model fits, apart from a linear plume frequency in the total coral cover model that was used to improve model convergence. After the best functional form for individual covariates and possible interactions were identified, models were also fitted with a first- or second- order autoregressive structure on the response variables for each sampling year with each reef. A first order autoregressive term significantly improved model fit of coral and *Acropora* cover models (LOO: -14510.59, -3572.44), but a second order autoregressive term was found to be more suitable for the *Acropora* growth form model (LOO: -2301.21). Model fit was then evaluated using several

graphical posterior predictive checks (Gelman & Hill 2007; Gelman, Hwang & Vehtari 2014) using the bayesplot package in R (Gabry 2016). The specific posterior predictive check tests were 1) density overlay plot of the predicted simulations versus the observed response density, 2) scatter plot of the average coral cover of the predicted simulations versus the observed, 3) a scatter plot of two key summary parameters (mean and standard deviation), 4) the maximum expected response and 5) the proportion of zeros for the GAMMs with zero-inflated Beta likelihood.

Results

Coral and Acropora

A total of 1036 coral cover observations collected from 93 reefs during 23 years were analysed, of these 346, 352 and 338 records belonged to north, central and southern regions, respectively, from the inner-, mid- and outer-shelves (Table 5.1). Overall, the averaged GBR-wide cover of all corals combined and all acroporids displayed similar patterns over time. Trends of total cover varied among regions being stable in the north, consistently declined in the central region, and dynamic in the south – characterised by a rapid decline from 2006-2010 followed by a rapid recovery until 2013 to a slight decline in 2014 (Figure 5.2). Prior to the rapid decline in the south, coral cover trends fluctuated from 1992-2005 but unlike total coral cover, *Acropora* showed a rapid increase in the initial four years of monitoring (Figure 5.2, 1992-1996). During the recovery phase from 2010-2013 in the south, both coral and *Acropora* cover reached 60% of values prior to decline. In general, both total coral and *Acropora* cover were higher in the southern region where estimates were also the most variable, followed by the north and central regions based on the 95% credible intervals. Notably, a number of southern reefs showed rapid recovery from 2010 which may contribute to the high uncertainty found in the south (Figure 5.2).

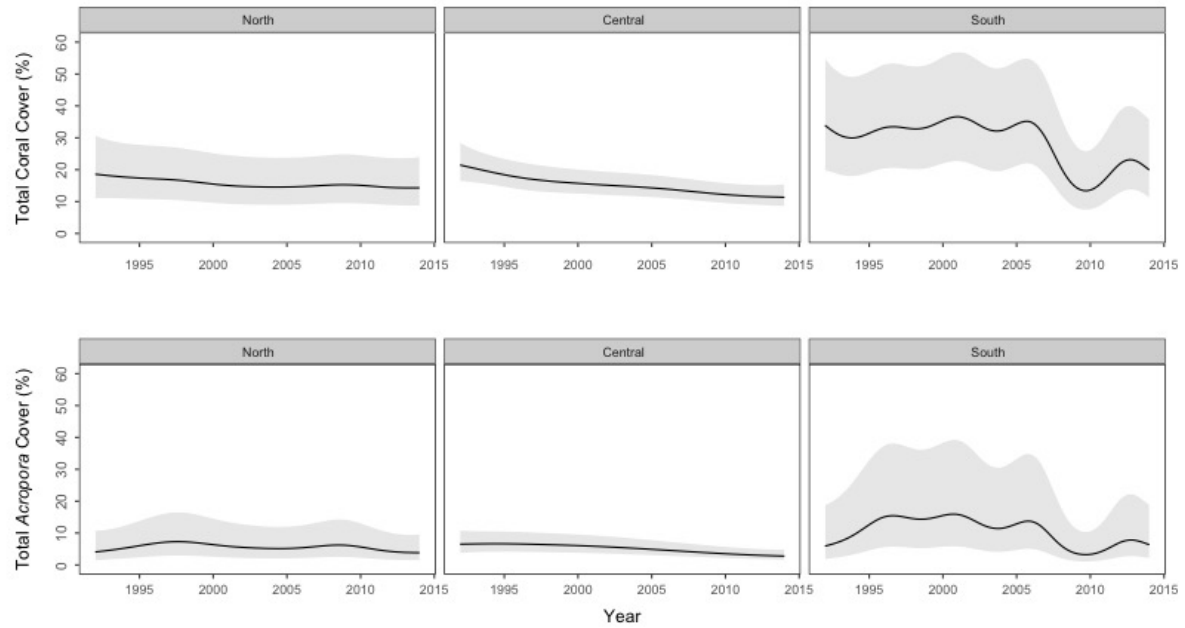


Figure 5.2 Predicted coral (top) and *Acropora* cover (bottom) in the north, central and southern GBR from the best fit coral and *Acropora* models.

Shaded bands represent 95% credible intervals.

Both coral cover and that of acroporids exhibited similar responses to environmental perturbations, whereby DHW had no significant effect but COTS and wind stress emerged as significant drivers in both models (Table S 5.1, Table S 5.2), although COTS had a stronger (negative) impact (Figure 5.3, Figure 5.4). COTS impacts varied among regions (Figure 5.3, Table S 5.1, Table S 5.2), being the greatest in the south (because of impact on the Swains) where extremely high densities were encountered (Figure 5.3; logged density ranges, north: 0-1.05, central: 0-2.25, south: 0-4). Great uncertainty of the coral-COTS relationship at high COTS densities was found because extreme COTS densities were not recorded in the north and central regions.

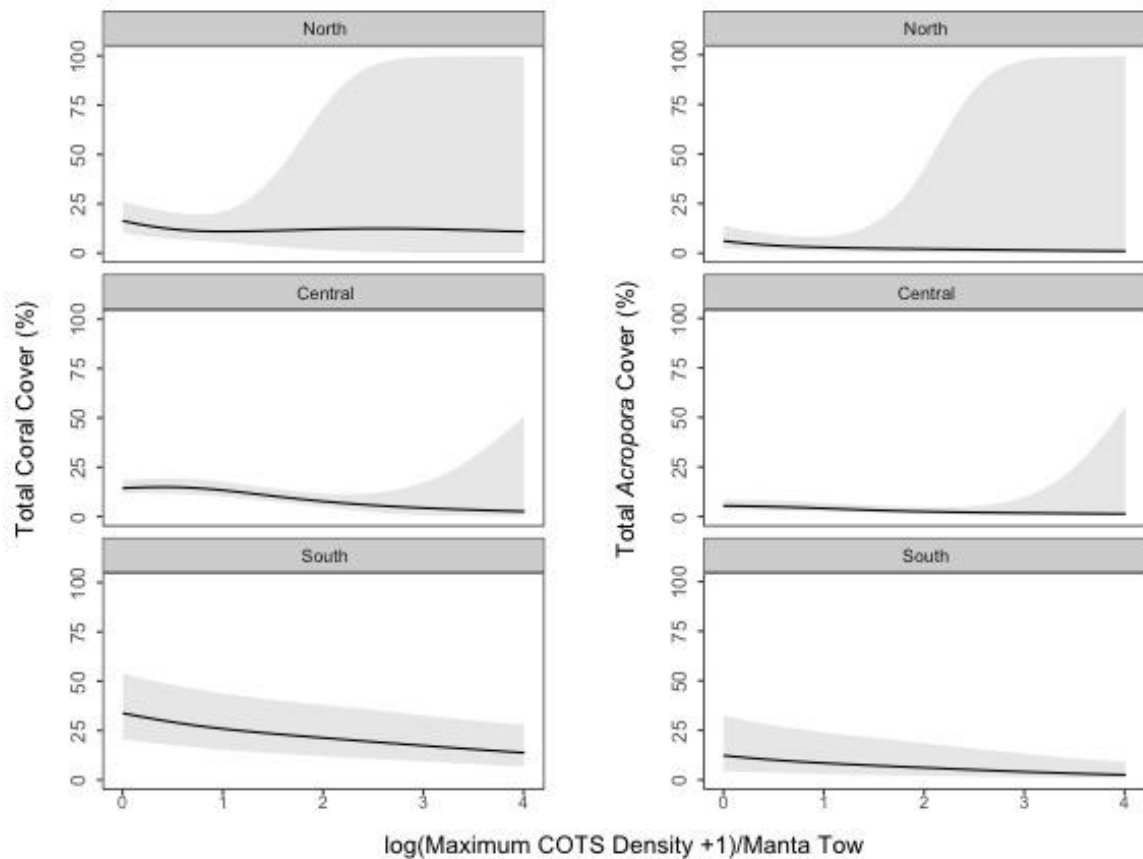


Figure 5.3 Negative relationship between COTS and coral (left) and *Acropora* cover (right) in the north, central and southern GBR.

Shaded bands represent 95% credible intervals.

The overall negative relationship between wind stress and coral cover was highly uncertain as indicated by the large credible intervals of the smoothing term (Figure 5.4; coral model: 0.08-18.80; *Acropora* model: 0.11-19.68). Although the effect of wind stress was borderline significant in the *Acropora* model (-0.01, 0.11, Table S 5.2), a hypothesis test gave 93% certainty of an effect (Figure 5.4). Analysis of changes in coral cover related to cyclone categories revealed diverse coral responses (Figure 5.5), whereby 60%, 30% and 31% of the reefs showed a positive response in coral cover after a cyclone category 1, 2 and 4 hit the reefs respectively (Table 5.2), implying that cyclones had heterogeneous effects on corals.

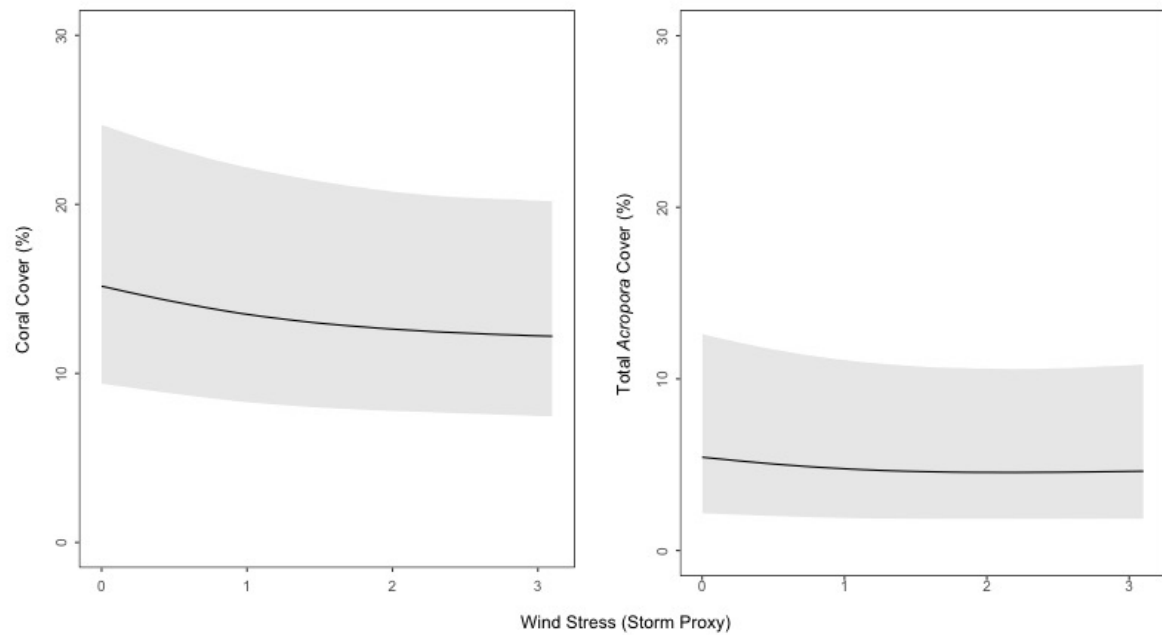


Figure 5.4 Negative relationship between wind stress and total coral cover (left) and total *Acropora* cover (right).
Shaded bands represent 95% credible intervals.

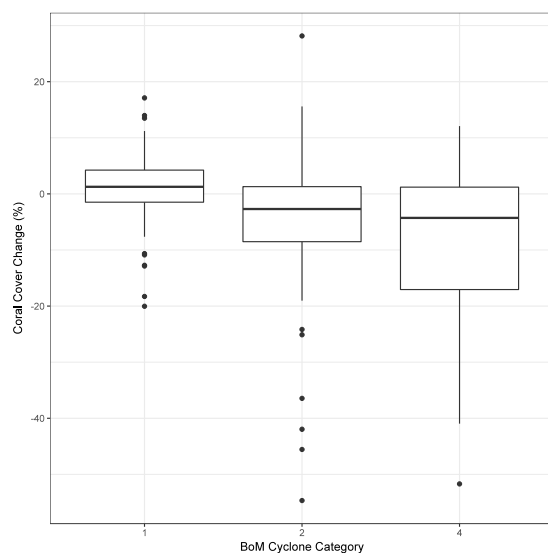


Figure 5.5 Coral cover change on LTMP reefs during years hit by cyclones.

Table 5.2 Direction of coral cover change on reefs in years hit by a cyclone.

NA indicates instances where cover change is unknown because data prior to cyclone is absent (21 cases).

<i>Cyclone Category/ Cover Change</i>	<i>Positive</i>	<i>Negative</i>	<i>No Change</i>	<i>NA</i>	<i>Total Cases</i>
1	64	38	1	1	103
2	45	84	0	20	129
4	13	29	0	0	42

Acropora growth forms

The overall abundance of acroporids by lifeform was tabulates > branching > others (Table S3). Unlike coral and *Acropora* models, most fixed drivers (maximum COTS density, wind stress, DHW and plume frequency) had significant effects on at least one *Acropora* growth form (Table 5.4). The exception was plume frequency (Table 5.4), which had a marginally negative effect on tabulates and other acroporid growth forms, but was associated with a slight increase in the cover of branching *Acropora* until plume frequency exceeded 0.6 (Figure 5.7D). In general, the effect of COTS and wind stress paralleled results reported for coral cover and *Acropora* (Figure 5.7A, Figure 5.7B), apart from the slight positive effect of wind stress on other *Acropora* (digitate, encrusting and submassive growth forms). DHW had a slight negative effect on both branching and other *Acropora*, but the cover of tabulates was found to increase up to 5.7 DHW after which cover declined rapidly (Figure 5.7C).

Table 5.4 Significance of driver effects on different *Acropora* morphologies.

The – and + signs represent a significant negative and positive effect of individual drivers on coral abundance. When nonlinear effects take different directions, the numerical ranges of drivers corresponding to the increase and decrease of coral abundance are indicated separately in square brackets. The * sign indicates a borderline driver effect with evidence ratio (percent certainty) in parentheses. N.S. represents not significant.

<i>Acropora Morphology</i>	<i>Max. COTS density</i>	<i>DHW</i>	<i>Maximum Wind Stress</i>	<i>Plume Frequency</i>
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Branching	–	– *(79.6%)	N.S.	+ [0-0.6] – [>0.6] *(78.4%)
Tabulate	–	+ [0-5.7] – [>5.7]	–	– *(57.4%)
Others	–	N.S.	+	– *(86.5)

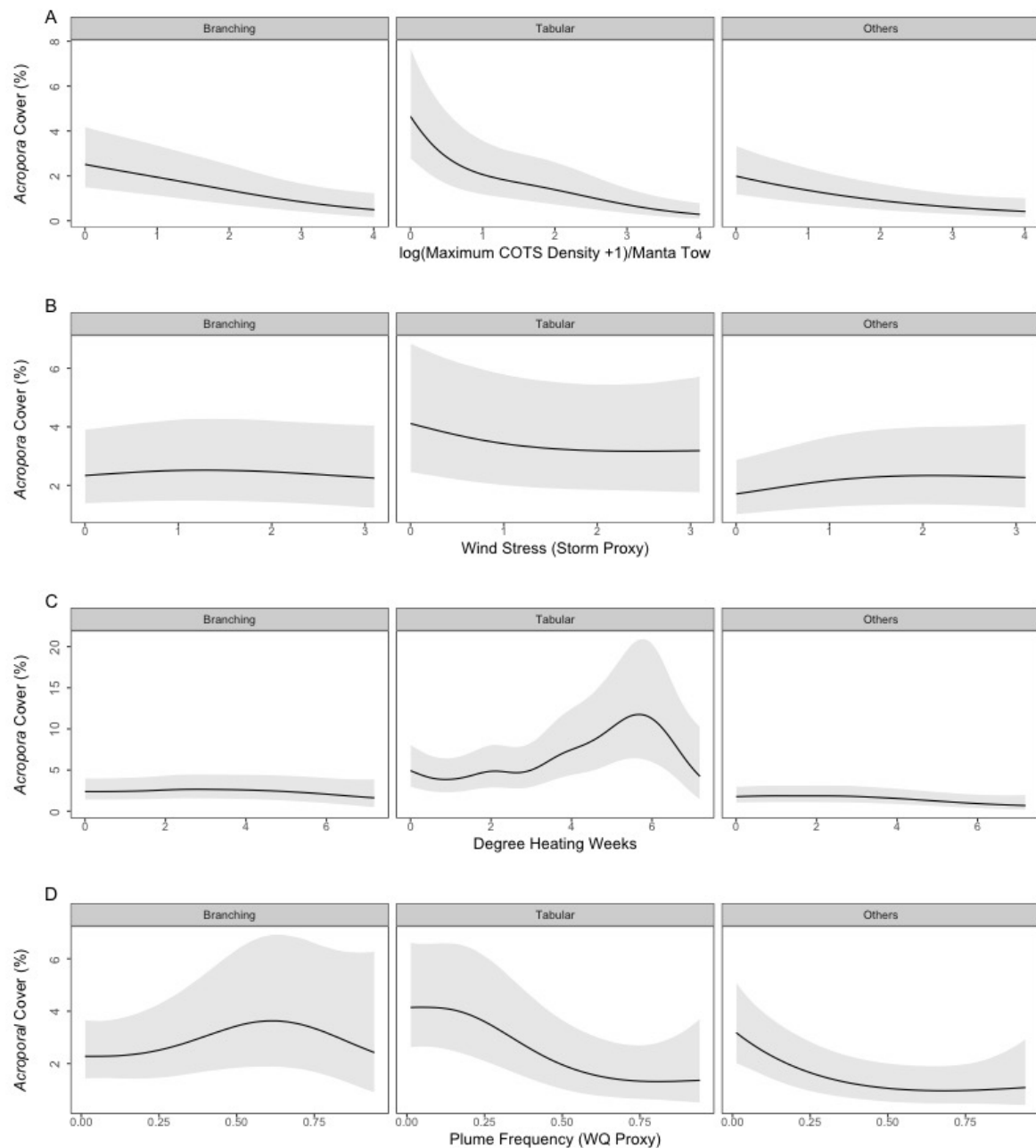


Figure 5.6 Relationship between (A) COTS density, (B) wind stress, (C) degree heating weeks, (D) plume frequency and branching, tabulate and other acroporid growth forms.

Shaded bands represent 95% credible intervals.

Structured spatial effects reflect residual coral cover heterogeneity unaccounted for by the model including covariates, covariate functional forms and model data likelihood. So those reefs with positive residuals reflect higher than expected heterogeneity in coral cover given

the fitted model – negative residuals reflect lower than expected coral cover. Cover estimates were consistently lower for the Swain (south) and higher for the Cooktown/Lizard (north) region in all three models (Figure 5.7). In the coral model, estimated cover was also higher for Townsville outer reefs and the Whitsundays but lower around the Capricorn-Bunker reefs (south, Figure 5.7A). Whereas for *Acropora*, higher estimates were found in the inner Whitsundays and lower estimates in outer Pompey Complex (Figure 5.7B). In general, there were less extreme positive and negative values once coral morphologies were incorporated, with the exception of a lower estimate for outer Pompey Complex in the model for acroporid growth forms (Figure 5.7C).

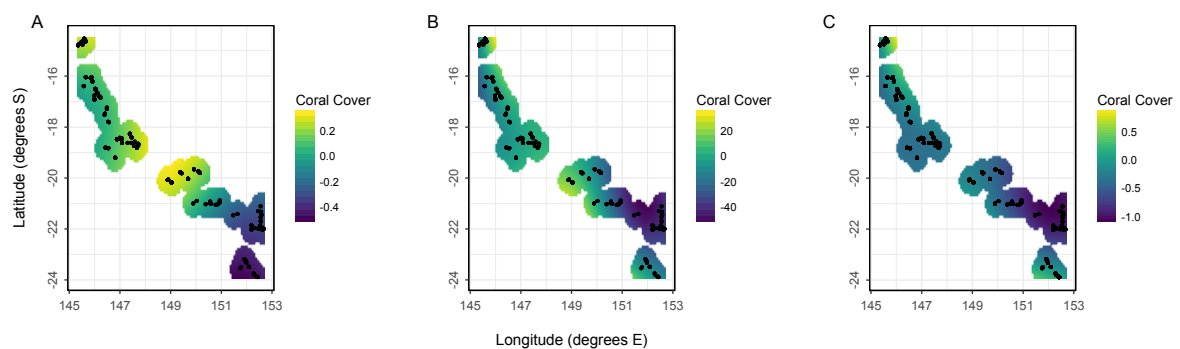


Figure 5.7 Structured spatial effect in (A) total coral cover, (B) total *Acropora* cover and (C) *Acropora* morphology model.

Colour scales represent centred and scaled residual values, where + and – values indicate higher and lower than expected coral cover.

Finally, posterior predictive checks of density, average coral cover, mean and standard deviation, maximum values and proportion of zeros showed good fits between predicted simulations and observed data (Figure 5.8, Figure S 5.1, Figure S 5.2). The exception being the simulated standard deviation were in general lower than the observed data for the *Acropora* and acroporid growth form models (Figure S 5.1, Figure S 5.2).

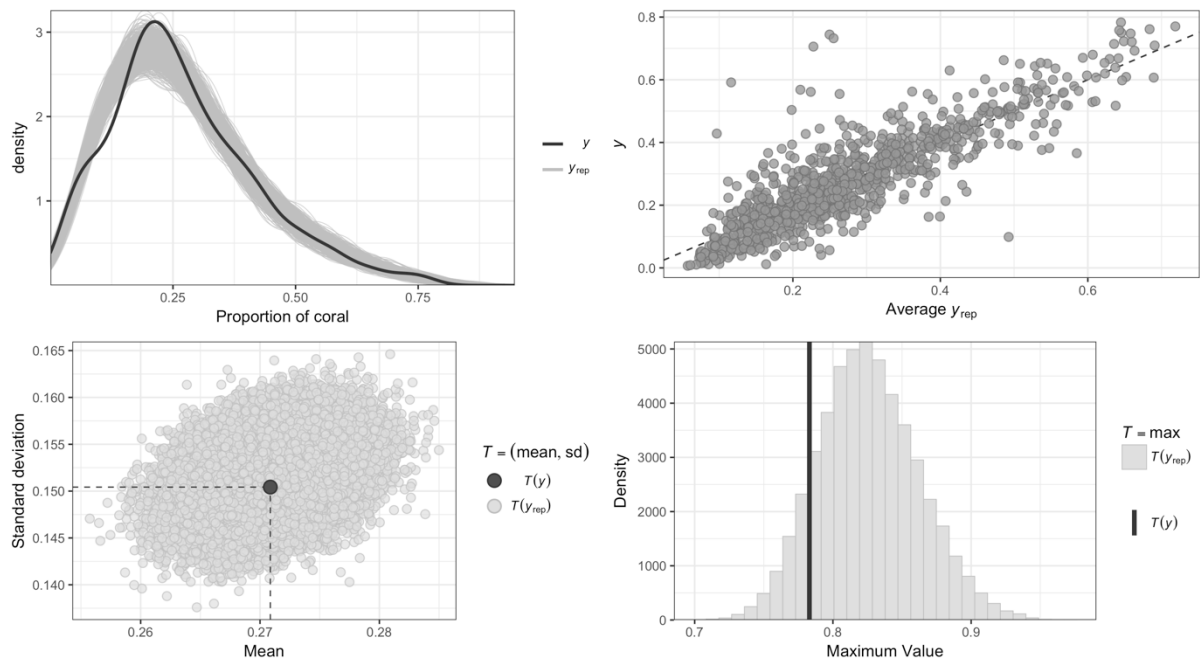


Figure 5.8 Graphical posterior predictive checks of a) density overlay b) scatter plot of average of coral cover c) scatter plot of mean and standard deviation summary parameters and d) histogram of maximum value of observed data and predicted values from best fit total coral cover model.

Discussion

Coral dynamics on the GBR have been studied extensively, mostly using the comprehensive data from the AIMS Long-Term Monitoring Program, including manta tows (Miller, Jonker & Coleman 2009; Osborne *et al.* 2011; Sweatman, Delean & Syms 2011; De'ath *et al.* 2012; Johns, Osborne & Logan 2014; Cheal *et al.* 2017; Osborne *et al.* 2017; Vercelloni *et al.* 2017). Here, we aimed to provide further insights into non-linearities in their dynamics – using Bayesian regression models – and incorporate the importance of spatial effects, the appropriate model likelihood, a chronic water quality measure, in addition to acute drivers (storms, COTS and bleaching) known to affect corals on the GBR. We also disaggregated dynamics of the dominant coral genus (*Acropora*) to account for generic and morphological differences in the response to putative drivers. Coral cover showed high spatial and temporal variation, with COTS and storms having the most consistent and significant impacts of all the drivers investigated. The effects of bleaching and water quality were only found to be significant when acroporid life forms were incorporated into the models, with individual

drivers affecting specific morphologies differently. The analysis of acroporid life forms highlight differing functional relationships with drivers. While all morphologies displayed negative responses to COTS, storms had a positive effect on other morphologies and a negative effect on tabulates. Elevated seawater temperature had negative effects on branching forms and a non-linear threshold effect on tabulates; whereas the increased plume frequency had negative effects on tabulates and other morphologies, but a non-linear threshold effect on branching forms. More importantly, our results demonstrate that the incorporation of valuable traits (e.g. coral growth forms) can help reveal drivers of coral dynamics such as bleaching and water quality, which may go undetected if only total coral cover metrics were used.

COTS are a well-known threat to the GBR (Done 1985; De'ath *et al.* 2012; Babcock *et al.* 2016). Our models demonstrate a consistent negative relationship of COTS with coral and *Acropora* cover. The uncertain relationship at higher COTS densities in the north and central regions reflect the limited scale of COTS impacts on reefs in that area compared to southern reefs where extremely high densities had been recorded during the study period. The highest COTS densities recorded were from Turner, Gannet Cay and Wade Reefs, reflecting a primary outbreak in the Swain region from 2001-2003 (Sweatman, Delean & Syms 2011; Miller *et al.* 2015). Although our results suggest that COTS are more important in the south, COTS generally affect the mid- and outer-shelf reefs to a much greater extent than inshore reefs (Brodie *et al.* 2005). The fact that there are no inner reefs in the southern dataset (Table 5.1) may partly account for the pronounced COTS effects in this area. To clarify, our spatial results do not suggest COTS are more important in the southern GBR, but rather reflect the uncertainty in predictions owing to the patchy distribution of COTS among the survey reefs in the northern and central sections. All acroporid life forms were negatively associated with COTS, with tabulate *Acropora* exhibiting the strongest relationship, consistent with known COTS feeding preferences (Endean & Stablum 1973a; De'ath & Moran 1998). Even at low densities, COTS rapidly reduce the amount of tabulates showing high preference over other morphologies (Keesing 1990) (Pratchett 2007).

Storms had a highly uncertain overall negative relationship with coral cover. Further examination indicated numerous cases where coral cover remained stable or increased even when a storm was recorded within a reef's vicinity, reflecting the highly localised and patchy nature of cyclonic wave impacts (van Woesik, Ayling & Mapstone 1991; Done 1992a;

Beeden *et al.* 2015; Wolff *et al.* 2016). The modelling of cyclone risk from 1969-2003 showed that only about a third of cyclone events are capable of significant damages in the GBR (Puotinen 2007), and this patchiness is demonstrated in numerous case studies. For example, Bramble Reef (Townsville subregion) remained intact despite being within the destructive wind zone caused by Cyclone Yasi (category 5) in 2011 (Beeden *et al.* 2015). Highly variable damages caused by Cyclone Ivor (category 3) were recorded within the Ribbon Reef area (Cooktown and Lizard Island subregion) (Done, Ayling & van Woesik 1991; van Woesik, Ayling & Mapstone 1991). A comparison between inshore and offshore reefs following Cyclone Ingrid (category 4) also confirmed high inconsistency of storm-inflicted damages, postulated to be influenced by reef location, coral community type and stage of reef development (Fabricius *et al.* 2008).

Consistent with the literature on hydrodynamic impacts on coral morphologies (Madin, Hughes & Connolly 2012), cyclonic waves significantly impacted tabulate *Acropora* because of their top-heavy growth forms but surprisingly had no effect on branching *Acropora*, believed to be especially vulnerable to mechanical damage (Scoffin 1993; Brown 1997; Madin & Connolly 2006). The inability to detect an effect of storms on branching *Acropora* may be due to unaccounted factors that affect the severity of coral mortality caused by storms, such as coral size (Madin *et al.* 2014), ecological history of the reef site (Rogers 1993), and/or the occurrence of partial mortality and rapid recovery post-disturbance (Rogers, Suchanek & Pecora 1982). Rapid recovery of branching *Acropora* was documented at the Keppel Islands in the GBR (Diaz-Pulido *et al.* 2009) and in Indonesia (Riegl & Piller 2001) resulting from the regeneration of existing living colonies, also known as the "Phoenix effect" (Krupp, Jokiel & Chartrand 1993; Diaz-Pulido *et al.* 2009). Moreover, branching corals are readily fragmented by storms (Lirman 2000) but surviving colonies tend to regenerate relatively quickly providing minimal tissue damage and the absence of further disturbances (Pearson 1981; van Woesik, Ayling & Mapstone 1991; Brown 1997). Cyclonic waves had a slight positive effect on other *Acropora* (lumped group consisting of digitate, encrusting and submassives) and can perhaps be explained by their relatively less susceptible growth forms to hydrodynamics, demonstrated in digitate *A. gemmifera* and submassive *A. palifera* (Madin & Connolly 2006).

The consideration of fundamental differences in the nature and intensity of impacts on corals is important when identifying the relative importance of drivers of reef dynamics. Taking the effect of COTS and storms on coral cover for example, De'ath *et al.* (2012) found that storms accounted for 48% of coral cover declines in the GBR, almost five times that of COTS but Osborne *et al.* (2011) found COTS-induced cover decline (42.2%) was more severe than storms (31.5%). Although our model estimates were alike Osborne *et al.* (2011) in finding stronger negative COTS impacts than storms, this does not necessarily suggest that COTS are the more important driver on the GBR. COTS actively target and feed on coral tissues (Endean & Stablum 1973b; Ormond, Hanscomb & Beach 1976), yet cyclonic impacts are often known to be complex and highly variable. First, local factors such as depth, topography and local shelter affect damage severity (Massel & Done 1993). Second, storm impacts take many forms, including partial mortality, sand burial, complete dislodgement, as well as structural damage (Scoffin 1993; Beeden *et al.* 2015). Hence, the effect of storms on coral cover may not be as evident or consistent as the effects of COTS predation.

Although bleaching is an important driver of GBR corals (Hoegh-Guldberg 1999; De'ath *et al.* 2012; Hughes *et al.* 2017b), no significant effects were found on both coral and *Acropora* cover in our models, despite major events in 1998 and 2002. The highest DHW recorded from the LTMP sites was 7.19, lower than the extreme temperatures (>8 DHW) known to cause widespread bleaching and mortality (Eakin *et al.* 2010). DHW values of over 4 induce coral bleaching but do not necessarily cause mortality (Kayanne 2017). An alternate explanation for the insignificant DHW effects on total cover is the existence of a protective mechanism (sub-bleaching stress) that minimises bleaching damage. Ainsworth *et al.* (2016) demonstrated this sub-bleaching stress occurred in 75% of the past thermal events in the GBR and decreased coral cell mortality and symbiont loss by over 50%.

Once acroporid life forms were incorporated into the model, significant effects of DHW were found on branching and tabulate acroporids and is supported for two reasons. First, the genus *Acropora* is particularly susceptible to bleaching (Fisk & Done 1985; Brown & Suharsono 1990; Loya *et al.* 2001) due to high levels of physiological integration (Gladfelter 1983; Veron 1986; Baird & Marshall 2002). Extensive bleaching and mass mortality of *Acropora* were documented in Pacific locations including the Maldives (Perry & Morgan 2017), Moorea (Pratchett *et al.* 2013), Kenya (McClanahan *et al.* 2004) and Indonesia (Brown &

Suharsono 1990). Second, branching and tabulate corals are particularly responsive to thermal stress (Marshall & Baird 2000). A study of 45 genera in the GBR concluded that both branching and tabulate *Acropora* were strongly affected by bleaching with 38% and 25% mortality respectively in the 1998 event (Marshall & Baird 2000). Most recently during 2016 on the GBR, branching (arborescent) and tabulate *Acropora* were shown to have extremely high bleaching susceptibility (>80%, Hughes *et al.* 2017b).

An unusual result occurred for tabulate *Acropora* such that coral cover was predicted to be higher at an intermediate level of DHW (5.7) above which it returned to baseline cover. Given that the higher DHW was not associated with coral mortality (because the predicted cover was identical to that at almost zero DHW), it is likely that this trend reflects a positive effect on coral growth rates and recovery during warmer – but not too warm – seasons. The implication is that average growth rates in tabulate acroporids benefit from warmer seasons that might approach the optimal for growth and calcification, beyond which temperature becomes stressful and growth rates then decline. Such parabolic functions are common and have been reported in corals such as in *Galaxea* and *Dendrophyllia* (Marshall & Clode 2004) and pocilloporids (Edmunds 2005). Similarly, (Fisk & Done 1985) noted an increase of tabulate *Acropora hyacinthus* during the 1982 bleaching event at Myrmidon Reef whereas (Roth, Koksall & van Woessik 2010) recorded higher *Acropora* growth rates at higher temperatures in 1998.

The adverse effects of poor water quality on reefs have been clearly documented, such as reduced light availability, toxin contamination bioaccumulation, lowered coral recruitment and skeletal density, enhanced bioerosion and reduced biodiversity (International Society for Reef Studies 2004; De'ath & Fabricius 2010). Although water quality has been proposed as an important driver of GBR reef dynamics (De'ath *et al.* 2012), most studies have compared sites along water quality gradients and focused on the inshore reefs where their effects are the most pronounced (Fabricius & De'ath 2004; Fabricius *et al.* 2013; Thompson *et al.* 2014). River runoff significantly affects water clarity of mid-shelf reefs up to 80km from the coast (Fabricius *et al.* 2014) and there is some evidence that offshore reefs can experience drastic changes in water quality, particularly in the north where the continental shelf is narrower (Fabricius *et al.* 2016). Our models did not detect a significant effect of water quality on overall coral and *Acropora*, but like the bleaching results, clearer relationships were revealed

once life forms were incorporated. Consistent to expectation, both tabulate and other acroporids declined when exposed to plumes. However, branching *Acropora* only decreased as plume exposure passed a threshold of 0.6, which might suggest that branching species are more tolerant to poor water quality. Branching corals are known to be less susceptible to sediments than other morphologies (Rogers 1990), such as *A. muricata* being adapted to sedimentary conditions (Browne 2012; Johnson *et al.* 2017). However, from previous studies, *Acropora* responses to water quality are not consistent. Fabricius *et al.* (2005) documented a higher *Acropora* abundance at poorer water quality sites in the Wet Tropics yet a separate study in the Whitsundays found a negative association of *Acropora* with poor water quality (Fabricius *et al.* 2012). Besides, plumes are associated with diverse aspects of water quality such as sediment, chlorophyll and nutrients (Devlin & Schaffelke 2009), likely to act differently on an overall coral cover metric that may explain the weak effects detected. Another possible explanation for the slight increase in branching *Acropora* at lower levels of plume exposure could be that an increase in water column phosphates may promote coral calcification and faster linear extension growth rates, as documented in *A. palifera* and *A. longicyathus* (Steven & Broadbent 1997; Koop *et al.* 2001).

Accounting for both structured spatial effects and unstructured (or reef-specific) random spatial effects, our study recognised the limitations of the predictors used in explaining complex coral dynamics in the GBR. Two regions stood out (Lizard/Cooktown and Swain subregions) where the potential effect of various covariates or predictors on expected coral cover was the most uncertain and longer-term studies are needed to fully disentangle these complex effects. Inference is strengthened also by including specific growth morphologies in the coral cover models – we showed that including specific acroporid growth forms reduced unaccounted heterogeneity in model fit. The *Acropora* growth form model also revealed associations with additional predictors (DHW and plume frequency) that would be otherwise undetected if only total coral cover data were used.

Our results find high spatial and temporal variation in coral dynamics across the GBR. Drivers and patterns are difficult to identify owing to the inherent local variation in coral cover trajectories, even when reefs are exposed to similar biophysical conditions and separated by only a few hundred metres (Vercelloni *et al.* 2017). The challenge is to incorporate the interaction of cover and stressors at both spatial and temporal scales (Levin

1992; Connell, Hughes & Wallace 1997), and our findings suggest the need to monitor factors at a resolution that can provide a nuanced interpretation of coral dynamics. By incorporating trait information in the analysis of long-term reef monitoring data, the different nonlinear relationships between drivers and coral dynamics are made apparent and may help predict future reef trajectories in the context of global change.

Supporting Information

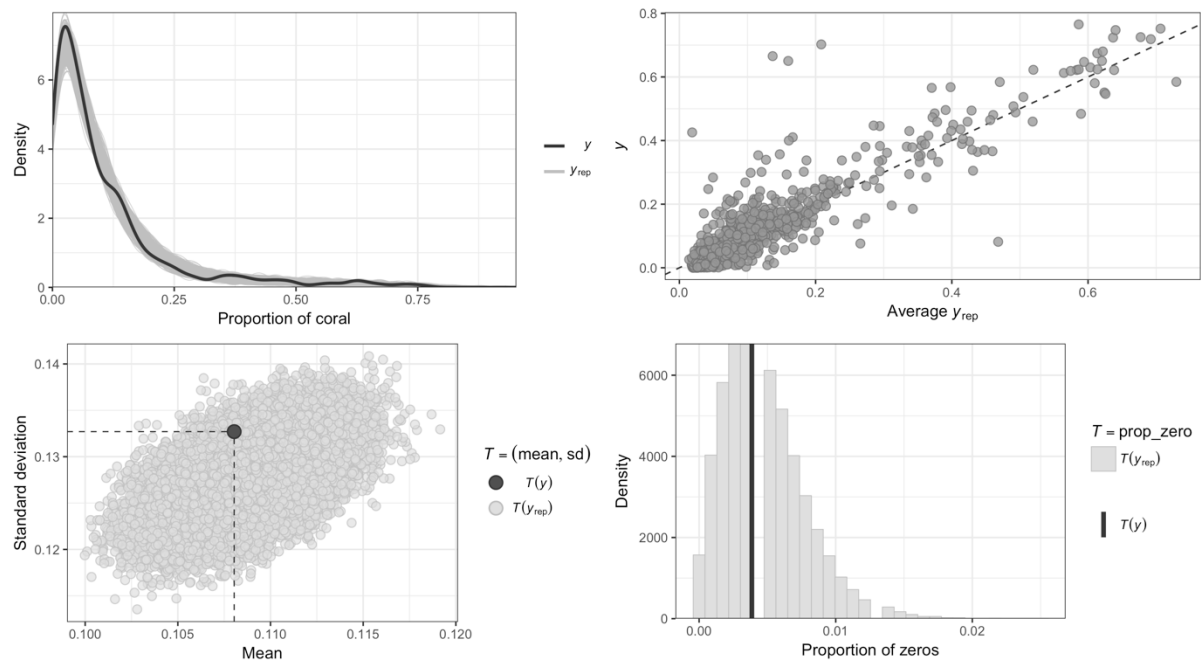


Figure S 5.1 Graphical posterior predictive checks of a) density overlay b) scatter plot of average of coral cover c) scatter plot of mean and standard deviation summary parameters and d) histogram of proportion of zeros found in the observed data and predicted values from best fit total *Acropora* cover model.

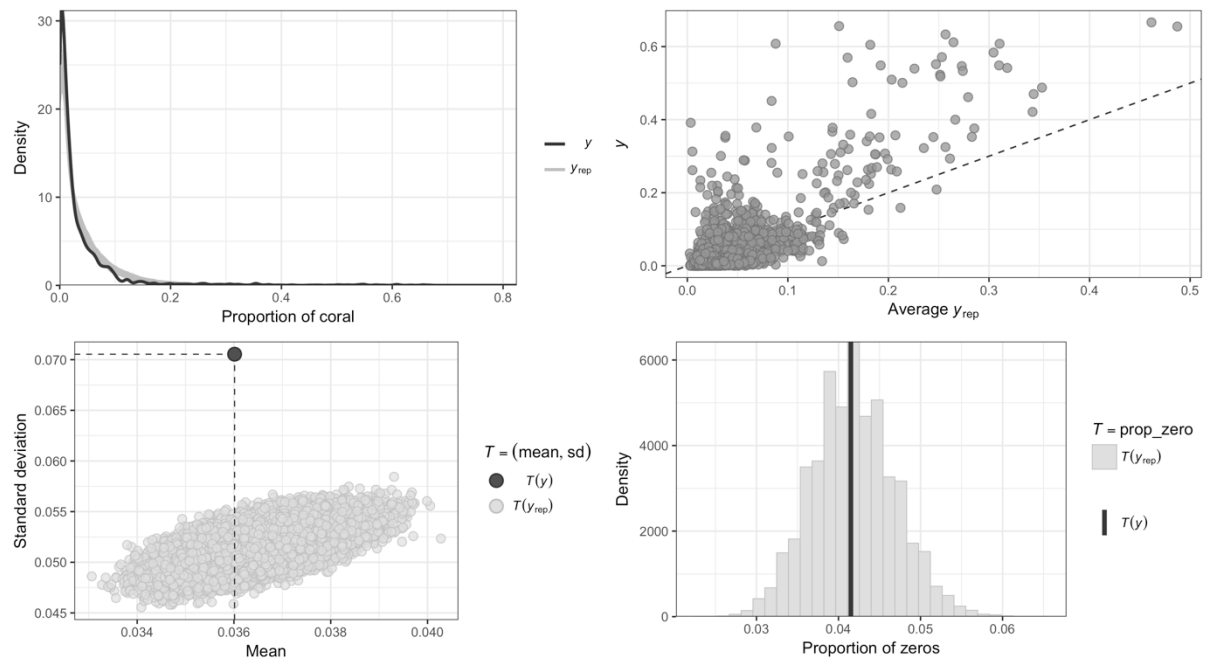


Figure S 5.2 Graphical posterior predictive checks of a) density overlay b) scatter plot of average of coral cover c) scatter plot of mean and standard deviation summary parameters and d) histogram of proportion of zeros found in the observed data and predicted values from best fit *Acropora* growth form model.

Table S 5.1 Model estimates for the coral cover model.

<i>Factors</i>	<i>Estimate</i>	<i>SD</i>	<i>Lower CI</i>	<i>Upper CI</i>	<i>Effective samples</i>	<i>Rhat</i>
Reef	0.19	0.03	0.14	0.25	16380	1
Year	0.11	0.03	0.06	0.17	17537	1
ARR (1)	3	0.12	2.76	3.24	50000	1
Intercept	-2.00	0.23	-2.43	-1.53	18847	1
Region: Central	-0.19	0.24	-0.69	0.27	23320	1
Region: South	0.70	0.34	0.04	1.38	23503	1
Plume Frequency	0.06	0.1	-0.14	0.26	19012	1
s(Year) North	-0.10	0.25	-0.62	0.45	19717	1
s(Year) Central	-0.24	0.19	-0.64	0.17	24203	1
s(Year) South	-1.19	0.57	-2.32	-0.09	21131	1
s(COTS) North	-0.12	0.55	-1.18	1.15	29246	1
s(COTS) Central	-0.09	0.28	-0.66	0.51	31809	1
s(COTS) South	-0.17	0.07	-0.33	-0.05	26721	1
s(Wind Stress)	0.06	0.02	0.02	0.10	50000	1
s(DHW)	0.01	0.08	-0.18	0.13	18433	1
t2 (1)	-0.14	0.36	-0.84	0.62	15895	1
t2 (2)	-0.05	0.34	-0.77	0.61	16018	1

t2 (3)	-0.18	0.38	-1.02	0.55	21142	1
phi	27.46	1.31	24.97	30.08	50000	1

Table S 5.2 Model estimates for the *Acropora* cover model

<i>Factors</i>	<i>Estimate</i>	<i>SD</i>	<i>Lower CI</i>	<i>Upper CI</i>	<i>Effective samples</i>	<i>Rhat</i>
Reef	0.35	0.04	0.27	0.43	17075	1
Year	0.09	0.04	0.01	0.18	10274	1
ARR (1)	3.73	0.19	3.35	4.11	50000	1
Intercept	-2.80	0.33	-3.42	-2.10	20994	1
Region: Central	-0.22	0.38	-0.97	0.53	24822	1
Region: South	0.58	0.51	-0.40	1.61	23929	1
s(Year) North	0.35	0.53	-0.61	1.49	22678	1
s(Year) Central	-0.11	0.27	-0.53	0.56	18955	1
s(Year) South	-0.19	0.67	-1.51	1.09	24296	1
s(COTS) North	-0.23	0.56	-1.28	1.08	26546	1
s(COTS) Central	-0.06	0.31	-0.61	0.69	23332	1
s(COTS) South	-0.23	0.10	-0.46	-0.07	23572	1
s(DHW)	-0.10	0.20	-0.61	0.14	12414	1
s(Wind Stress)	0.05	0.03	-0.01	0.11	50000	1
s(Plume)	-0.05	0.32	-0.54	0.77	14370	1
t2 (1)	0.03	0.51	-1.00	1.02	20769	1
t2 (2)	-0.12	0.48	-1.07	0.86	21061	1
t2 (3)	-0.15	0.66	-1.58	1.05	20168	1
phi	28.31	1.41	25.62	31.14	50000	1

Table S 5.4 Model estimates for the *Acropora* morphology model.

<i>Factors</i>	<i>Estimate</i>	<i>SD</i>	<i>Lower CI</i>	<i>Upper CI</i>	<i>Effective samples</i>	<i>Rhat</i>
Reef	0.38	0.04	0.31	0.46	12119	1
Year	0.11	0.03	0.05	0.199	10058	1
ARR (1)	-1.16	0.21	-1.56	-0.75	50000	1
ARR (2)	-0.74	0.21	-1.15	-0.34	50000	1
Intercept	-3.55	0.38	-4.24	-2.74	10498	1
Region: Central	-0.06	0.41	-0.88	0.73	14601	1
Region: South	0.89	0.47	-0.02	1.84	13832	1
Morph: Tabulate	0.59	0.04	0.52	0.66	38298	1
Morph: Others	-0.18	0.04	-0.27	-0.10	38467	1
s(Year) North	0.04	0.29	-0.43	0.70	15844	1
s(Year) Central	0.54	0.50	-0.40	1.57	17273	1
s(Year) South	0.44	0.57	-0.73	1.51	15645	1

s(COTS) Branch	-0.19	0.09	-0.39	-0.02	21962	1
s(COTS) Tabulate	-0.49	0.13	-0.77	-0.27	18182	1
s(COTS) Others	-0.18	0.08	-0.34	-0.01	22926	1
s(Wind Stress) Branch	0.00	0.03	-0.06	0.07	50000	1
s(Wind Stress) Tabulate	0.07	0.03	0.01	0.13	50000	1
s(Wind Stress) Others	-0.08	0.03	-0.14	-0.01	50000	1
s(DHW) Branch	-0.14	0.18	-0.59	0.09	12121	1
s(DHW) Tabulate	-0.91	0.35	-1.65	-0.29	14677	1
s(DHW) Others	-0.10	0.18	-0.49	0.28	16791	1
s(Plume) Branch	-0.25	0.29	-0.84	0.25	5949	1
s(Plume) Tabulate	0.06	0.30	-0.49	0.63	5895	1
s(Plume) Others	-0.30	0.28	-0.82	0.25	6799	1
t2 (1)	0.15	0.60	-0.98	1.37	15222	1
t2 (2)	-0.13	0.57	-1.23	1.00	15626	1
t2 (3)	0.21	0.81	-1.33	1.82	13543	1
phi	31.08	1	29.14	33.07	50000	1

6. GENERAL DISCUSSION

Synthesis

Coral communities and dynamics are a result of numerous ecological processes, functions and feedback mechanisms (Scheffer *et al.* 2001). A major goal in the management of coral reef ecosystems is to prevent undesirable shifts (i.e. coral to algal-dominated systems) (Scheffer & Carpenter 2003; Walker *et al.* 2004) and central to this endeavour is to understand how corals respond to and recover from perturbations. A thorough understanding of the different components that govern the resilience of coral reef ecosystems is needed to ensure reefs can adapt to change in face of global changes (Hughes *et al.* 2010). Multiple environmental factors affect reef functioning, either positively or negatively (Hughes *et al.* 2003,) and areas with varying levels of ecological complexity and disturbance regimes are likely to exhibit different resilience (Mumby *et al.* 2015). Moreover, reefs with different biophysical attributes require tailored management strategies to preserve and/or enhance their resilience values (Maynard *et al.* 2010).

Coral reef system dynamics are complex and hard to predict (Graham, Nash & Kool 2011; Sasaki *et al.* 2015), often yielding ecological surprises (Hughes 1994; Paine, Tegner & Johnson 1998). To date, there are mechanistic models that analyse and forecast the resilience of reefs but require specialist knowledge and extensive data for parameterisation. Data mostly come from controlled experiments on the functional relationships between different parameters to fill knowledge gaps (Mumby, Hastings & Edwards 2007; Fung, Seymour & Johnson 2011), but there is a wealth of data amassed from global long-term monitoring programmes yet to be utilised (Peters 2010). Little guidance is available on how best to interpret long-term monitoring data to infer insight on reef resilience (Flower *et al.* 2017). Current resilience approaches come in a 'one-size-fits-all' perspective for coral reefs, an ecosystem characterised by a variety of habitats that are under the influence of different biophysical attributes (Marzloff, Little & Johnson 2016), such as proposing the same set of

resilience metrics to be used in different geographical regions. Also, there is no clear guidance on how to translate measurements of 'resilience' to indicate best coral reef management practices (Maynard *et al.* 2015).

The broad objective of this PhD was to improve the way monitoring data are used to inform resilience. My thesis had four main objectives to address this gap: (1) to review resilience-related concepts and evaluate resilience measurement approaches in coral reef systems; (2) evaluate how resilience-based management has influenced metrics monitored; (3) identify key drivers of coral cover dynamics on the inshore Great Barrier Reef; and (4) identify key drivers and disturbance impacts on acroporid life forms focusing on the mid- and off-shore GBR. In addressing these objectives in coral reef resilience and monitoring science, lessons are learnt from some of the best monitoring datasets in the GBR and how that might refine what should be valued when conducting a resilience and/or monitoring study. Additionally, some insights into the design of monitoring programs is presented, based on an alternate set of limitations revealed when sophisticated statistical analyses were applied on long-term datasets.

In the next section, I briefly summarise the context, gaps and issues, conduct and the main findings and implications of the Thesis chapters.

Demystify the measurement of reef resilience

There is widespread interest in the quantification of resilience in ecological systems (Standish *et al.* 2014), but the term resilience has evolved into a boundary object used differently across various disciplines over the past decades (Baggio, Brown & Hellebrandt 2015). Often found to be overly vague for quantification (Hodgson, McDonald & Hosken 2015; Olsson *et al.* 2015), this ambiguity has led to an assortment of methods for measuring reef resilience, with no clear consensus on how to address different management goals and priorities. A critical overview of the current state of knowledge on reef resilience science is urgently needed and is addressed in **Chapter 2**. Based on a comprehensive review of reef resilience literature, I created a conceptual framework with seven potential measurement approaches with an assessment of strengths and limitations. Frameworks identified include ecological resilience, precariousness, current attractor, short-term recovery rate, long-term reef performance, absolute vulnerability and relative vulnerability. In selecting the most appropriate approach,

key considerations such as ease of implementation, cost of data collection, skill constraints and the management questions/goals to be answered/achieved should be considered. Apart from clarifying the full suite of potential approaches to measure reef resilience, I also recommend appropriate approaches in light of diverse management objectives. The results of this chapter highlight the need to move beyond measurements and consider how resulting resilience values can be used to improve the conservation and management of coral reefs.

Evaluate influence of RBM on reef monitoring

The concept of resilience has evolved from largely theoretical underpinnings to the current focus on facilitating operationalisation to better inform management (Anthony *et al.* 2015). This new approach to reef management is known as resilience-based management (RBM), yet it is unknown how RBM has changed the way coral reefs are monitored and assessed. In **Chapter 3**, I systematically evaluated the influence of RBM on global coral reef monitoring activities by comparing metrics utilised by conventional monitoring programs versus those by resilience assessments. My results provide clear evidence of substantial differences between the metrics used in monitoring and resilience assessments, and confirm that RBM has altered the way people conduct monitoring. Resilience metrics are more diverse and focused on factors that are likely to predict the response and recovery behaviour of reefs, such as ecological processes and exposure to environmental drivers. Monitoring, on the contrary, had a focus on reef states providing greater taxonomic resolution on benthic community changes. The diversity of resilience metrics documented underscores the reliance on proxies for hard to measure ecological processes. Surprisingly, a substantial proportion of monitoring metrics can be used as potential proxies if duly interpreted using a resilience perspective. Thus, with the appropriate tools and frame of reference, there is considerable potential in using existing monitoring data for the application of RBM on coral reefs.

Identify drivers of inshore reef dynamics

Coral reefs are dynamic systems characterised by alternate periods of recovery and decline (Connell 1997). Our knowledge of coral dynamics mostly comes from relatively healthy mid- and off-shore reef systems, yet far less is known about long-term inshore reef dynamics closer to anthropogenic stress (Guest *et al.* 2016b) (Mumby 2017). In **Chapter 4**, I assessed the spatial and temporal coral cover dynamics on a 10-year dataset from the inshore GBR

using a multivariate state-space modelling approach (MARSS). Modelling results demonstrated that inshore reefs, like their offshore counterparts, are chiefly governed by acute disturbances albeit different ones depending on locality. The major drivers identified are storms (northern GBR) and floods (southern GBR), with disease, juvenile coral density, macroalgal and turf cover found driving coral cover at specific catchments. Correlated negative trends in water quality and coral cover were not detected, and one hypothesised reason is because the decline of water quality on the GBR was linked to early European settlement (McCulloch *et al.* 2003; Perry *et al.* 2008; Kroon *et al.* 2012). Corals have likely responded to water quality effects decades ago and recent dynamics may not show observable changes. Water quality mechanisms are clearly affecting coral dynamics manifested in flood as a key driver and further work is needed to help unpack causality. This case study illustrates the difficulty in detecting subtle and nuanced mechanistic impacts of chronic pressures over and above the conspicuous impacts of acute drivers.

Incorporate traits to analysis of long-term dynamics

One of the more comprehensive analyses of reef dynamics from a time-series of 27 years established storms, bleaching and crown-of-thorns starfish (COTS) as the main cause for coral decline in the GBR system (De'ath *et al.* 2012). Studies on the impacts of multiple drivers on reef dynamics have tended to be somewhat simplistic, focusing on total coral cover and acute disturbances. In **Chapter 5**, I assessed the spatial and temporal coral cover dynamics using a 22-year dataset (with a focus on mid- and off-shore reefs) using Bayesian regression models. Albeit from an intensively studied environment, value was added by incorporating chronic water quality effects, trait information (acroporid life forms), as well as structured and unstructured spatial effects. I also focused on *Acropora* dynamics as one of the most dominant taxa in the GBR and its importance in driving reef recovery (Osborne *et al.* 2011; Vercelloni *et al.* 2017). Overall, COTS and storms emerged as the main negative drivers of total coral and *Acropora* cover, with COTS impacts more consistent and apparent than storms. Interestingly, associations of bleaching and chronic water quality with cover were only detected when corals were disaggregated into life forms. Varying, and somewhat surprising, relationships were detected between drivers and acroporid growth forms, such as the nonlinear threshold effects of elevated seawater temperature on tabulate *Acropora*. The final case study underscores the value in considering additional traits when investigating coral reef resilience and dynamics.

Overarching implications

Ultimately, the results from my thesis has contributed to a small part within the larger context of operationalising coral reef resilience. Using a range of techniques, I have addressed the need to improve the retrospective analyses of long-term monitoring data in the context of resilience-based management (**Chapter 2**), focusing on the data collection (**Chapter 3**) and analysis components using two of the world's best monitoring datasets as case studies (**Chapters 4 and 5**). The overall novel contributions of this thesis are as follows:

1. The comprehensive review of resilience literature in **Chapter 2** presents an original conceptual framework for reef resilience measurement approaches and illustrates how each approach can address different management questions – bridging the gap between the measurement of resilience for the application of resilience-based management.
2. Comparison of existing monitoring and resilience assessment protocols in **Chapter 3** presents a new finding: clear evidence that resilience-based management has influenced on-the-ground monitoring with a shift in reef metrics being measured.
3. Through the analysis of key drivers and reef dynamics on the Great Barrier Reef, **Chapters 4 and 5** present two case studies on the retrospective analysis of long-term monitoring data using state-of-the-art statistical methods, identifying key predictors of coral dynamics on the inshore and mid-offshore GBR. The varying relationships revealed between drivers and different life forms add value to existing knowledge on GBR coral dynamics.
4. The synthesis of results and extracting lessons learnt for future resilience assessments here in **Chapter 6** provides insights into future research avenues to improve monitoring activities and highlights issues to be aware of for the successful operationalisation of resilience-based management on coral reefs.

Making metrics matter

The practice of resilience-based management relies on the ability to detect, quantify and manipulate components of a system that affects resilience (Spears *et al.* 2015; Hughes *et al.* 2017a). A conventional way to measure resilience is to collect data in the form of metrics, hence, this process has important implications on the operationalisation of resilience-based management. In this section, I will discuss several relevant themes highlighted from the results of my research (Figure 6.1) and the corresponding limitations under each category, leading to future research suggestions and priorities.

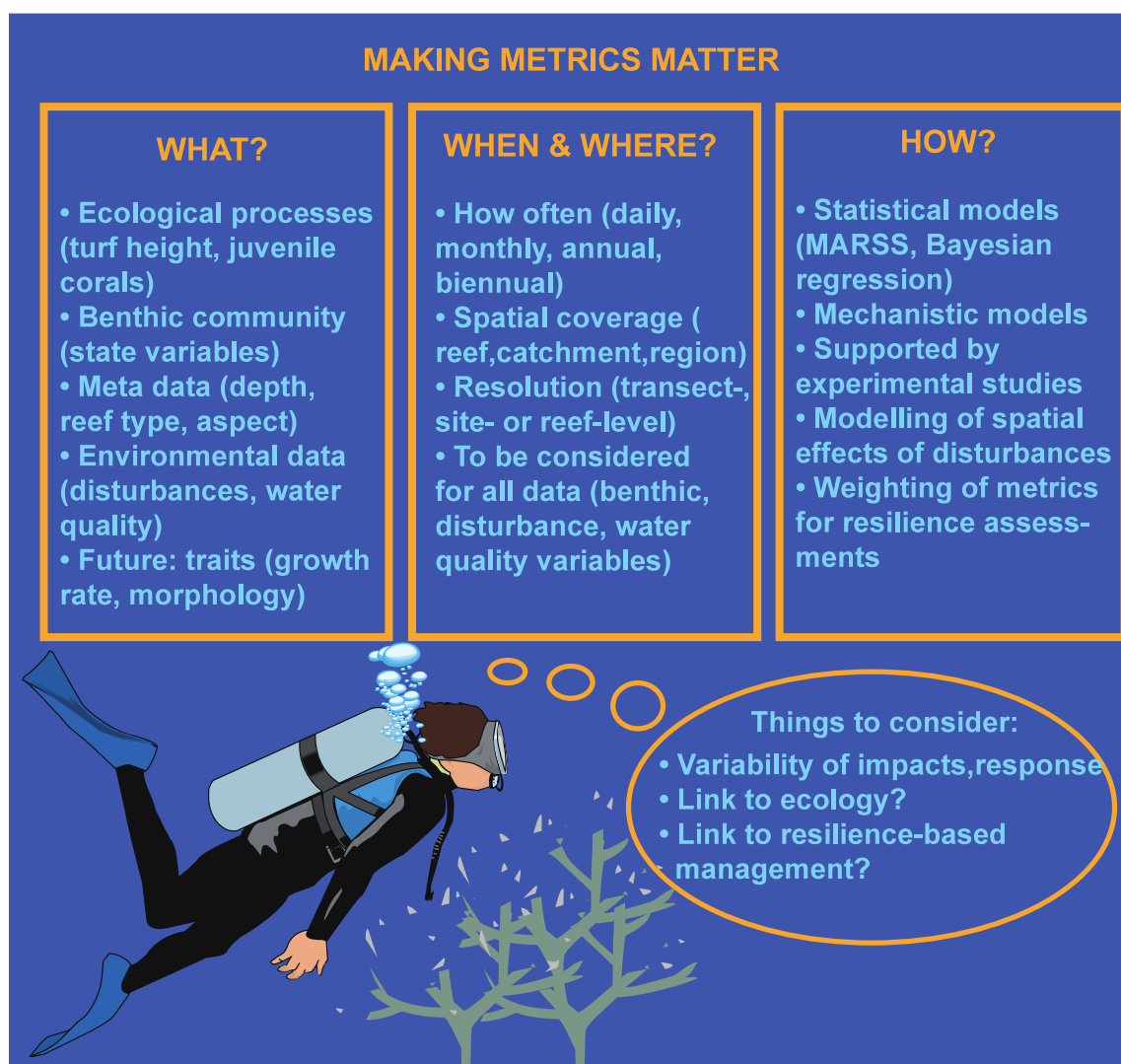


Figure 6.1 Making monitoring metrics matter: things to consider.

Choice of metrics

Contrary to monitoring programs that focus on documenting detailed changes of reef state, resilience assessments (by definition) should investigate ecological processes that determine resistance and recovery, as demonstrated in **Chapter 3** (Figure 3.2). For both future monitoring and resilience assessments, metrics should be chosen carefully covering both state and process variables. Information that are currently not commonly measured in monitoring programmes can provide great insight on reef resilience, such as turf canopy height. For instance, additional turf canopy height information in **Chapter 4** can help shed light on the mechanisms responsible for the lack of coral recovery in the Burdekin catchment. Turf height directly informs on herbivory and recruitment processes, as low turf height indicates high levels of herbivory and leads to an increase in available substrate for coral recruitment, thus facilitating coral recovery (Mumby & Steneck 2008). The presence of thick turfs in the Burdekin would provide data that is consistent with the regime shift theory, whereby the reef is locked in an algal-dominated attractor by reinforcing feedbacks preventing coral recovery as the system becomes inhospitable to coral recruits.

The inability to detect water quality effects over and above the impacts of acute disturbances on corals in **Chapter 4** highlights the importance of appropriate monitoring of key environmental drivers (Table 4.2). Monitoring programmes focus on the changes of response/state variables (i.e. benthic community cover) but often collect limited information on potential drivers of trends (Keith *et al.* 2015a). Environmental drivers are frequently assembled from separate studies, such as water quality variables from independent satellite-derived data used in both **Chapters 4 and 5**. Amassing environmental data from different sources can lead to potential issues, such as the mismatch between the spatial and temporal scales of drivers and response and can cause complex relationships to go undetected (Fabricius & De'ath 2004). Hence, I urge the collection of potential drivers at the same scale and resolution of organisms of concern, for example, the collection of water quality metrics at every reef site to capture differences in exposure which may have considerable consequences on local reef trajectories. Moreover, the successful incorporation of factors influencing the observation of coral cover into MARSS (e.g. proportion of clay and silt on visibility) underscores the value of observation covariates in the analyses of survey data (Clark & Bjørnstad 2004; Connors *et al.* 2014; Stanton *et al.* 2016). Future data analyses can

consider potential observation covariates such as photographic equipment (e.g. camera resolution), changes in survey methods, and observer bias, and steps should be taken to ensure meta-data (e.g. depth, aspect) is recorded in an organised way for future use. Since the spatial coverage expansion of sampling sites significantly raises monitoring costs, strategies to offset costs should be considered, such as water quality sensors placed within reef sites that require minimal maintenance or satellite-based data. Alternatively, monitoring can focus on specific components of metrics such as maximum values and the duration of reefs exposed to water quality that passes pre-defined thresholds known to cause mortality in corals (Berkelmans, Jones & Schaffelke 2012).

In addition, **Chapter 5** highlights the utility of moving beyond coral cover by incorporating additional trait information (such as coral morphology) to reveal additional insight on the underlying mechanisms governing coral dynamics (Table 5.4). Trait information is routinely overlooked during analysis of population dynamics and can provide clues on ecological mechanisms and population abundances with an emphasis on environmental gradients and physiology (McGill *et al.* 2006). Functional traits, such as morphology as demonstrated in **Chapter 5**, help identify general patterns by providing insight on underlying mechanisms that drive ecological processes such as coral-algal competition (Swierts & Vermeij 2016) leading to appropriate predictions of population dynamics. The incorporation of information on three coral morphologies (branching, tabulate and others) revealed additional significant associations of thermal stress and water quality within the LTMP dataset. Different life forms are known to have varying resistances to disturbances, are vulnerable to different forms of impact, and have divergent recovery trajectories (Madin & Connolly 2006; van Woesik *et al.* 2012). The knowledge of how groups of taxa are likely to respond to stressors and their respective rate of recovery enable an informed prediction on how reefs with different coral communities may respond to and recover from future stress. For example, a reef composed mostly of branching corals is likely to be more heavily impacted by storms compared to a reef with largely massive corals, yet the former reef is also likely to recover quickly because of the fast growth rates exhibited by branching species. To that effect, resilience assessments can incorporate morphological information which are weighted in terms of their resistance and recovery capacity when impacted by disturbances and be directly integrated into resilience values for reefs.

Data collection

An important component in data collection is on the frequency and intensity of monitoring and how those metrics can be translated into meaningful ecological understanding through analyses and interpretation (Hill & Wilkinson 2004; Reynolds 2012). Spatial and temporal scales should be carefully considered for individual variables in relation to study goals (de Gruijter *et al.* 2006). Most coral reef systems exhibit high heterogeneity, variability and patchiness (Houk & van Woesik 2013; Vercelloni *et al.* 2017), but whether the objective is to get a mean value or to detect the passing of a threshold will determine how the data should be collected. For example, in a coral reef context, the mean benthic cover of different taxa over time may be of interest, but when looking at water quality would likely be more concerned with the passing of specific thresholds and how that affects the survival and processes of coral reefs (De'ath, Fabricius & Authority 2008; Wooldridge 2009).

Water quality variables are site specific and hard to detect, characterised by high estimation error and poorly captured by temporal aggregation owing to seasonal fluctuations (Baffaut *et al.* 2015). The results in **Chapters 4 and 5** illustrate the limitations of the water quality component, whereby all samples were pooled temporally (either annually or throughout the time-series to represent chronic effects) to obtain a compatible resolution with the response variable (coral cover) when modelling dynamics. However, water quality metrics were at a lower resolution than coral cover and the same water quality value (reef-level) had to be extended for both reef sites. Moreover, water quality metrics collected using the same sampling method were found to be highly correlated (e.g. satellite-derived variables such as coloured dissolved organic matter, non-algal particulates and chlorophyll were correlated with each other; as were sediment grab samples such as nitrogen and carbon content in **Chapter 4**) and led to the exclusion of most water quality metrics. Because of the coarse and infrequent nature of the water quality sampling, I recommend an improvement in the spatial and temporal resolution of water quality data collected near reef sites with the placement of site-level in-situ loggers for a continuous estimate of water quality variability. Although being a resource-intensive strategy, studies have shown high local variability in water quality, even under natural conditions, and monthly samples are inadequate for capturing bloom effects from storms and floods that are frequent in the GBR (Brodie *et al.* 1997; Devlin *et al.* 2001). To address the mounting cost issue brought about by the intensification of water

quality monitoring as discussed previously (see 'Choice of metrics' section), here, the findings suggest a possibility of cost reduction by eliminating highly correlated metrics, with a preference of selecting the least expensive and easiest variables to monitor. In addition, follow up studies should attempt to get an orthogonal design across major gradients of water quality with a view to disaggregating the importance of correlated effects (Fukami & Wardle 2005). The gradient analysis approach originates from the plant community ecology, and studies can take two forms with gradients established either in the laboratory or naturally established gradients (Whittaker 1967; Vitousek & Matson 1991). Examples on coral reef systems include investigating the effects on coral communities along changing gradients of pH, fishing pressure (Weijerman, Fulton & Parrish 2013), anthropogenic impacts (Sandin *et al.* 2008) and water quality (Fabricius *et al.* 2005). To disentangle and look at the isolated effects of water quality effects on different growth forms, a possible future piece of research is to conduct manipulative experiments where different coral growth forms are exposed to stratified levels of water quality in the laboratory. Experiments can also be used to evaluate the various effects of different water quality metrics separately to overcome confounded variables and their effects.

Simple differences in survey design and data collection can have serious consequences on data analyses (Reynolds 2012). Taking disturbance impacts on coral reefs as an example, storm effects on coral cover in **Chapters 4 and 5** illustrate how different data collection methods can affect the detection of drivers and dynamics of reef systems in the subsequent analyses. In **Chapter 4**, the disturbance data on inshore reefs were collected from scuba searches and only impacts that were observable on reefs were recorded, indirectly minimising the inherently patchy effects of storms that were illustrated with the cyclone-tracks satellite derived storm (wave) impacts used in **Chapter 5** (Wolff *et al.* 2016). Although effects of storms were found to be significant in both datasets, the results from **Chapter 5** reflected a much higher uncertainty (Figure 5.4). Further examination of reef-level data confirmed that not all storms caused a negative impact on coral cover (Figure 5.5), and signifies that caution should be applied when using *in-situ* observations of reef impacts. First, if a reef was not impacted or was resistant to the impact showing no signs of observable damage, the disturbance may go unrecorded (false negative). Second, it is hard to distinguish impacts on reefs with multiple concurrent and/or consecutive disturbances, evident in the dataset, such as Fitzroy catchment in **Chapter 4**. Monitoring more frequently can partially address this issue,

especially when major impacts are known to have occurred on the reef to avoid misidentifying the cause of coral decline (Rogers & Miller 2016) but is often logistically difficult for large region of reefs such as the GBR and hence the advantage of satellite data. Also, satellite/remote-sensing data can be complemented by in-situ data or vice versa to assess impacts of disturbances on individual reef sites. Future analyses should consider the goals for monitoring to decide the best way to account for natural variability while allowing for ecological patterns to be detected from inherently variable datasets (Houk & van Woesik 2013). Balancing broad scale surveys with finer scale modelling of disturbance impacts to elucidate spatial and temporal heterogeneity can help identify reefs that have persistent refugia from certain stressors, such as cyclones (Wolff *et al.* 2016; Cheal *et al.* 2017). Results of these finer scale studies will be useful in resilience assessments, where areas of refugia will be given weight accordingly based on conservation objectives (Game *et al.* 2008).

Nuances of data treatment

The issue of aggregation of ecological data of different scales and time is central to the treatment of long-term monitoring data prior to analyses (Clark & Avery 1976; Levin 1992). Data can be aggregated spatially, temporally or taxonomically (Erickson, Gray & Eager 2017). Common in large-scale analysis, aggregation is often needed when response and environmental variables are collected at different spatial scales and resolution and when conclusions need to be drawn at a larger (i.e. regional scale) for management or reporting purposes (Schneider 2001). However, the aggregation of variables leads to loss of individual-level information that can lead to the masking of certain relationships when interpreting complex ecological dynamics (Wakefield & Lyons 2010). For example, Erickson, Gray and Eager (2017) cautioned that MARSS can produce biased estimates on linear trends when applied to aggregated environmental monitoring data.

To use an explicit example, in **Chapter 4**, I wanted to estimate catchment-level coral cover trends in the inshore GBR – an ecological fallacy of making multilevel reference based on a single level of analysis (Clark & Avery 1976). Ecological fallacy occurs when there are differences in the detection of associations based on different levels of data (i.e. site, reefs, catchments) (Wakefield & Lyons 2010). Through critical thinking about the data, I finally decided on the current resolution of models – reefs within each catchment had drastically

different trajectories (Figure S4.1-S4.10) and thus a generalisation of catchment-level trends would be meaningless. Moreover, MMP reefs were inherently different as sites were chosen at a gradient of water quality within each catchment (Thompson *et al.* 2016), so it was more meaningful to predict individual reef trajectories from an ecological perspective.

Fundamentally, inferring catchment cover averages will be difficult with the data collected from this survey design. The example fully illustrates the importance of cross-validation between modelling estimates with site-level raw data to ensure that appropriate ecological conclusions are being made in the right context (Wakefield & Lyons 2010; Rogers & Miller 2016). One way of overcoming the issue of spatial scales would be to model the data using a hierarchical approach, as demonstrated by (Vercelloni *et al.* 2017) at the site-, reef-, habitat- and subregional-levels on *Acropora* cover of GBR reefs.

Another important issue was the treatment of environmental variables to ensure their effects can be detected by the models. Much effort was used to improve the disturbance data used in **Chapter 4** to account for historical effects, allowing us to explain the varying initial conditions for individual reefs. Disturbances often leave legacy effects that continue to affect reef structure and processes (Magnuson 1990; Turner *et al.* 2003b), such as in the inshore Burdekin catchment. Coral cover showed signs of historical degradation and remained low and stable throughout the survey period, likely linked to increased sediment discharge because of European settlement since the 1870s. To account for past environmental disturbances, a literature search was conducted to document the possible disturbances that occurred within the 15 MMP reefs during the 10 years prior to the start of the initial survey. However, this was not feasible for the much bigger LTMP dataset of 93 reefs used in **Chapter 5**, as reef histories were not as well documented by the literature, especially the additional reefs that were added after the rezoning of the Great Barrier Reef. Some research had used palaeoecological reconstructions to address the historical changes of reefs, such as in the Pelorus Island of central GBR (Roff *et al.* 2013) and inshore GBR reefs (Perry *et al.* 2008), and future studies should incorporate environmental histories of reef sites to improve assessments of reef dynamics and resilience (Hughes 1989; Thurstan *et al.* 2015). Simple metrics such as initial coral community composition can be considered as a first step in resilience assessments, as this metric indirectly reflects disturbance histories and physical features important for reef condition (Graham *et al.* 2014).

Implications for resilience assessments

The implications of my PhD research are novel insights on resilience from the retrospective analyses of long-term monitoring data, in particular on that would change the way people conduct and interpret a resilience assessment. From the analyses of long-term monitoring data, **Chapter 4** has shown that recent acute disturbances may be the key drivers of coral dynamics in the relatively short time-scales field monitoring data addresses. Observed data show that reefs with relatively high coral cover can be found in places with poor water quality and vice versa. Thus, having poor water quality does not necessarily mean that a reef has low resilience, especially if *Acropora* is present. Moreover, a change in chronic water quality may not be transferred immediately into and be reflected by reef dynamics. Historical changes should be considered when making inferences using variables measured in a resilience assessment. Changes in physical parameters may have happened decades ago, such as sediment impacts on coral reefs from early human settlement in the GBR (McCulloch *et al.* 2003). This insight differs from how many existing resilience assessments are currently conducted, whereby reefs with poor water quality are routinely scored lower for resilience (Obura & Grimsditch 2009; Maynard *et al.* 2010), which may not be appropriate given the time-scales being considered. Based on the finding that disturbance events can be quite influential on recent reef dynamics, one way to improve the accuracy of resilience assessments is to incorporate the risks of various acute disturbances such as flooding, COTS, storms and bleaching, which seem to have a greater impact on reef dynamics at the temporal spans of monitoring programmes.

Chapter 5 is a second example demonstrating the need to re-evaluate how physical data should be interpreted in a resilience context. Normally, an increase in thermal stress will lower reef resilience scores because of the mortalities associated with bleaching. However, the results of Chapter 5 showed a positive relationship of tabulate corals with DHW, which illustrates the importance of distinguishing between thermal stress that cause direct mortality and levels that induce thermal tolerance by preparing and exposing corals to minor stresses (Ainsworth *et al.* 2016). Moreover, DHW values experienced by reefs in the LTMP dataset were below the extreme threshold of 8 known to cause widespread bleaching and mortality (Eakin *et al.* 2010). In fact, corals may be recovering faster in warmer conditions if they have not exceeded their thermal optimum. While this finding does not necessarily suggest that

corals will continue to recover fast under climate change, it may be an indication that DHWs may not be the most important factor affecting coral dynamics in the short-term.

Suitability of analytical tools

Much of the understanding on what drives systems has come from statistical analyses of long-term datasets supported by short-term experimental studies. To gain further insight on the coral reef dynamics of the inshore and offshore GBR, I applied two independent cutting-edge statistical frameworks available. In this section, I discuss and illustrate the advantages and disadvantages of these modelling techniques using **Chapters 4 and 5**.

The first approach was multivariate state-space modelling (MARSS). MARSS includes two models: one for the population process and another for the observation of that process (Dennis *et al.* 2006; Holmes, Ward & Scheuerell 2014). The advantages of the model have been fully stated in **Chapter 4**, but briefly, MARSS can: 1) handle missing response data; 2) estimate true underlying population trends; 3) separate process (natural) and observed variability; and 4) incorporate specific variables to influence both process and observation models (Ward *et al.* 2010). However, the flexibility of MARSS can result in many possible combinations that are computationally demanding and challenging to implement, as extensive numerical simulation and integration is required (Dennis *et al.* 2006).

Despite difficulties in MARSS model formulation caused by aggregation issues and large spatial variability in the MMP dataset as described above (see 'Nuances of data treatment' section), I made progress in resolving some drivers of coral dynamics on the inshore GBR with a 10 year time-series of 30 sites. However, MARSS modelling is most effective when longer time-series (>20 years) are available as demonstrated in most fisheries studies (Hinrichsen & Holmes 2009; Siple & Francis 2016; Stanton *et al.* 2016; Erickson, Gray & Eager 2017). A limitation when dealing with short-term data is illustrated by **Chapter 4**, difficulties were encountered in identifying drivers for the inshore GBR catchments that exhibited static response dynamics (e.g. Burdekin and Mackay). Statistical modelling techniques are predicated on the detection of associations between changes in the explanatory and response variables (Bruno & Selig 2007). If there is no change in the response variable, how can the drivers of change be detected by statistical associations? As hypothesised in

Chapter 4, the non-dynamic catchments are likely to have responded to anthropogenic impacts decades ago and this phenomenon is not uncommon in reef systems (McCulloch *et al.* 2003; Bahr, Jokiel & Toonen 2015). Some alternative reasons can be because of low disturbance frequency and stable communities (e.g. sheltered inshore reefs dominated by relatively stable submassive and encrusting long-lived corals), sampling that is not frequent enough to detect subtle increases and decreases (see 'Data collection' section) and too much variability in predictor and response variable (i.e. noise) to detect changes. Additionally, changes in coral community composition and structure cannot be detected from an overall metric like coral cover and the potential lagged effects of drivers can also add to the difficulty of identifying drivers of coral cover trajectories in reef systems. Apart from the use of a longer time-series that help determine whether historical or lagged effects exist, alternative methods (e.g. mechanistic models, intensifying *in situ* observations) should be considered for a better perspective of the reason behind reefs with stable trajectories.

The second approach applied in **Chapter 5** used Bayesian geospatial varying coefficient generalised additive mixed regression models (GAMMs). Diverse and complex disturbance regimes cause challenges in the understanding of underlying coral population dynamics and perturbations have varying effects on ecological processes, reef resistance and recovery (Hughes *et al.* 2003; Fabricius & De'ath 2004). One major issue while dealing with the datasets is the high variability inherent in all coral reef ecosystems, nested within different levels of the collected dataset including transect-level, site-level and reef-level data. A recent study by Vercelloni *et al.* (2017) investigated different spatial scales and concluded that local variation in the GBR is key in estimating trends in coral trajectories, sites close to each other (a few hundred meters) displayed largely different trajectories. This parallels the point above whereby extra consideration should be paid when analysing aggregated environmental data, as results and conclusions may be biased (Erickson, Gray & Eager 2017).

The two case studies in this thesis illustrate how one can apply an array of statistical techniques to existing long-term monitoring datasets and successfully achieve novel insights on the dynamics of reef ecosystems. However, my work also substantiates how the use of comprehensive datasets is not the be all and end all – it is still a difficult process to arrive at meaningful ecological conclusions and there is a need to carefully interpret the mechanisms and reasons behind the statistical results obtained. The analysis of long-term monitoring data

should also be supported by other approaches such as mechanistic models and experimental field research to resolve specific components to better understand coral reef systems. For example, Udy *et al.* (2005) used remote sensing, *in situ* data collection and fixed sensors at reef site to collect information on water quality metrics and Doropoulos *et al.* (2016) combined field observations with experiments in both the lab and field to understand the mechanisms underlying coral recruitment. Although the above-mentioned studies focused on specific components of the coral reef system, this approach should also be implemented to understand reef dynamics with long-term monitoring data.

Concluding remarks

In conclusion, this thesis has captured the current state of knowledge of reef resilience science and demonstrated how sophisticated analytical techniques can be used on existing monitoring data to further understand about the resilience of our systems. I have used a range of techniques, ranging from qualitative literature review to sophisticated quantitative analytical techniques to explore the link between monitoring, time-series analyses and reef resilience. The improvement of monitoring programmes to address conservation issues and realise effective management decisions is a continuously evolving field, accompanied by advances in computational techniques and the understanding of reef systems, mechanisms and processes. Thoughtful consideration of how data can be used for resilience-based management can enhance the value of monitoring data in contributing to the effective management and conservation of global reef systems.

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