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The population dynamics and functions of corals on post-bleach coral reefs

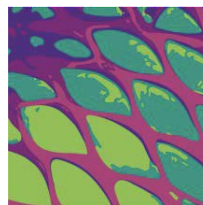
Thesis submitted by
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January 2024



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This work was carried out in the Research Hub for Coral Reef Ecosystem Functions and the Bellwood Reef Fish Lab in the College of Science and Engineering at James Cook University in Townsville, Australia.



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Statement of the Contribution of Others

This thesis was conducted under the supervision of Prof. David Bellwood and Dr. Renato Morais. I was responsible for the project's conception and design, data collection and curation, development of figures and tables, statistical analyses and interpretation, and the writing, editing, and submission of manuscripts and reports. My supervisors provided intellectual guidance throughout the research projects, providing assistance with fieldwork, technical and editorial support, as well as financial backing. I also benefited from the contribution of Sterling Tebbett in **Chapters 2, 3, 4, and 5**, who provided guidance on data collection, analysis and writing. In **Chapter 2**, I also benefited from a collaboration with Prof. Morgan Pratchett, especially with regards to the writing and editing process.

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Abstract

Climate change is rapidly transforming ecosystems globally. Coral reefs are at the forefront of this environmental transformation, with bleaching-induced coral mortality leading to abrupt changes in the structure, biodiversity, productivity and functioning of reefs. While our knowledge of how coral reefs respond to these changes has progressed greatly in the last few decades, a single indicator has prevailed in evaluations of coral reef health: coral cover.

As coral cover declines globally, a deeper understanding of the consequences of thermal stress on the status, recovery and function of reef corals will require new metrics beyond coral cover. A demographic approach appears to be the best candidate to move forward, as it not only captures key processes, such as recruitment and growth, but also provides a predictive framework with which to evaluate how key ecosystem processes on coral reefs, such as their structure, are affected by climate change. Furthermore, reef-building corals are major contributors to the topography and structural complexity of coral reefs, providing shelter and food for numerous invertebrates and fish species, with their role being mediated by their individual population dynamics. Quantifying these dynamics will be critical if we wish to understand the future trajectories of corals and reef-associated communities on post-disturbance reefs, especially in a scenario of shortening "recovery" windows between disturbance episodes.

In this thesis, I used demographic data collected across Lizard Island, on the Great Barrier Reef (GBR) over six years that encompassed three bleaching events and one significant recovery event. This systematic investigation of the demographic processes ruling coral assemblage dynamics in response to severe coral mortality incorporated an extensive analysis across multiple spatial and temporal scales. Through four data chapters (2 to 5), I addressed the following main questions: a) How do the demographic strategies of the two dominant coral genera, massive *Porites* and *Acropora*, differ given their contrasting life histories and bleaching susceptibility? b) Do small-scale

hydrodynamic regimes affect among-genera differences in bleaching susceptibility? c) How long does the structure of coral colonies persist following mortality, and how is the loss of coral structure related to estimated erosion rates? and d) What is the time frame of natural coral recovery following extensive bleaching mortality, and how can this information guide more effective restoration initiatives?

To investigate the difference in demographic strategies between coral genera with distinct bleaching susceptibilities, in **chapter 2**, I tracked the fate of 1069 individual *Acropora* and massive *Porites* coral colonies for 5 years, spanning three bleaching events. This chapter revealed remarkable genus-level differences in demographic responses to bleaching (in mortality, growth, and recruitment). Although *Acropora* colonies suffered 100% mortality, substantial local recruitment and fast growth revealed a marked capacity for recovery with a 1000% increase in the number of colonies. By contrast, almost all massive *Porites* colonies survived, and the majority grew in area (by an average of 21%), yet no new colonies were detected over the five years. These results highlighted contrasting dynamics of boom-and-bust vs. protracted declines in two major coral groups.

In **chapter 3**, I explored how small-scale hydrodynamic regimes (i.e., that occur across hundreds of metres to a few kilometres) may impact bleaching in the low-bleaching susceptible massive *Porites*. I quantified bleaching in 108 massive *Porites* colonies during the 2016 bleaching event. I investigated how hydrodynamic exposure levels and colony size contribute to local variability in bleaching prevalence and extent. The results of this chapter indicated that corals situated in exposed sites were less affected by bleaching, whereas those in lagoonal environments showed a greater prevalence of bleaching and more extensive colony-level bleaching. In particular, coral colonies located in the frontal lagoon were twice as likely to bleach compared to their counterparts in the exposed areas and were about 1.5 times more susceptible than those in the back reef locations. This variation in bleaching incidence may stem from the extended duration of warm

water temperatures in lagoon areas and highlights the importance of considering location-specific factors when assessing coral health.

Chapter 4 explored coral colonies after the bleaching-induced mortality. To answer the question ‘c’ (How long does the structure of coral colonies remain following mortality, and how is the loss of coral structure related to estimated erosion rates?), I followed the fate of 143 recently dead individual coral colonies, with complex growth forms, that died following bleaching events. These dead coral colonies were tracked for up to 5 years, across the Lizard Island reef complex, allowing detailed examination of erosion rates and post-mortality structural persistence. The results of this chapter revealed rapid erosion of dead coral colonies, with an average of 79.7% of dead colonies completely disappearing within 60 months. Remarkably, I found no effect of estimated parrotfish bioerosion, wave exposure, or coral growth form, on observed erosion rates, suggesting that our understanding of the erosion of dead corals may be more incomplete than previously thought. The rapid coral colony loss across all study sites calls for a re-evaluation of the role of corals with complex growth forms in reef growth and of the role of parrotfishes in reef erosion.

Finally, in **chapter 5**, I used coral reefs as a case study to explore how demographic insights from natural ecosystem recovery can inform and guide restoration projects. Following the local extirpation of fast-growing *Acropora* corals following the back-to-back bleaching events in 2016 and 2017, I tracked the growth of 809 individual *Acropora* recruits over two years across the 16 km² wide Lizard Island reef complex. This chapter aimed to assess the potential for natural coral recovery driven by fast-growing *Acropora* spp. and to examine how the physical setting (wave exposure), traits (growth form), and colony density affected the growth of recently settled recruits. Recruited *Acropora* corals grew to coral cover levels equivalent to the global average within just two years. Furthermore, I discovered that only 11.5 *Acropora* recruits per square meter were sufficient to achieve this cover, within this period of two years. I also found that wave exposure, growth form and colony density had a marked effect on recovery rates. My results underscore the importance of

considering natural recovery in management and restoration and highlight how lessons learnt from natural reef recovery can inform our understanding of recovery dynamics in high-diversity climate-disturbed ecosystems.

In conclusion, this thesis has systematically analysed the demographic responses of coral communities following acute and repeated environmental stressors induced by climate change. The approach adopted here, studying responses to bleaching across different genera, hydrodynamic regimes, post-mortality structural changes, and the potential for natural recovery, not only advances our scientific understanding but also provides critical insights for reef conservation and restoration strategies. The results and conclusions drawn from this thesis underscore the complexity of coral ecosystems and the varied resilience of coral species. They also highlight the necessity of integrating ecological nuances into the management of these vital marine habitats. Overall, this work contributes significantly to the field of coral ecology and offers hope and direction for future efforts to preserve our invaluable coral reef ecosystems in a rapidly changing world.

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Chapter 1. General Introduction

1.1 Coral reefs in the Anthropocene

Over the past 500 years, human activity has emerged as the primary catalyst for transformation of our planet, resulting in a new geological epoch known as the Anthropocene (Lewis & Maslin 2015; Folke *et al.* 2021). This emerging epoch is already evident in the climatic and geological record of the Earth (Summerhayes & Zalasiewicz 2018) with natural consequences such as declines in the diversity and abundance of many ecosystems around the world. Species and population losses have been revealed for many well-studied groups of organisms. For example, terrestrial vertebrate population sizes have declined by a third, with many mammals experiencing declines of at least 80% over the last century (Ceballos *et al.* 2017). Also, approximately, half of all amphibians are endangered, 2.5% of which have recently been declared extinct (González-del-Piiego *et al.* 2019). Additionally, bird numbers have fallen by 2.9 billion since 1970 across North America alone (Rosenberg *et al.* 2019). In most instances, the ensuing shifts in ecosystems have been further aggravated by the impact of worldwide climate change (Barlow *et al.* 2018; Bruno *et al.* 2018; Nolan *et al.* 2018; Smith *et al.* 2023). The current scenario increasingly diverges from an optimistic one as thermal disturbances are only forecast to intensify in the near future (Urban 2015; Sévellec & Drijfhout 2018; Trisos *et al.* 2020).

Coral reefs, like most ecosystems, are being exposed to these increasingly intense disturbances (Hughes *et al.* 2018b; Bellwood *et al.* 2019a; Hoegh-Guldberg *et al.* 2019; Vercelloni *et al.* 2020). Coral reefs host one of the highest biodiversity densities of all ecosystems, also comprising some of the oldest structures of the earth built by living organisms (Carpenter *et al.* 2008; Budd & Pandolfi 2010). Like trees in a rainforest, that create the essential environment for a wide variety of interconnected wildlife, reef-forming scleractinian corals establish the fundamental living space and

shelter for an immensely diverse range of associated animals (Connell 1978). The complex structures formed by the calcium carbonate skeletons of both living and dead coral colonies provide a 3-dimensional environment that supports an estimated one million species of reef organisms, many of which remain to be described (Fisher *et al.* 2015; Brandl *et al.* 2018). Thus, in sustaining this great biological and genetic diversity, coral reefs play a fundamental role in the ecological processes and dynamics of marine ecosystems (Moberg & Folke 1999; Graham & Nash 2013; Kerry & Bellwood 2015). Furthermore, coral reefs have immense global ecological and economic value providing millions of people with essential ecosystem services. For example, food provision, carbon sequestration, tourism, structural materials, coastal protection, and a major source of new biochemicals; coral reefs are vital for human societies and industries (Souter & Lindén 2000; Chen *et al.* 2015; Woodhead *et al.* 2019; Eddy *et al.* 2021; Carlot *et al.* 2023). The world's coral reefs hold an approximate economic worth exceeding \$350 billion annually (Costanza *et al.* 1998, 2014), with the Great Barrier Reef alone supporting 64,000 jobs and contributing \$56 billion per year to Australia's economy. (O'Mahoney *et al.* 2017). All of this, however, pales in comparison to the intrinsic value of coral reefs, and their evolutionary role as a cradle, museum and testing stage for planet Earth's biodiversity. Yet, climate change is rapidly altering the functioning of tropical reef ecosystems (Bellwood *et al.* 2004; Graham *et al.* 2015; Hughes *et al.* 2017b, 2018b; Duarte *et al.* 2020; Cornwall *et al.* 2021) and placing their future at risk.

Globally, sea surface temperature (SST) increased by 0.08 °C per decade from 1950 to 2011 (Lough 2012). Furthermore, the most recent (2023) assessments by the Intergovernmental Panel on Climate Change (IPCC) suggest that there is more than a 50% probability that the increase in global temperatures will reach or exceed 1.5°C between 2021 and 2040. Under scenarios where emissions remain high, this temperature rise threshold is likely to be met even earlier. For example, in a scenario where carbon emissions continue to grow at a high rate, the rise in global temperatures by the end of the century could be between 3.3°C and 5.7°C (IPCC 2023). While certain ecosystems may be slower in showing the effects of climate change, coral reefs are already revealing the impacts of

climate change with consecutive bleaching events, indicating a tight linkage between these ecosystems and climate variability. Indeed, coral mortality from these massive ocean-wide bleaching events has been increasing in frequency and intensity in the last few decades (Eakin *et al.* 2010; Hughes *et al.* 2018a; Sully *et al.* 2019; Vercelloni *et al.* 2020). More specifically, coral reefs have already faced three global bleaching events (1998, 2010 and 2014-2017) (Skirving *et al.* 2019). Additionally, other disturbances such as acidification, overfishing, pollution, tourism, crown-of-thorns starfish (CoTS), cyclones, and coral disease outbreaks further threaten the future of coral reefs as we know them (Diedrich 2007; Hoegh-Guldberg *et al.* 2007; McLeod *et al.* 2013; Zaneveld *et al.* 2016; Pratchett *et al.* 2017; Dixon *et al.* 2022; Burke *et al.* 2023).

1.2 The effect of thermal anomaly events on coral population dynamics

It is widely reported that different types of coral vary in their susceptibility to thermally-induced bleaching (Marshall & Baird 2000; Van Woesik *et al.* 2011; Burn *et al.* 2023). For instance, branching and corymbose growth forms of corals (e.g., *Acropora*, *Pocillopora*, *Stylophora*, *Seriatopora*) tend to be more susceptible to thermal disturbance, while massive and encrusting growth forms, (e.g., massive *Porites* and *Dipsastraea*) tend to be more resistant (Loya *et al.* 2001; Harrison *et al.* 2019; McClanahan *et al.* 2020; Pratchett *et al.* 2020; Burn *et al.* 2023). However, growth form alone is not enough to explain this disparity in coral susceptibility. Corals that rely exclusively on symbionts to source their energy are more likely to die in bleaching events, while corals that also feed on plankton when they lose their symbionts (i.e., that are more heterotrophic) have more chance of survival (Grottoli *et al.* 2006). Likewise, corals with thinner tissues can run out of nutrients more quickly during or after bleaching events (Loya *et al.* 2001). On coral reefs in the Maldives, for example, high bleaching mortality during 2016 and 2017 among acroporids created reefs dominated by pocilloporids and poritids (Pisapia *et al.* 2019). This was a fundamental change in the dynamics of coral populations that involved the decline in abundance and size of susceptible

coral species and the increase of more resistant coral groups (Riegl & Purkis 2015; Pisapia *et al.* 2020). Thus, investigating the differences in susceptibility, mortality and recovery from thermal disturbances is essential to completely understanding how coral assemblages will shift in the face of climate change (Alvarez-Filip *et al.* 2011; Kayal *et al.* 2018; McWilliam *et al.* 2018; Burn *et al.* 2023).

Shift in population structure may also change the functions provided by corals to reef-associated communities (Graham & Nash 2013; Coker *et al.* 2014). Indeed, the physical structure of habitats plays an important role in the maintenance of associated biodiversity and ecosystem functioning (MacArthur & MacArthur 1961). Structural complexity's vital role in ecosystem functioning is evident across diverse habitats; from terrestrial (Tews *et al.* 2004), to freshwater (Kalacska *et al.* 2018), to marine ecosystems (Graham & Nash 2013). On coral reefs, scleractinian corals are the most important reef framework builders, having thus a disproportional importance in sustaining ecological processes and services (Spalding *et al.* 2001). In addition to their importance for the diversity and abundance of reef-associated communities (Graham & Nash 2013; Coker *et al.* 2014), coral reefs may also provide an indispensable service as the first line of coastal protection from inundation (Elliff & Silva 2017; Reguero *et al.* 2018; Carlot *et al.* 2023). This flood protection service may benefit millions of people living in coastal cities and has been valued at around US\$1.8 billion just for the USA. (Storlazzi *et al.* 2019) and US\$9 billion per year worldwide (Cesar *et al.* 2003). Indeed, both ecological and physical protection services have been linked with coral growth that supports positive carbonate budgets and maintains the reef structures. However, this growth may be threatened (Perry *et al.* 2018; Cornwall *et al.* 2021). Thermal disturbances can result in both coral mortality and growth in survivors, potentially weakening the structural integrity of dead colonies (Leggat *et al.* 2019). The damaged structures of some growth forms may be prone to rapid erosion, which may lead to a deficit in the carbonate budget. It has been suggested that this degradation poses a serious threat to the ecosystem services supplied by the reef, including biodiversity support, coastal protection, and carbon storage, ultimately jeopardizing the reef's resilience (Cornwall *et al.* 2021; Carlot *et al.* 2023; Hughes *et al.*, 2017). Thus, there is a critical need for a thorough

understanding of the dynamics of coral populations as they confront the challenges posed by a changing climate.

1.3 Coral cover and the demographic approach

With the ongoing escalation of reef disturbance regimes, investigating and managing these phenomena across extensive spatial, temporal, and taxonomic scales is a challenge. Notably, ecological data remain largely deficient. The methodology most commonly used in studies to assess the impact of this disturbance, especially after bleaching events, is typically based on measurements of the overall percentage benthic cover of hard corals. There is a long and successful record of using live coral cover to measure the condition of coral communities (Hughes 1994; Connell *et al.* 1997; Bruno *et al.* 2007). “Coral cover”, defined as the percentage of live tissue cover of corals (e.g., total cover or cover from specific groups of corals) from a planar perspective, has been for many decades the most widely used metric to quantify coral reef health (Gardner *et al.* 2003; Bellwood *et al.* 2004; De’ath *et al.* 2012; Hughes *et al.* 2018b). Declines in coral cover are considered negative outcomes for reef health, while increases in coral cover are considered positive (De’ath *et al.* 2012; Hughes *et al.* 2018b).

Coral cover is an intuitive and inherently simple metric, which can be estimated in a variety of ways. It can, for instance, be approximated from the ratio between the number of intersecting points over coral colonies and the total number of systematically allocated points in point-count surveys along transects (English *et al.* 1997). It can also be measured using software to distribute random points over planar photographic images of coral reefs (Kohler & Gill 2006), or even in 3D models (Storlazzi *et al.* 2016). However, despite its continued and sometimes almost unrestricted use in coral reef research (De’ath *et al.* 2012), coral cover has several significant limitations. These

are evident when assessing critical properties of coral populations, particularly from a demographic perspective (Edmunds & Riegl 2020; Cant *et al.* 2022). Firstly, coral cover alone does not show how live tissue area is distributed among colonies (*i.e.*, many small or few large colonies?). Secondly, it does not inform the processes driving observed changes in coral cover through time, particularly recruitment, persistence, and mortality. Finally, it does not allow projections of how coral cover will change in the future (Connell 1973; Hughes & Jackson 1985; Edmunds *et al.* 2014). For instance, coral reproduction and recruitment were historically understudied due to the open nature of coral populations and the challenges of tracking larval dispersal (Caley *et al.* 1996). However, there is now increasing focus on this aspect as concerns arise about the capacity of natural coral recovery after severe thermal disturbances (Graham *et al.* 2011; Kayal *et al.* 2018; Dietzel *et al.* 2020; Edmunds 2023). Thus, there have been numerous pledges to move towards other, more informative approaches (Loya 1978; Pichon 1978; Hughes & Tanner 2000; Pisapia *et al.* 2020; Cant *et al.* 2022).

These limitations can be addressed by using a demographic approach (Dietzel *et al.* 2020; Edmunds & Riegl 2020; Cant *et al.* 2022). Demographic data are collected by measuring the size and tracking the fate of individual colonies, allowing the investigation of changes in colony size, partial or total mortality, and recruitment (*i.e.*, the appearance of new colonies) throughout space and time (Bak & Meesters 1998). To quantify the effects of thermal disturbance in coral populations with enhanced precision, measurements of the same colony (*i.e.*, size, survival/mortality outcome), as well as population recruitment, are critical. Furthermore, because it provides relevant systematic information, the demographic approach allows projections of likely (or plausible) future dynamics of corals (Caswell 2001; Kayal *et al.* 2018; Pisapia *et al.* 2020; Pratchett *et al.* 2020). In this sense, Edmunds and Riegl (2020) highlighted the importance of adjusting existing and new coral reef monitoring efforts to address demographic bottlenecks on coral reefs. To do this, they suggested some tasks that would facilitate these adjustments. First, increasing the frequency of sampling of the same areas of the reef (*i.e.*, time-series, surveying the same populations and coral colonies over multiple years). Second, increasing effort to collect data at the species level. Third, avoiding line

intercepting methods, and favouring image-based techniques to record coral communities. Image-based techniques allow, for example, the opportunity for retrospective analyses, including coral colony sizes and related, derived demographic properties. Only a flexible collection of demographic data in addition to coral cover will allow predictions that will be critical for research on changing reefs (Edmunds *et al.* 2014; Edmunds 2015).

1.4 Thesis aims and outline

Demographic data are crucial for understanding the varied responses of different coral groups in a changing climate, as well as assessing the impacts on ecosystem functions during disturbances and the subsequent recovery processes after coral mortality. Clearly, with the increased frequency of thermal stress events threatening the survival of corals and the functions and services they provide, there is an urgent need to enhance our understanding of coral dynamics and their functional roles. This task will require comprehensive demographic data. To fill these important knowledge gaps, the primary aim of this thesis is to understand how bleaching events affect the population dynamics and functions provided by corals. This overarching aim was addressed in four separate data chapters.

Firstly, in **Chapter 2** I explored the population dynamics of two of the most common coral groups, *Acropora* and massive *Porites*. Specifically, I tracked the fate of individual coral colonies over 5 years to investigate their responses to a severe bleaching event, including susceptibility to bleaching, mortality and recruitment during and after bleaching events. Building upon the findings of **Chapter 2**, in **Chapter 3** I investigated the spatial dynamics of coral bleaching across Lizard Island. Specifically, I explored the spatial patterns of bleaching prevalence and the potential influence of small-scale hydrodynamic exposure levels and colony size on bleaching in massive *Porites* colonies.

Extending the thesis beyond bleaching, in **Chapter 4**, I wanted to understand what happens to coral colonies after mortality. I, therefore, tracked the fate of dead coral colonies to measure erosion rates, estimating how long a colony's physical structure remains. Additionally, I explored variables that may influence the ecological process of erosion in dead coral colonies, including parrotfish-driven bioerosion, wave exposure level, and coral colony growth form. Finally, in **Chapter 5**, the thesis turns its attention to the natural recovery potential of coral populations post-disturbance. By examining the patterns of coral recruitment, growth, and survival rates, this chapter seeks to quantify and characterize the recovery trajectories of corals, contributing to a deeper understanding of resilience mechanisms in reef ecosystems. Furthermore, this chapter aims to explore how lessons learned from natural recovery processes can help to inform restoration projects and management strategies.

Chapter 2. Dangerous demographics in post-bleach corals reveal boom-bust versus protracted declines

Chapter 2.

Dangerous demographics in post-bleach corals reveal boom-bust versus protracted declines

This chapter is published as:

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2.1 Abstract

Thermal-stress events have changed the structure, biodiversity, and functioning of coral reefs. But how these disturbances affect the dynamics of individual coral colonies remains unclear. By tracking the fate of 1069 individual *Acropora* and massive *Porites* coral colonies for up to 5 years, spanning three bleaching events, we reveal striking genus-level differences in their demographic response to bleaching (mortality, growth, and recruitment). Although *Acropora* colonies were locally extirpated, substantial local recruitment and fast growth revealed a marked capacity for apparent recovery. By contrast, almost all massive *Porites* colonies survived and the majority grew in area; yet no new colonies were detected over the 5 years. Our results highlight contrasting dynamics of boom-and-bust vs. protracted declines in two major coral groups. These dangerous demographics emphasise the need for caution when documenting the susceptibility and perceived resistance or recovery of corals to disturbances.

2.2 Introduction

Climate change is rapidly transforming global ecosystems (Hughes *et al.* 2017b; Duarte *et al.* 2020). On coral reefs, bleaching-induced coral mortality has led to abrupt changes in their structure, biodiversity, productivity and functioning (Graham *et al.* 2015; Darling *et al.* 2017; Hughes *et al.* 2018b; McWilliam *et al.* 2018; Cornwall *et al.* 2021). However, the majority of studies examining coral population dynamics have been based on coral cover or colony counts (Gardner *et al.* 2003; De'ath *et al.* 2012; Hughes *et al.* 2017b, 2018b; Madin *et al.* 2018; Dietzel *et al.* 2020). Only rarely is the fate of individual colonies considered over multiple years, especially during the critical post-bleaching 'recovery' period (Claar & Baum 2019; Claar *et al.* 2020; Edmunds 2021b; Hall *et al.* 2021). Long term evaluations of colony level changes enable the separation of immediate vs. delayed and partial vs. total colony mortality (Madin *et al.* 2014; Edmunds & Riegl 2020). Furthermore, if considered across multiple bleaching events, colony-tracking may reveal cumulative impacts and allow the identification of genus and colony-level variation in the response to bleaching impacts.

Using an extensive spatial design of fixed photo-quadrat locations (**Fig. 2.1**), we tracked the fate of 1069 coral colonies (in 362 quadrats spread across 16 km² on the Lizard Island reef complex) over 5 years (2016-2021), encompassing three mass bleaching events on the Great Barrier Reef (GBR). Lizard Island was at the epicenter of the first of these bleaching events on the GBR, and represents a critical arena in which to explore long-term responses of corals to bleaching (Hughes *et al.* 2017b, 2019b). We focus on colonies within two dominant coral genera, with contrasting life-histories and differences in bleaching susceptibility: massive *Porites*, which are slow-growing (Hughes *et al.* 2015) and resistant to bleaching (Cantin & Lough 2014), and *Acropora* (all growth forms), which are fast growing but susceptible to bleaching (Victor *et al.* 2009; Linares *et al.* 2011; Hughes *et al.* 2015). Our goal was to evaluate the extent, magnitude and variability of colony-level

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susceptibility to successive bleaching events, as well as the potential demographic consequences and their implications for recovery.

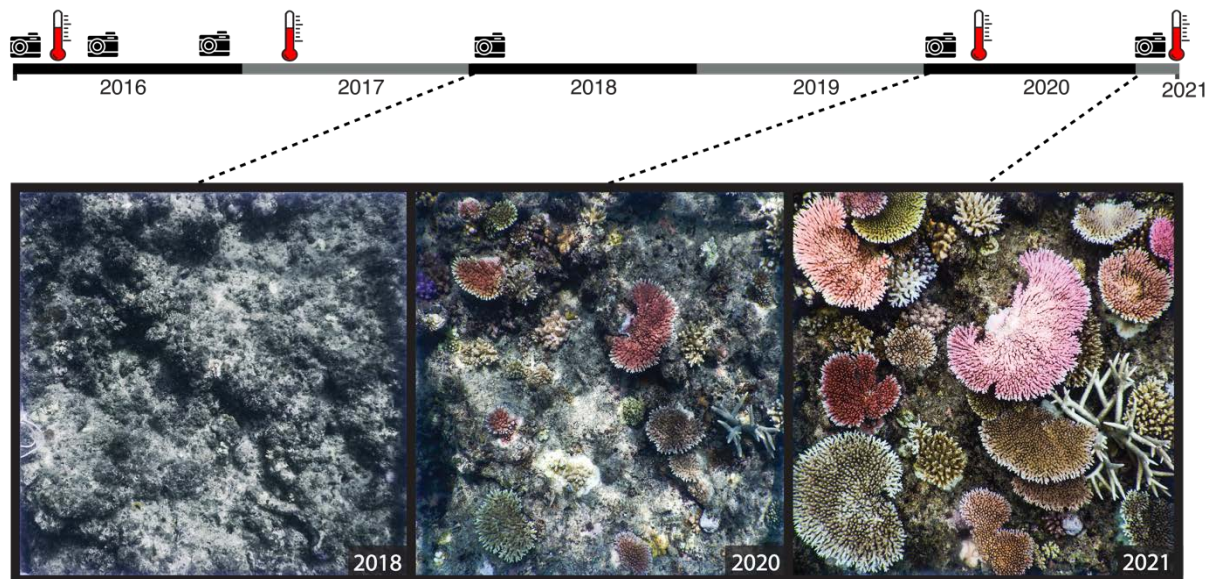


Figure 2.1 | Timeline of the study. Data collection instances (camera icons) and bleaching events (temperature gauges) with examples of quadrats (1 m²) of the same reef section across repeated sampling periods showing the growth of new *Acropora* colonies. January 2018, 24 months after first sampling, January 2020, 48 months after first sampling, and February 2021, 60 months after first sampling. All photographs taken at Lizard Island by SB Tebbett.

2.3 Methods

2.3.1 Study area and Sampling

Tracking of individual colonies was based on a comprehensive photo-quadrat census at Lizard Island, (14°40' S, 145°28'E) in the northern region of the Great Barrier Reef (GBR), described in Wismer et al., (2019a, 2019b). This region experienced two prolonged thermal events between February and April 2016, as well as between January and March 2017, leading to extensive coral bleaching (Hughes *et al.* 2017b; Madin *et al.* 2018). During the first sampling period, a total of 19

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permanent transects (between 50 – 210 m in length, as constrained by reef morphology) along the reef 'crest' (at 0-4 m below chart-datum) were established around Lizard Island (Supplementary Fig 2). Along each transect, between 12 and 38 quadrats (1 m² area), approximately 5 m apart, were sampled. These transects were revisited five times: in April 2016 (2-3 months after first sampling); October 2016 (9 months after first sampling); January 2018 (after 24 months); January 2020 (after 48 months) and January/February 2021 (after 60 months).

Using SCUBA, each quadrat was photographed in each of the six sampling periods (Camera: Nikon Coolpix AW130) from a planar 'bird's-eye' view between 09:00 and 16:00 h. To survey each transect on subsequent trips, the starting location was identified based on a GPS mark taken on the first sampling trip. Since the quadrats were not marked permanently (to minimize the impact on the site), the same quadrat area had to be accurately relocated on each sampling trip using a secondary underwater camera. This camera held all prior images of each quadrat in chronological order, serving as a guide to find the exact same reef section and enabling the tracking of individual coral colonies over time (see Wismer et al., 2019a for a sensitivity analysis of this method). A total of 362 photo-quadrats were sampled across the entire study. Around each quadrat there was also a buffer area (**Fig. 2.1**) where individual colonies could also be located and followed. We therefore tracked and quantified the fate of individual colonies within the quadrats and in the 10 cm wide buffer area around each quadrat. This resulted in a censused area of 1.44 m² per quadrat, and a total censused area of 521.2 m². All colonies from the two studied groups (*Acropora* spp. and massive *Porites* spp.) within the photo-quadrats and within the buffering area were recorded, identified (to species level whenever possible) and had their live tissue area determined from the photographs (please see Supplementary Figure 2.3). Live tissue area of each colony was determined by tracing around the visible live coral tissue to obtain the planar area in cm² relative to the quadrat area (10,000 cm²). Coral cover was calculated as the sum of the areas of individual coral colonies within the 1 m² quadrat and the surrounding buffer area. To offer a comprehensive metric of the island's general

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coral cover, all quadrats were included in this calculation, even those without any coral colonies. All images were processed using the software ImageJ (Abràmoff *et al.* 2004).

2.3.2 Data analysis

We considered ‘growth’ to be the difference in live tissue area of each colony between the first and subsequent sampling periods. For *Acropora* colonies, growth was calculated from recruitment onwards (for colonies that recruited in 2018 or 2020), and was expressed as increase in live tissue area per year. Because there were no recruits detected for *Porites*, all colonies were present at the start of the study. Thus, growth for massive *Porites* colonies represents growth over 5 years. To facilitate comparisons among colonies, we standardized live tissue area using the area from the first sampling period as the reference. The same method was used when we detected ‘recruit’ colonies (i.e., new colonies of a visible size in the quadrat) in the subsequent samples.

For massive *Porites* colonies that bleached, we also measured the proportion of bleached planar area on each colony during the 2016 bleaching event. We tested for the hypothesis that bleaching severity had an effect on the change in live tissue area (loss or gain) for massive *Porites* colonies following this event. ‘Bleaching severity’ was defined as the highest proportion of tissue area observed to bleach for each coral colony across all trips in which bleaching occurred. To test this hypothesis, we used a generalized linear mixed effects model (GLMM) with tissue area change as the response variable and ‘bleaching severity’ as the predictor. We also included quadrat, nested in transect, as random intercepts in the model to account for repeated sampling and any lack of spatial independence in the data. We used a Gamma error distribution with a log link function. Because the data was slightly right skewed, we used model selection to find the best error distribution to fit the model. We compared models fitted using the Gaussian distribution, the lognormal distribution (i.e.,

a Gaussian distribution with a log link), and the gamma distribution (also with a log link), using Akaike's Information Criterion. Model selection showed that the gamma distribution model was the one that best balanced fit and parsimony, and therefore was the one chosen. Model fit and assumptions were assessed using residual plots, all of which were satisfactory. Statistical modelling was performed in the software R (Team 2020), using the glmmTMB package (Brooks *et al.* 2017).

2.4 Results and discussion

There were dramatic differences in the response to successive bleaching between the two coral types investigated (**Fig. 2.2**). *Acropora* colonies underwent complete local extirpation (i.e., 100% loss across all quadrats) in the 2 years following the first bleaching episode. Remarkably, however, there was also massive recruitment (i.e., the appearance of previously undetected colonies greater than 3 cm²) of *Acropora* starting 2 years after the first bleaching, resulting in a 1000% increase in the number of colonies relative to the start of the study (**Fig. 2.2b**). New colonies showed rapid growth, with an average 201% increase in colony size per year by the end of the study period (**Fig. 2.3**). Despite a 10-fold increase in numbers and rapid growth, mean *Acropora* cover only increased from approximately 1% to 3%. Thus, it still remained low (<3%) compared to historical levels of *Acropora* cover (from ~15-30% between 1995 and 2014 (Madin *et al.* 2018), likely reflecting an early 'recovery' trajectory (**Fig. 2.2a**).

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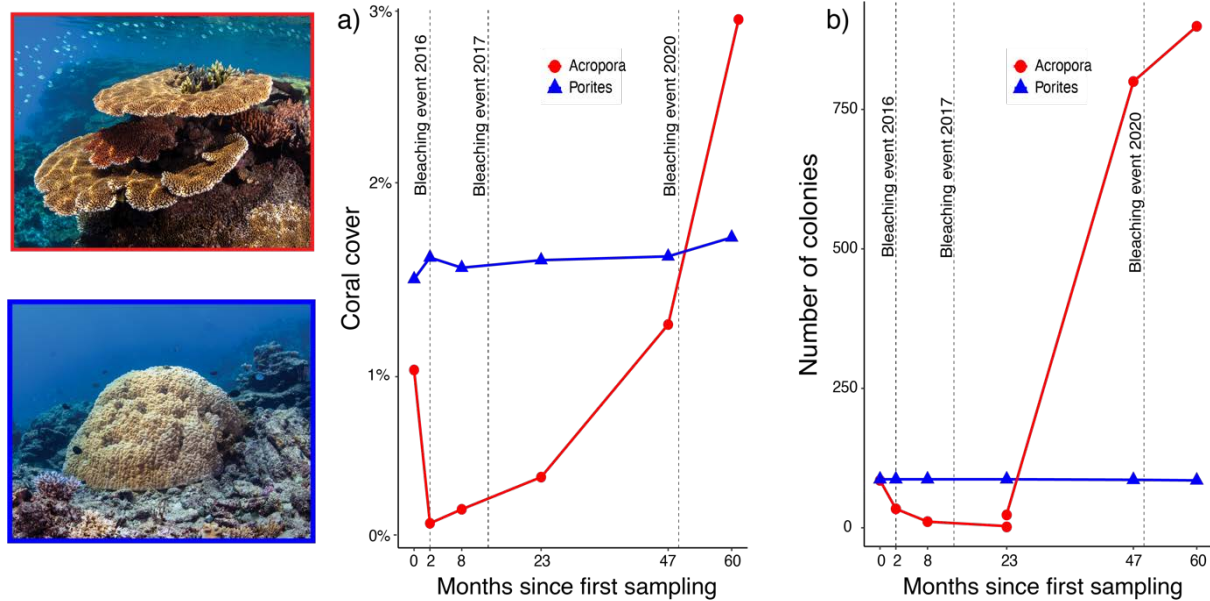


Figure 2.2 | Cover and total number of colonies of *Acropora* and Massive *Porites*. a) Coral cover of *Acropora* and massive *Porites* based on 362 quadrats over the 60 month time period. b) Total number of *Acropora* and massive *Porites* coral colonies tracked over the 60 month time period spanning three bleaching events at Lizard Island, northern Great Barrier Reef. Photographs: Victor Huertas.

By contrast, the number of massive *Porites* colonies remained stable: there was only a 2.3% loss of colonies (2 colonies). But no new colonies were detected over the 5 years (Fig. 2.2). Surviving colonies showed an average increase in colony area of 21%, however, there was extensive among-colony variation in live tissue area changes (Fig. 2.3). Indeed, approximately half of the colonies suffered tissue loss. The extent of tissue loss was relatively well predicted by bleaching severity at the individual level (i.e., relative area of bleached tissue in the April 2016 bleaching event, Fig. 2.4). Thus, *Acropora* corals appear to be responding with a pronounced boom-and-bust pattern (Wilson *et al.* 2019; Pratchett *et al.* 2020), while massive *Porites* colonies exhibit a precarious degree of resilience, increasing in area but with an underlying recruitment deficit and a strong negative response in tissue area to bleaching severity (Fig 2.4b).

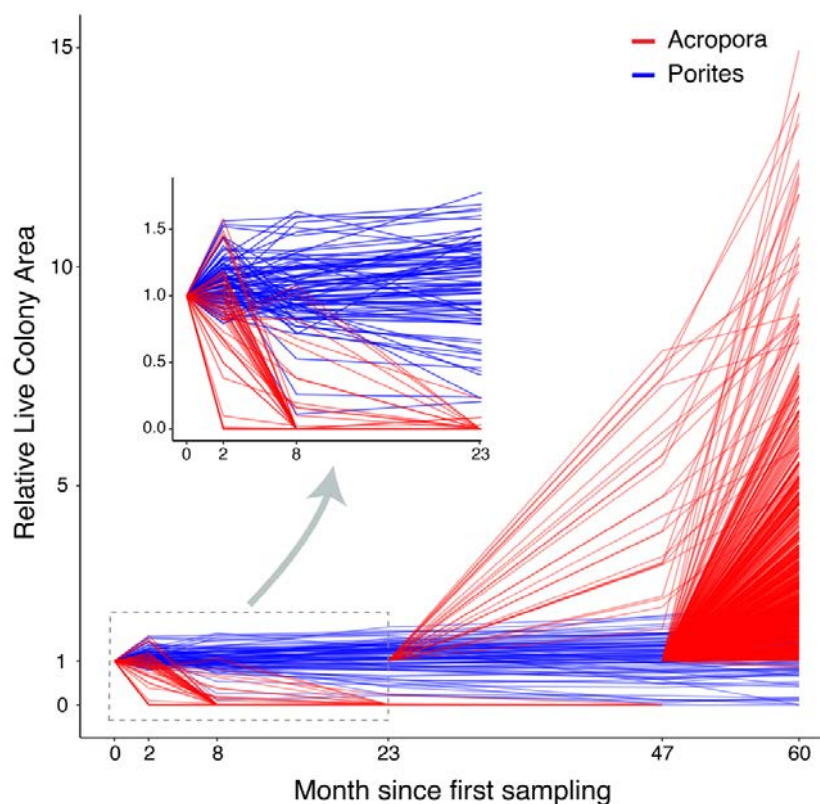


Figure 2.3 | Relative live colony area of *Acropora* and massive *Porites* colonies over 60 months (each line represents an individual colony). Relative live colony area is the horizontal planar area of living tissue on a colony relative to the value at first detection. The small inner graph represents a zoom showing the standardized live area of *Acropora* and massive *Porites* colonies during the first 24 months since first sampling.

Our findings agree with previous studies that show a high-susceptibility to thermal stress in *Acropora* (Loya *et al.* 2001; Van Woesik *et al.* 2011; McWilliam *et al.* 2020) and a degree of resistance to thermal stress in *Porites* (Marshall & Baird 2000; Loya *et al.* 2001). These contrasting responses to disturbances play an important role in structuring coral communities and are now more apparent than ever given the frequency and severity of disturbances impacting coral reefs (Graham *et al.* 2014; Pratchett *et al.* 2020). While the devastating effects of climate change on corals have been emphasized numerous times (Van Woesik *et al.* 2011; Hughes *et al.* 2017b, 2018b; Madin *et al.* 2018; Sully *et al.* 2019), the fate of individual coral colonies has rarely been tracked over multiple

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bleaching events over multiple years, particularly in conjunction with key demographics traits such as recruitment and growth. Quantifying these dynamics is critical to understand future trajectories of coral populations subject to changing disturbance regimes, especially in a scenario of shortening 'recovery' windows (Gilmour *et al.* 2013; Hughes *et al.* 2019a; Vercelloni *et al.* 2020).

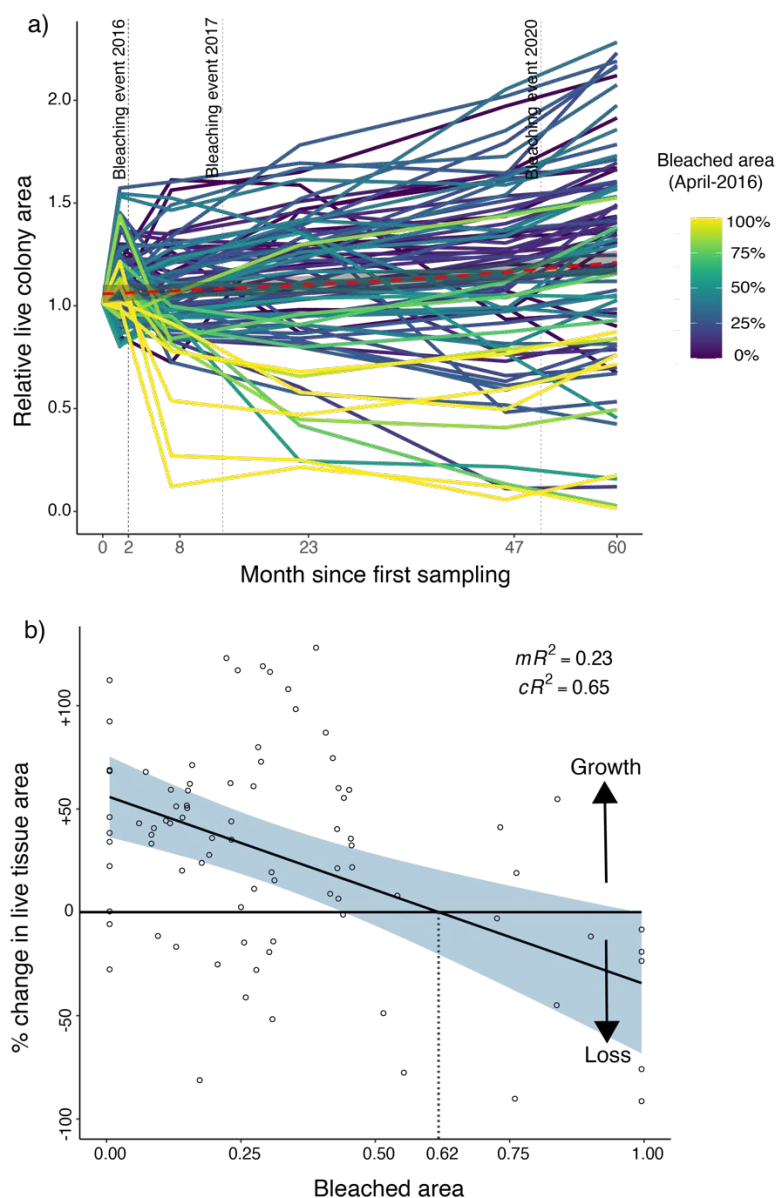


Figure 2.4 | a) Relative area of live tissue on massive *Porites* colonies over 60 months. Each line represents a single colony, with line colors representing the proportion of bleaching in each colony (during the 2016 bleaching event). The red dotted line represents the average increase of 21% in colony area of massive *Porites*. b) Effect of the proportional bleached area (in April-2016) on the subsequent relative change in live tissue area

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of massive Porites. Line and band show the prediction and 95% confidence intervals of a Gamma GLMM, while dots show raw data points. Modelling was performed in the software R (Team 2020), using the glmmTMB package (Brooks et al. 2017). The solid horizontal line and arrows indicate where colonies effectively increased or decreased live tissue area. The dotted vertical line represents the minimum bleached area required, on average, to trigger tissue loss. mR2 = marginal R2 and cR2 = conditional R2.

Acropora colony density at the start of the study was relatively low (85 trackable colonies, > 3cm, across 362 quadrats (521.2 m²) in 2016). This was primarily due to two back-to-back cyclones in 2014 and 2015 (Madin *et al.* 2018). Following these disturbances, the severe bleaching events in 2016 and 2017 led to complete loss of *Acropora* in our censused area. After this widespread mortality period, we documented a >10-fold increase in colony numbers between 2018 and 2021 (relative to the first sampling period), with 897 new colonies by 2021 (1.72 new colonies m⁻²). These seemingly high levels of population replenishment were observed despite large (89%) declines in coral settlement across GBR, especially in *Acropora*, following the bleaching events in 2016 and 2017 (Hughes *et al.* 2019a). It was anticipated that the GBR-wide decline in settlement would have severely compromised the recovery capacity of these corals, as it was estimated that recovery would take at least a decade, even for faster-growing corals such as *Acropora* (Hughes *et al.* 2019a). Although coral replenishment can be highly variable across spatial scales (Hughes *et al.* 2019a; Evans *et al.* 2020), the rate of appearance of new colonies in our study, especially following such a sharp decline in coral numbers, offers some hope for the future of coral reefs.

Not only did new colonies of *Acropora* recruit in substantial numbers, but they also rapidly increased in size. Colonies initially detected in January 2018 had grown, on average, by 393% over 24 months. Peak detection of new colonies occurred in January 2020, and new colonies detected in 2020 and 2018 grew, on average, 211% between January 2020 and January 2021 (**Fig. 2.3**). Such fast growth is likely to underpin the perceived 'potential recovery' of *Acropora*, even as these 'recovery' windows between disturbances become shorter and shorter (Hughes *et al.* 2019a). However, the

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realized long-term recovery of reef systems will depend on the capacity of these corals to persist in a scenario of increased frequency of extreme thermal events over the coming years (Pratchett *et al.* 2020; Carlot *et al.* 2021). The growth we observed resulted in a mean *Acropora* cover of just 3%, far below pre-bleach levels of coral cover. It may represent, therefore, just a short-term boom in a new Anthropocene configuration, where fast-growing corals persist but are unlikely to attain their former abundance due to successive disturbances and suppression of recovery dynamics (Hughes *et al.* 2018b; Bellwood *et al.* 2019a; Pratchett *et al.* 2020). Nevertheless, the responses we observed over five years highlight the remarkable potential for ‘boom and bust’ dynamics in *Acropora*, providing evidence that degraded coral reefs may still maintain some potential for apparent *Acropora* recovery, at least for a limited time and at the colony level.

However, our findings also highlight the need for caution. Although massive *Porites* shows ecosystem-level resistance to bleaching, responses of individual colonies are highly variable (Loya *et al.* 2001; Pratchett *et al.* 2020). Indeed, individual bleaching susceptibility (indicated by the maximum proportion of colony area observed to bleach) was able to predict long-term (60 month) individual massive *Porites* colony tissue loss (**Fig. 2.4a**). Colonies that bleached more intensely also suffered heavier tissue loss, while those that bleached less intensely often grew in tissue area (Fig. 4b). Nevertheless, even when massive *Porites* colonies suffered intermediate to high bleaching (in proportion to live colony area), their likelihood of recovery was much higher than *Acropora* colonies as noted previously (Loya *et al.* 2001). Most importantly, however, despite censusing 521.2m² of reef in extreme detail over 5 years, we did not record a single new massive *Porites* colony. This lack of apparent recruitment over half a decade suggests that massive *Porites* could be rare, a pattern supported by the examination of coral recruitment on tiles across large spatial scales post-bleaching (Hughes *et al.* 2019). However, the apparent rarity of *Porites* recruits could also be magnified by the difficulty of detecting *Porites* recruits in photos. Indeed, due to a combination of cryptic colouration, small size and slow growth, *Porites* recruits are likely to be harder to detect than *Acropora* recruits in photographs, potentially leading to an underestimation of relative recruitment in *Porites*. (Baird *et al.*

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2012; Hughes *et al.* 2019a). Nevertheless, the scarcity of massive *Porites* recruitment throughout our study highlights the potential for protracted declines and storage effects (Edmunds 2000; Foster *et al.* 2007). Such protracted declines may be even more concerning than sudden dynamic shifts, as in *Acropora* abundance, as they may be easier to overlook or ignore, and harder to reverse (Hughes *et al.* 2013).

Thus, our data has revealed how the colony-level population dynamics of two archetypical coral types, massive *Porites* and *Acropora*, have responded in distinctly different manners over multiple disturbances events caused by thermal stress and a short-term 'recovery' window. For weedy, fast-growing *Acropora* colonies, high susceptibility to bleaching and complete mortality was followed by substantial recruitment and fast growth, revealing a marked capacity for apparent 'recovery'. However, the lifespan of these new colonies is already being tested as a fourth bleaching event began to unfold in January/February 2021, with marked paling of these new *Acropora* colonies (Supplementary Figure 2.1). We also demonstrated the well-documented resistance of stress-tolerant colonies of massive *Porites*, with net positive growth over five years. However, the complete lack of new colonies over this same time frame (despite intensive sampling) suggests that recruitment is rare and, potentially, unpredictable. Without replacement, increasing repetitive bleaching events (Hughes *et al.* 2018a; Sully *et al.* 2019), may drive a slow, protracted decline of massive *Porites* that could be easily overlooked. These markedly different demographic patterns offer grounds for both optimism and concern. Massive *Porites* are resistant, but potentially compromised in the long-term, while *Acropora* are vulnerable, but have greater capacity to recover in the aftermath of major disturbances (Gilmour *et al.* 2013; Pratchett *et al.* 2020). In both cases their dangerous demographics require caution when interpreting the susceptibility and perceived resistance of corals to disturbances.

Chapter 3.

Hot spots of bleaching in massive *Porites* coral colonies

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3.1 Abstract

Coral bleaching events have become more frequent and severe due to ocean warming. While the large-scale impacts of bleaching events are well-known, there is growing recognition of the importance of small-scale spatial variation in bleaching and survival probability of individual coral colonies. By quantifying bleaching in 108 massive *Porites* colonies spread across Lizard Island, Great Barrier Reef, during the 2016 bleaching event, we investigated how hydrodynamic exposure levels and colony size contribute to local variability in bleaching prevalence and extent. Our results revealed that exposed locations were the least impacted by bleaching, while lagoonal areas exhibited the highest prevalence of bleaching and colony-level bleaching extents. Such patterns of bleaching could be due to prolonged exposure to warm water in the lagoon. These findings highlight the importance of considering location-specific factors when assessing coral health and emphasize the vulnerability of corals in lagoonal habitats to rapid and/or prolonged elevated temperatures.

3.2 Introduction

Severe marine heatwaves have intensified coral bleaching events in recent years, leading to high coral mortality rates (Lough *et al.* 2018; Sully *et al.* 2019). While there is some evidence of localized natural recovery after these disturbances (Holbrook *et al.* 2018; Morais *et al.* 2023), a shortening in the recovery window has led to ongoing regional-scale impacts on coral populations (Vercelloni *et al.* 2020; Hughes *et al.* 2021). Large spatial scale (hundreds to thousands of square kilometres) bleaching impacts on coral reefs are now well documented (e.g. Sully *et al.* 2019; Dietzel *et al.* 2021b). However, the effects of bleaching events can also vary at small spatial scales, spanning from just tens to hundreds of meters (Green *et al.* 2019; Grimaldi *et al.* 2023). For individual coral colonies, small-scale spatial variation in exposure to heatwaves may mean the difference between life and death.

At small spatial scales there are various factors that may shape the extent of coral bleaching. For example, variation in reef morphology can interact with water flow, causing some reef areas to heat more than others (Lenihan *et al.* 2008; Green *et al.* 2019; Grimaldi *et al.* 2023). These hydrodynamic process can either exacerbate (DeCarlo *et al.* 2017) or mitigate (Schmidt *et al.* 2016) thermal stress from heatwaves. Furthermore, there is evidence to suggest that colony size has an impact on the susceptibility of corals to bleaching (Hughes and Jackson 1985; Shenkar *et al.* 2005; Wagner *et al.* 2010; Pratchett *et al.* 2013). Finally, the specific coral taxa present at a location may also influence bleaching rates as some corals, such as massive *Porites*, are known to be relatively bleaching resistant (Harrison *et al.* 2019; Pratchett *et al.* 2020; Morais *et al.* 2021), while others, such as *Acropora*, tend to be highly susceptible to bleaching (Van Woesik *et al.* 2012b; Burn *et al.* 2023). Given the high mortality rates of susceptible corals (Loya *et al.* 2001; Pisapia *et al.* 2019), it has been suggested that in some circumstances corals that are more thermally tolerant, such as massive *Porites*, may become the dominant coral taxa (Pisapia *et al.* 2019; McClanahan *et al.* 2020; Pratchett

et al. 2020). Although there is a significant body of literature on massive *Porites* bleaching responses across small-spatial scales (<5 km) using artificial bleaching methods (e.g. Barshis et al. 2018; Klepac and Barshis 2020, 2022), our understanding of how this response varies in populations at small scales, across different hydrodynamic exposure levels during natural bleaching events remains limited.

As massive *Porites* may be a key group of corals on some Anthropocene reefs, understanding how bleaching impacts in this genus varies across small spatial scales could be important in helping predict the impacts of heatwaves in the future. To examine this variation, we measured bleaching prevalence (% colonies) and individual extent (% colony area) in 108 massive *Porites* coral colonies during a severe bleaching event in 2016 on Australia's, Great Barrier Reef (GBR). Subsequently, we investigate how hydrodynamic exposure levels and colony size may help explain observed variability in bleaching in *Porites* colonies spread across Lizard Island's 16 km² coral reef system.

3.3 Methods

3.3.1 Study area and sampling

Data were collected at Lizard Island (14°40' S, 145°28'E), a mid-shelf island group in the northern region of the GBR. Between February and April 2016, an intense marine heatwave resulted in a severe coral bleaching event in this northern region of the GBR (Hughes *et al.* 2021). Within this timeframe, the average water temperature at a depth of 0.6 m consistently surpassed 30°C (see Supplementary Figure 3.3). In April/May 2016, during this bleaching event, and after ~8 Degree Heating Weeks (DHW) (Bainbridge 2017), a series of 19 permanent transects (distances between

individual transects ranged from 0.15 to 4.7 km) were surveyed along the reef 'crest' (0–4 m below chart-datum, details in Wismer et al. 2019; Tebbett et al. 2022) (Supplementary Figure 3.2a). Each transect comprised 12 - 38 quadrats (1 m² area). Within transects, each quadrat was placed approximately 5 meters apart (with the number of quadrats dependent on reef extent) and photographed (Camera: Nikon Coolpix AW130) from a planar view. All photographs used in the analysis in this study were taken between April 27th and May 5th 2016, which ensures that timing of individual surveys had a minimal effect on bleaching data.

3.3.2 Image processing

From the photographs, we selected all quadrats that included at least one massive *Porites* colony and recorded the number of *Porites* colonies and their bleaching status (i.e. bleached or not bleached). Note that five transects with no quadrats containing at least 1 massive *Porites* colony were excluded from our analysis. To determine the live tissue area, each colony was measured by tracing around visible live coral tissue to obtain the planar area of live tissue in cm² (this planar area was considered as the 'colony size'). When a colony was bleached (ranging in colour from paled, i.e. light bleaching, to white, i.e. severe bleaching; all categorized as bleached herein), we also traced around the visibly bleached area, as above. Subsequently, the relative extent of coral bleaching on each colony was calculated based on the planar bleached area as a percentage of the total planar live tissue area. It should be noted that, due to the constraints of our photographic methods, our analysis was limited to the planar area of each colony, which represents a two-dimensional, top-down view of the coral colony surface. Bleaching does not occur uniformly across a coral colony. Typically, areas not exposed to direct sunlight exhibit less bleaching compared to the colony's uppermost parts that receive more sunlight. Therefore, to keep estimates consistent, all photographs were taken from the same perspective, ensuring that we compared equivalent portions

of each colony (the planar area). All images were processed using the ImageJ software (Schneider *et al.* 2012) with the 1 m² quadrat serving as a scale.

3.3.3 Statistical analyses

To compare the bleaching prevalence, i.e. the proportion of massive *Porites* colonies that bleached in each exposure level, we used a Bayesian generalized linear mixed effects model with a binomial distribution and logit link. Bleaching status (0 = not bleached, 1 = bleached), was used as the response variable and exposure level (exposed, front lagoon, back lagoon, and back reef), as well as colony size, were treated as interacting fixed effects. The exposure categories were determined based on the transect locations' orientation relative to the prevailing south-east trade winds following (Morais *et al.* 2022). To investigate the extent of bleaching (% of colony area bleached; the response variable) in bleached massive *Porites* colonies (only colonies with measurable bleaching extent were used in this model [n = 84]), we used a Bayesian generalized linear mixed effects model with a gamma distribution and log link. Again, exposure level and colony size were treated as interacting fixed effects. In both models, transect identity was also included as a random effect to account for any lack of spatial independence in the sampling design. Each model was based on 3 MCMC chains with 5000 iterations, including 1000 iterations to warm-up and a thinning interval of 3, with weakly informative priors. Model fits and assumptions were assessed using residual and autocorrelation plots, supplemented by metrics of effective sample size (neff) and sampling efficiency (rhat) scores, all of which were satisfactory and showed that the MCMC chains were well mixed and converged. Both Bayesian models were performed in Stan (Stan Development Team 2021) via the *brms* package (Bürkner 2017) in the software R (R Core Team 2020).

3.4 Results and Discussion

There were clear differences in the bleaching response of massive *Porites* colonies among exposure levels at Lizard Island during the 2016 bleaching event. Out of the 108 colonies recorded, 84 (77.7%) experienced bleaching to some extent. Exposed locations had the lowest bleaching prevalence with a total of 53% of the colonies bleaching (varying from 40% to 62% among the exposed transects). By contrast, virtually all colonies in the lagoonal habitats were bleached. In the front lagoon, 100% of the colonies experienced bleaching. Meanwhile, in the back lagoon, a total of 86.6% of colonies were bleached, with this percentage varying from 50% to 100% at the transect level. Additionally, there was a high prevalence (total = 71%, ranging from 44% to 75% at the transect level) of colony bleaching on back reefs (**Fig. 3.1a, b**). Importantly, our model estimated colonies in the front lagoon to be twice as likely to bleach compared to those in exposed locations and around 1.5 times more likely compared to those in the back reef (**Fig. 3.1c**, Supplementary Table 3.3). This highlights the spatial variability of bleaching prevalence and the importance of considering location-specific factors when assessing coral responses to disturbance. Indeed, these findings align with earlier studies that also observed a higher prevalence of coral bleaching and/or coral loss following bleaching within lagoonal habitats for a variety of coral groups (Van Woesik *et al.* 2012a; Green *et al.* 2019; Tebbett *et al.* 2022a). However, prior-exposure of coral colonies to higher and more variable temperatures (such as those that occur in coral reef lagoons), have also been found to facilitate thermal acclimatization and adaptation of corals to acute temperature stress (Van Woesik *et al.* 2012a; Ainsworth *et al.* 2016; Safaie *et al.* 2018). While our results align with the first example from previous studies, rather than the latter, both examples highlight the marked spatial variation that can occur across coral reef systems in terms of coral colony bleaching.

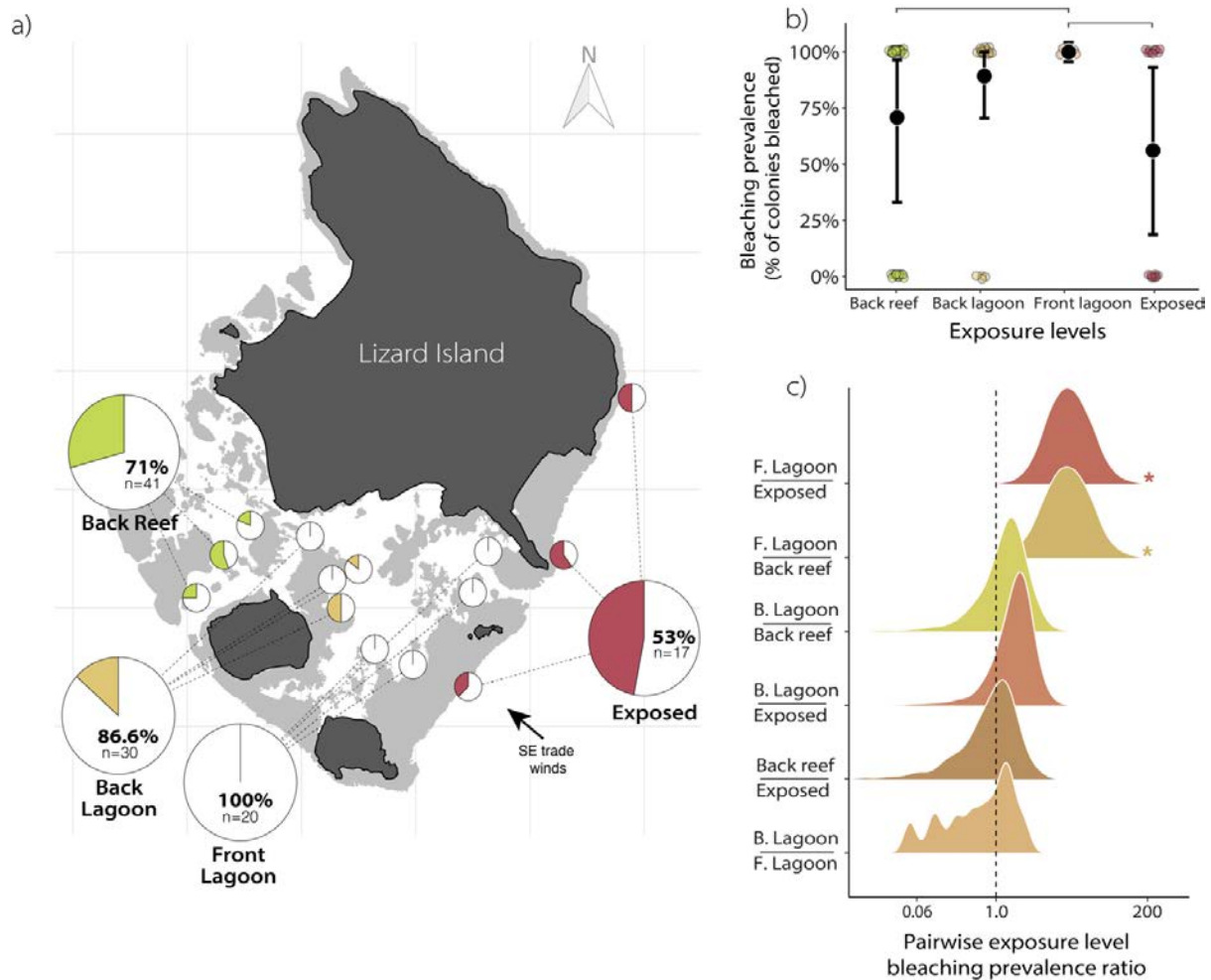


Figure 3.1 | Spatial variation of massive *Porites* bleaching prevalence among exposure levels at Lizard Island, Great Barrier Reef; a) Map showing the bleaching prevalence (i.e., proportion of massive *Porites* colonies with any signs of bleached tissue) on the different transects (small pies) and aggregated by exposure level (large pies). In the pie charts, white segments represent bleached colonies, while colorful segments represent colonies that were not bleached. “n” represents the total number of colonies (bleached + not bleached) sampled in that specific exposure level; b) colony-level bleaching outcomes (coloured dots, 0 = not bleached, 100 = bleached) and the posterior probability of bleaching for massive *Porites* colonies in the different exposure levels. Model fits originated from a binomial Bayesian generalized linear mixed model (with transect as a random effect); c) pairwise comparisons (ratio) of the posterior probability of bleaching for massive *Porites* colonies in the different exposure levels. Distributions with values predominantly exceeding 1 indicate that the exposure level in the numerator had higher probability of bleaching, while distributions with values predominantly lower than 1 indicate that the exposure level in the numerator had lower probability of bleaching. Horizontal bars in ‘b’ and asterisks in ‘c’ represent strong evidence of differences between the categories.

Our results of spatial variation in bleaching prevalence were mirrored by patterns of bleaching extent in massive *Porites* colonies. Specifically, of the corals that experienced some bleaching (77.7% of colonies), ~30% of the live tissue area was bleached, on average, although there was again marked spatial variation in this bleaching extent (**Fig. 3.2**). As in prevalence, the most severe bleaching impacts, on average (\pm SD), were recorded in the front and back lagoon locations with 32.3 ± 25 % (varying from 36% to 64% among back lagoon transects), and 48.1 ± 26 % (ranging from 21% to 42% among front lagoon transects) of the live tissue area bleached (**Fig. 3.2**), while relatively little (12.6 ± 6 %, ranging from 9% to 23% at the transect level) of the live tissue area was bleached on colonies in exposed locations. Colonies on back reefs experienced intermediate levels of bleaching (26 ± 12 % of live tissue area, ranging from 16% to 32% at the transect level) (**Fig. 3.2**). Therefore, the areas that experienced the highest prevalence of bleaching (in terms of percentage of colonies bleached) also experienced the most severe bleaching (in terms of the relative extent of live tissue area bleached). Furthermore, this spatial variation in bleaching extent was supported by our model which revealed strong evidence (i.e. the 95% high posterior intervals did not intersect 0) for differences between all exposure levels (except between the front lagoon versus back reef location, **Fig 3.2c**, Supplementary Table 3.5).

In a previous study, we found that massive *Porites* colonies that experience bleaching on 62% or more of their live tissue area tend to experience substantial levels of partial mortality in the months following the bleaching event (Morais *et al.* 2021). Of the colonies measured herein, 17% had more than 62% of their live tissue area bleached and almost all of these colonies (98%) were found in lagoonal habitats. Given the spatial distribution of bleaching extent this, therefore, suggests a substantially higher likelihood of tissue loss for massive *Porites* corals in these lagoonal habitats following bleaching.

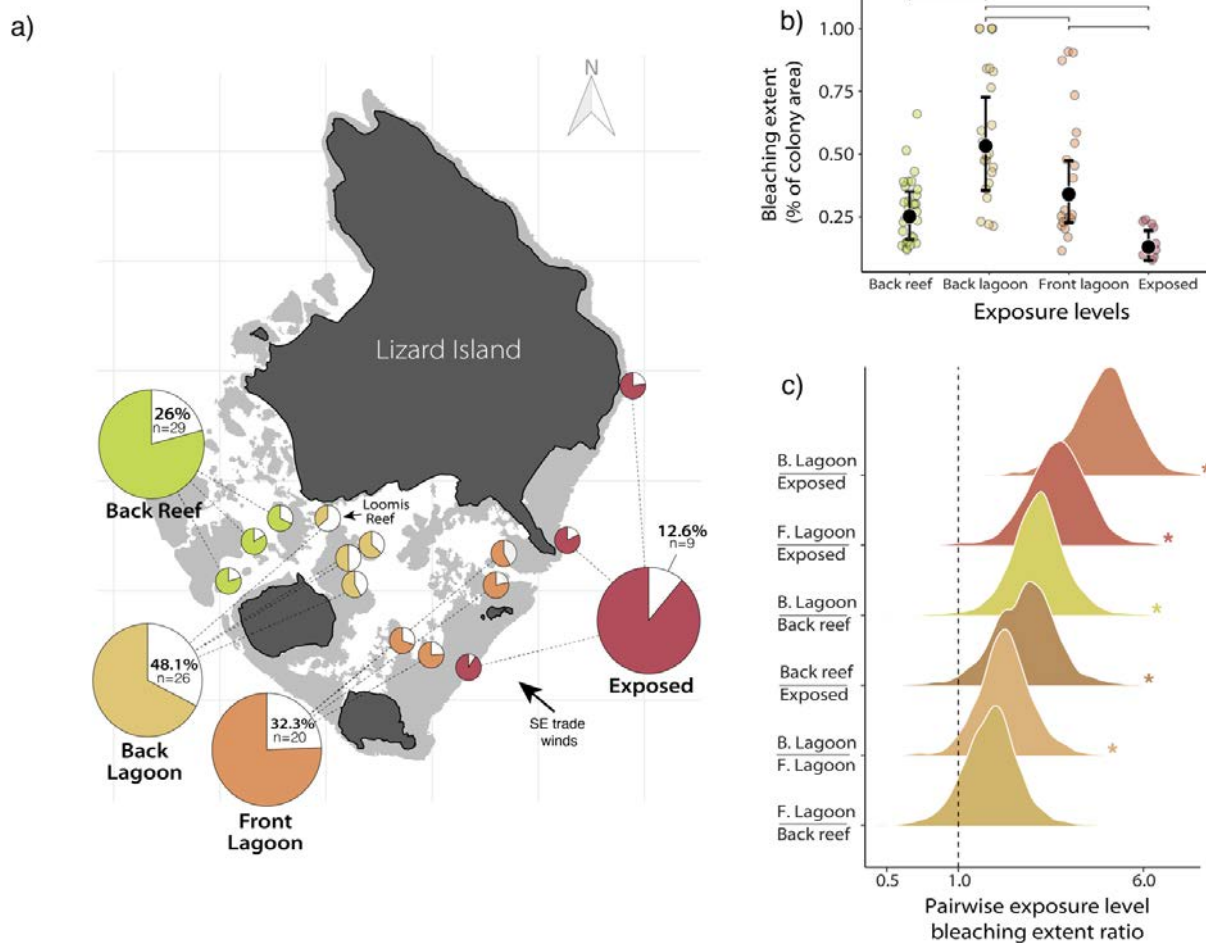


Figure 3.2 | Spatial variation of massive *Porites* bleaching extent among exposure levels at Lizard Island, Great Barrier Reef; a) Map showing the average bleaching extent (i.e., average percentage of colony live tissue bleached) on the different transects (small pies) and aggregated by exposure level (large pies). In the pie charts, white segments represent % of the live tissue area bleached, while colorful segments represent % of the live tissue area not bleached. “n” represents the total number of bleached colonies in that specific exposure level; b) posterior probability of bleaching extent for massive *Porites* colonies in the different exposure levels. Model fits pertain to a gamma Bayesian generalized linear mixed model (with transect as a random effect), while coloured dots represent individual massive *Porites* colonies (raw data points); c) pairwise comparisons (ratio) of bleached area extent between the different exposure levels (interpretation of Fig 2c is the same as in Fig 1c). Horizontal bars in 'b' and asterisks in 'c' represent strong data evidence of differences between paired categories.

It is important to recognize that thermal regimes on coral reefs strongly depend on the interaction between water movements and reef morphology (Lenihan *et al.* 2008; DeCarlo *et al.*

2017; Grimaldi *et al.* 2023). Specifically, while exposed sites benefit from strong currents, which can bring cooler water up the fore reef slope (Schmidt *et al.* 2016; Storlazzi *et al.* 2020; Wyatt *et al.* 2020), lagoonal habitats can experience limited cooler water inputs (Rogers *et al.* 2016; Grimaldi *et al.* 2023). Consequently, lagoonal sites can be more prone to rapid local warming, making coral communities there more susceptible to bleaching. However, not all types of water movement on reefs lead to thermal stress reduction. Indeed, at the transect level, the highest average bleaching extent (64%) was located at the sheltered (western) fringe of the main lagoon (Loomis Reef) (**Fig 3.2a**). This particular reef is also exposed to some of the highest average current speeds around Lizard Island (Tebbett *et al.* 2022b) (Supplementary Figure 3.2). The accelerated water flow, combined with the prevailing current direction, means that Loomis Reef forms a bottleneck for water being discharged from the lagoon (Tebbett *et al.* 2022b). This water exiting the lagoon is likely to be relatively warm (Green *et al.* 2019; Grimaldi *et al.* 2023). Therefore, corals situated in this area likely faced a high flow of heated water, increasing bleaching risk, and presumably explaining the highest *Porites* bleaching prevalence and extent in this area.

Beyond the interaction between reef morphology and hydrodynamics, colony size can also play a role in determining bleaching susceptibility, with an extensive body of literature identifying this relationship for a variety of corals (e.g. Edmunds 2005; Shenkar *et al.* 2005; Wagner *et al.* 2010; Pratchett *et al.* 2013; Burn *et al.* 2023). However, our models indicated that the size of colonies had no effect on either the prevalence or the extent of bleaching in massive *Porites* (**Fig. 3.3**, Supplementary Figure 3.1, Supplementary Table 3.1, 3.2, 3.4, 3.6). The lack of effect found herein may be attributed to the difference in the size range examined in our study compared to other studies. For example, past studies that investigated bleaching using colony size as a variable, explored a relatively small size range of small colonies (e.g. $>16 \text{ cm}^2$ to $<60 \text{ cm}^2$ [Shenkar *et al.* 2005]) or compared juvenile colonies ($\leq 5 \text{ cm}$ diameter) with adults ($>5 \text{ cm}$ diameter) (e.g. Burn *et al.* 2023). In contrast, when compared to Burn *et al.* (2023), our study focused only on adult colonies

(>5 cm diameter), and when compared to Shenkar et al. (2005,) our study considered a much larger size range (30.4 cm² to 3408.8 cm²). Indeed, when compared to the size range in Shenkar et al. (2005), only 4.6% of our colonies were smaller than their largest size colony (i.e. <60 cm²). To deepen our understanding of the effect of colony size on bleaching susceptibility, future research may also consider the variation in bleaching colour gradient (Chow *et al.* 2016). A thorough investigation of these aspects could shed even more light on the differential bleaching responses among colonies of varying sizes.

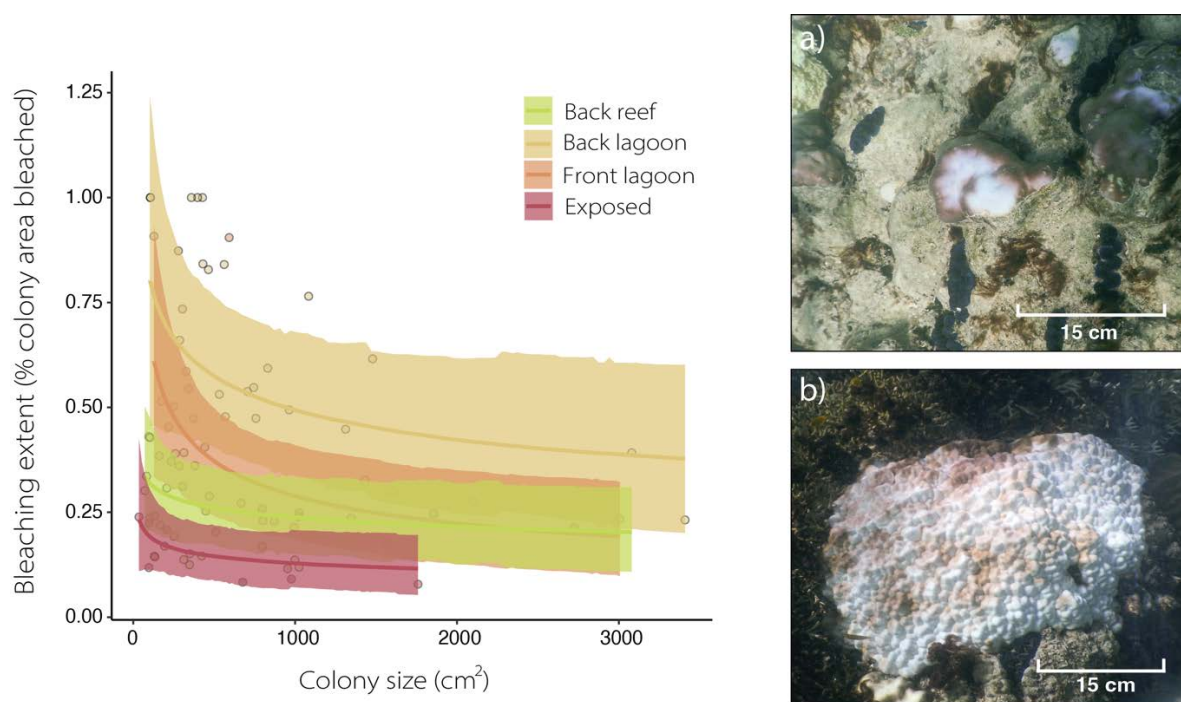


Figure 3.3 | Interaction between colony size and wave exposure level in determining the extent of bleaching on individual massive *Porites* colonies. Note most of the variability is among exposure categories while colony size did not have a large effect on bleaching extent. Model fits were based on a gamma distributed Bayesian generalized linear mixed model (with transect as a random effect). Lines represent model estimated marginal means for different exposure levels. Ribbons denote the 95% high posterior density intervals and points represent bleaching extent of individual massive *Porites* colonies. Photographs showing examples of bleaching

in a small (a) and a large (b) massive Porites colony at Lizard Island, Great Barrier Reefs. Photographs: RP Streit.

Overall, our study revealed that both the prevalence and extent of bleaching were spatially heterogeneous in massive *Porites* colonies around Lizard Island. Given that both the prevalence and extent of bleaching were highest in the lagoonal habitat, this suggests that corals in this area were either a) more sensitive to thermal stress, or b) exposed to more intense thermal stress during the heatwave. As past evidence has suggested that corals in lagoonal environments tend to be more tolerant of thermal stress (Ainsworth *et al.* 2016; Safaie *et al.* 2018), the latter mechanism may be the primary factor driving spatial variation in bleaching intensity. Restricted water circulation in lagoonal habitats may thus have led to more intense and prolonged exposure to warmer waters (cf. Rogers *et al.* 2016; Green *et al.* 2019). Indeed, the highest extent of bleaching was in the location where these lagoonal waters are likely to drain from the lagoon (i.e. Loomis Reef). These findings emphasize the importance of considering location-specific factors, especially reef morphology and hydrodynamics, in assessing coral health and bleaching susceptibility.

Chapter 4. On the fate of dead coral colonies

This chapter is published as:

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4.1 Abstract

Carbonate budgets dynamically balance production and loss of calcium carbonate (CaCO_3) on coral reefs. To sustain or expand the coral reef framework, CaCO_3 production by calcifying organisms must be higher than erosion. However, global climate change has been negatively impacting carbonate production, with bleaching events causing widespread coral mortality. While bleaching and coral mortality are well documented, the fate of coral colonies after their death, including their erosion rates, are still poorly known. We followed the fate of 143 recently dead individual coral colonies with complex growth forms (arborescent, caespitose, corymbose, digitate, and tabular), whose mortality was triggered by two consecutive bleaching events. These colonies, spread over 16 km² of the Lizard Island reef complex, were tracked for up to 5 years, allowing detailed examination of erosion rates and post-mortality structural persistence. We also tested how variables that are commonly used in coral reef erosion studies relate to spatial and temporal variability in the erosion rates of dead coral colonies. We revealed rapid erosion of dead coral colonies, with an average of 79.7% of dead colonies completely disintegrating within 60 months. The predicted half-life of a dead coral colony was 40 months, with limited variation among wave exposure levels. Remarkably, we found no effect of estimated parrotfish bioerosion, wave exposure,

nor coral growth form, on observed erosion rates. Our results suggest that our understanding of the erosion of dead corals may be more limited than previously thought. The rapid loss of coral colonies on our study sites calls for a re-evaluation of the role of corals with complex growth forms in reef growth and of parrotfishes in reef erosion.

Introduction

The physical structure of coral reefs is dependent on the dynamic balance between the production and loss of calcium carbonate (CaCO_3). In this "carbonate budget", production by calcifying organisms must be higher than erosion to sustain or expand the coral reef framework (Kleypas *et al.* 2001; Cornwall *et al.* 2021). Sustaining the physical structure of reefs is vital for maintaining the abundance, diversity and ecosystem functioning of reef-associated communities (Graham & Nash 2013; Coker *et al.* 2014) and key services to people, such as coastal protection from inundation during storms (Elliff & Silva 2017; Reguero *et al.* 2018). However, the persistence of positive carbonate budgets and reef structures may be at risk due to the increasing impact of climate change on coral reefs (Cornwall *et al.*, 2021; Hughes *et al.*, 2017; Perry *et al.*, 2018).

On coral reefs there are three main types of natural carbonate erosion: chemical, physical and biological. Chemical erosion occurs via carbonate dissolution. This process is slow, but has been forecast to increase due to acidification (Eyre *et al.*, 2018; Eyre, Andersson, & Cyronak, 2014; Schönberg, Fang, Carreiro-Silva, Tribollet, & Wisshak, 2017). Physical erosion is mostly caused by storms, including cyclones, which are often localised and short in duration (Puotinen *et al.* 2020). Biological erosion or 'bioerosion' refers to the removal of carbonate from the consolidated reef structure or from the skeletons of reef-building taxa (e.g., hard corals) by organisms (Kiene & Hutchings 1994; Hutchings *et al.* 2005). Bioerosion is the most widespread and consistent form of carbonate removal and is the primary form of erosion on most reefs (Scoffin *et al.* 1977). Of all bioeroding taxa, parrotfish are arguably the most important, delivering rates of bioerosion that may approach total calcification (Bellwood, Hoey, & Choat, 2003; Morgan & Kench, 2016). It is well known that estimated bioerosion rates, and the organisms that underpin this process, exhibit marked spatial variability across depths, habitats and exposure levels (Bellwood *et al.*, 2003; Brown *et al.*, 2021; Yarlett, Perry, Wilson, & Harborne, 2020). However, this is based on estimates of

removal, primarily using proxies e.g. fish abundances. Our understanding of the links between potential bioeroders and the disappearance of dead coral skeletons is in its infancy.

Given the context of ongoing, widespread coral bleaching events, it is important to quantify how long coral colony structure remains following mortality, and how the loss of coral structure relates to estimated erosion rates. To fill this knowledge gap, we tracked the fate of 143 individual coral colonies of complex growth forms spread across 16 km² on the Lizard Island reef complex for 5 years (2016-2021), following their bleaching-induced mortality. In addition, we investigate the effect of variables that are commonly used in bioerosion studies, to assess how these may help to explain spatial and temporal variability in dead coral colony erosion around Lizard Island.

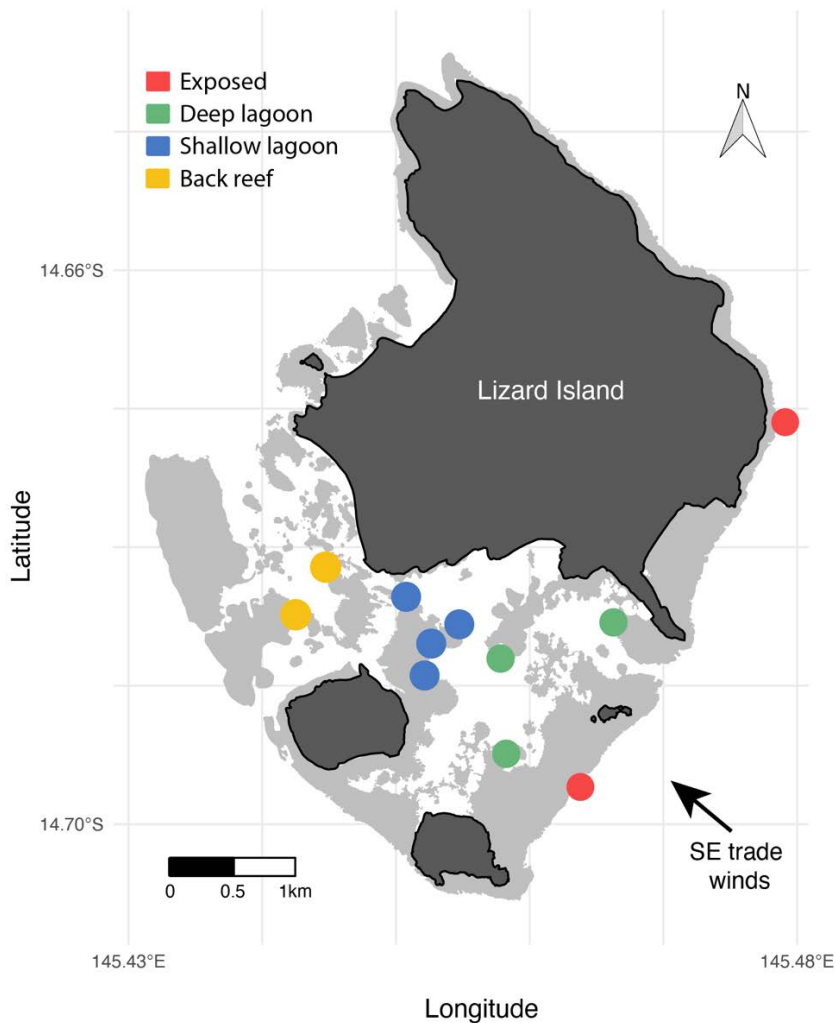


Figure 4.1 | A map of Lizard Island showing the 11 sampling locations and their depth/exposures categories. (relative to the prevailing south-east trade winds).

4.3 Methods

4.3.1 Study area and sampling

Data collection was based on a comprehensive series of photo-quadrat censuses at Lizard Island (14°40' S, 145°28'E), in the northern Great Barrier Reef (GBR) (**Fig. 4.1**). In 2016, a severe marine heatwave affected the GBR, including Lizard Island, triggering the most severe coral bleaching event recorded on the GBR (Hughes et al., 2021). In 2017 and 2020 the area experienced less intense bleaching events (Hughes et al., 2021). In February 2016, immediately prior to the major bleaching event, a series of 19 permanent transects, between 50 and 210 m in length (constrained by the nature of the reef) were established along the reef crest/edge (0–4 m below chart-datum) around Lizard Island. Each transect comprised between 12 and 38 quadrats (1 m² area) placed approximately 5 meters apart. These quadrats were photographed initially and on five additional field trips: in April 2016 (3 months since first sampling), October 2016 (9 months), January 2018 (24 months), January 2020 (48 months) and January/February 2021 (60 months). Using SCUBA, a bird's-eye-view photograph of each quadrat was taken in each of the six sampling periods using a Nikon Coolpix W300 camera. Note that the quadrat frames were not fixed in place. Instead, we used a second camera containing previous images of each quadrat, ordered from the start to the end of the transect, as a guide to enable quadrat frames to be placed in the same position on each sampling trip (see Wismer *et al.* 2019a for a sensitivity analysis of this method). For this study, we only used transects that included initially (in 2016) more than two visually trackable coral colonies, with the prerequisite that these colonies died at some point during the following five field surveys. This resulted in 11 transects in total, distributed among exposure regimes according to their position relative to the prevailing south-east trade winds (Fulton & Bellwood 2005). Two transects were in exposed locations, three on the windward side of the lagoon (henceforth 'deep lagoon'), four in the protected lagoon ('shallow lagoon') and two on the back reef (**Fig. 4.1**).

4.3.2 Erosion metrics

To investigate coral erosion of individual colonies, we tracked the fate of all corals with complex growth forms (i.e., arborescent, caespitose, corymbose, digitate, and tabular), that died during our sampling period (most died after the 2016 bleaching event). Massive corals were not tracked due to low mortality rates (Morais et al., 2021). We did not consider colonies that were already dead in the first sampling period, selecting only living colonies that could be tracked until their mortality to ensure we examined the entire post-mortality period.

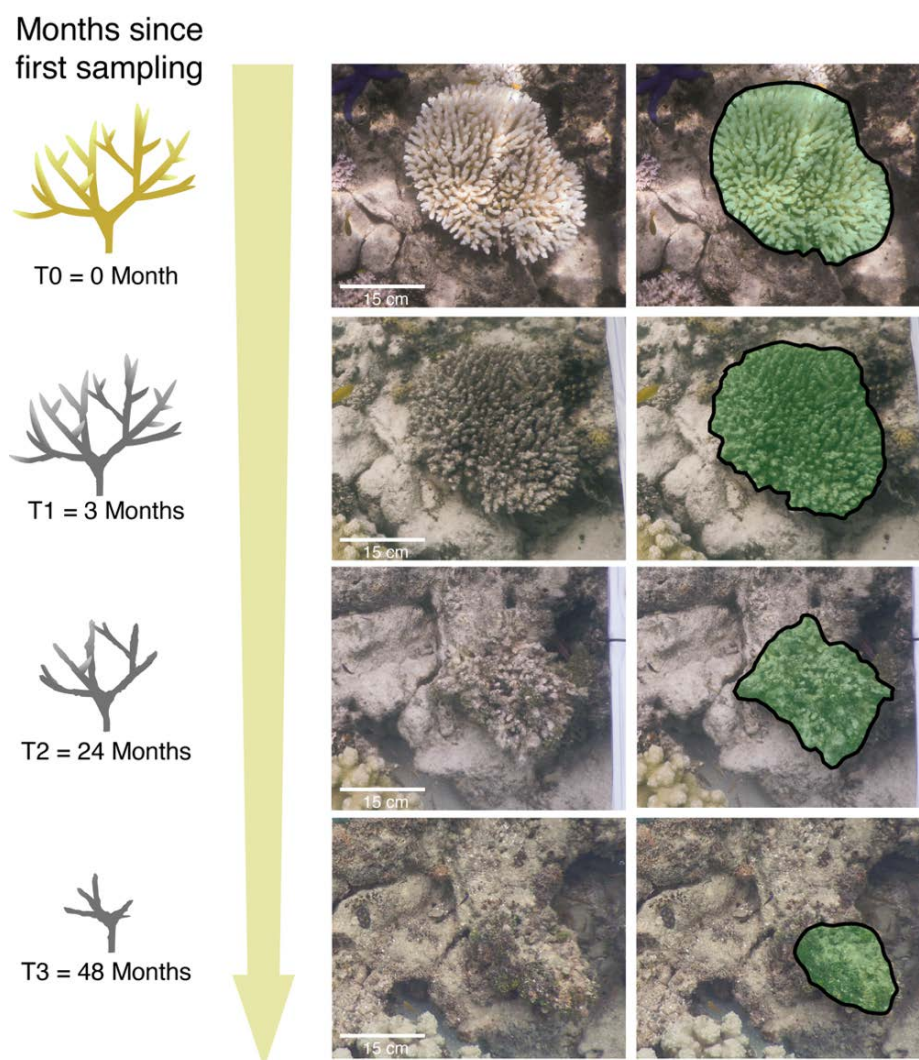


Figure 4.2 | Sequence of photos showing an example of an *Acropora* coral colony eroding over time. Left image, right showing the digitalized area.

To quantify erosion, estimates of individual coral colony volume are required. However, while there are now methods such as 3D photogrammetric approaches via Structure-from-Motion available that can facilitate this process (Pizarro *et al.* 2017; Bayley & Mogg 2020; Aston *et al.* 2022), such processes have a number of limitations, especially in terms of processing times and light requirements (House *et al.* 2018). Moreover, it is impossible to utilize this method post-hoc (i.e., after the corals have already died and begun to erode), limiting our capacity to understand how processes on the reef could have changed. However, it has now been repeatedly shown that 2D estimates of colony surface area are inextricably linked to 3D volume for corals of the same morphology (House *et al.* 2018; Urbina-Barreto *et al.* 2021; Husband *et al.* 2022). Therefore, by deriving relationships between 2D surface area and 3D volume, one can estimate colony volume from data on surface area alone. We utilized such an approach herein. Specifically, we used the software ImageJ (Abràmoff *et al.* 2004) to measure planar area (in cm^2) from the photographs of each colony in each sampling period (following Morais *et al.*, 2021). We then applied the relationships between planar area and colony volume provided in Urbina-Barreto *et al.*, (2021) to convert estimates of coral planar surface area from our photoquadrats to predict 3D colony volume (see Appendix S1 for further details and potential limitations of this method).

To comprehensively address all the comparisons and models in our study, the loss of calcium carbonate ('erosion') was expressed in five different ways.

(1) The changing volume of each colony (in cm^3) was predicted from its planar area based on the relationships in Urbina-Barreto *et al.*, (2021) (Supplementary Methods 4.1).

(2) To calculate the loss of CaCO_3 in grams per colony per year, we first calculated the mass of calcium carbonate in each colony by multiplying the estimated volume by species or genera-specific skeletal densities from the coral traits database (<http://coraltraits.org>; Madin *et al.*, 2016). Where multiple density values were available for a species, these were averaged. For coral species with no density data, data from the closest related species with the same growth form were used. Then we

calculated the difference in estimated calcium carbonate (g) between the largest size recorded for each colony and its size at the last sampling (i.e., the end of the study or when colony was undetectable, planar area = 0). Dividing the mass lost per colony (g) by the time in years (between the largest recorded size and the last sampling or when the colony was undetectable) provided the average carbonate loss in g per colony per year (this was calculated for each colony then averaged for each transect).

(3) To model erosion rates per colony we took the colony specific mass lost from (2) and standardized it by the initial colony size, to account for variation in initial colony sizes. Erosion rates in this case are therefore the loss of g carbonate per cm^2 of initial colony area, per year.

(4) To calculate total carbonate mass lost per unit area of reef (i.e. the loss of CaCO_3 in $\text{kg m}^{-2} \text{yr}^{-1}$), as in (2), we first calculated the mass of calcium carbonate in each colony by multiplying the estimated volume by species skeletal densities. Then, we calculated the differences in the mass of calcium carbonate (in kg) between the largest size recorded for each colony and its size at the last sampling period. To calculate carbonate loss per unit area (i.e. average carbonate lost per m^{-2} surveyed in each transect), the total loss of mass across all colonies, per transect, was divided by the area of the total number of quadrats in that transect (including quadrats that did not host colonies). This resulted in the total loss of CaCO_3 in kg m^{-2} (in each transect) over the five years, which was then divided by 5 to provide an annual rate of erosion per unit area of reef.

(5) To estimate the average erosion rates per unit area across all transects in $\text{kg CaCO}_3 \text{m}^{-2} \text{yr}^{-1}$, we simply averaged the values in (4) across all transects in the study.

4.3.3 Explanatory variable

In addition to erosion, we quantified a number of key explanatory variables. Specifically, we calculated potential parrotfish erosion at each transect location based on two 50 x 5m transect surveying all parrotfishes larger than 10 cm total length (TL). We specifically chose surveys of this size (covering an area of 500 m² at each location) because this is reflective of methods commonly used in the literature on parrotfish bioerosion (e.g. 240 – 720 m² per site; Alwany et al., 2009; Graham et al., 2018; Kuffner et al., 2019; Morgan & Kench, 2016; Perry et al., 2015). This was important because it ensured our results aligned with the methods commonly used in this research field, thus allowing our results to be placed into the context of this past research more directly. Our surveys included data on species identity, abundance, and size (total length, in cm) and were undertaken by the same experienced SCUBA diver (last author) between January and February 2021. We considered only excavating parrotfishes, which disproportionally dominate fish bioerosion (Bellwood & Choat, 1990). Only three excavating species were observed: *Chlorurus microrhinos*, *Chlorurus spilurus*, and *Chlorurus bleekeri*. All counts were conducted between 0930 and 1600 hrs. From the counts, potential bioerosion (in kilograms of CaCO₃ per m² of reef per year) for each transect was estimated by multiplying individual fish size by the proportion of bites that leave scars (from Hoey 2018), bite volume (mm³ bite⁻¹) (from Bellwood, 1995), feeding day length (in minutes) (from Bellwood, 1995, averaged across winter and summer), bite rate (bites per minute) (Bellwood & Choat, 1990 values for Lizard Island), and the abundance of each fish species, as well as an overall estimate of the carbonate density of the 'reef matrix' (following Bellwood, 1995). It is important to note that these methods for quantifying the process of bioerosion by parrotfishes from one-off surveys, inherently assumes that this process is consistent both spatially and temporally (e.g., Bellwood, 1995; Kuffner et al., 2019; Morgan & Kench, 2016; Perry et al., 2012).

In addition to potential parrotfish bioerosion, potential wave exposure and coral growth form, we also incorporated geometric and environmental factors: skeleton density, local coral cover, colony size (planar area), colony volume, and colony density (number of colonies per transect) which allowed us to control for potential morphological and environmental variation in our model. As per above, coral skeletal density was obtained from (Madin et al., 2016). Colony size was considered to be the largest size of the colony during our sampling period, which in all cases coincided with the last time the colony was seen alive or the first time it was recorded dead. Colony volume was the same as used above in metric #1. Colony density was the count of the number of colonies per transect. Finally, coral cover was determined from the photographs and was calculated by determining the cover under 40 randomly positioned points per quadrat using the software Photoquad v.1.4 (Trygonis & Sini 2012).

4.3.4 Data analyses

To estimate the rates of loss of individual coral colonies and the predicted 'half-life' of coral colonies as a recognisable physical structure following mortality, we used a Bayesian generalized linear mixed effects model with a binomial distribution and logit link. The fate of the colony at each survey occasion (i.e., if completely eroded or retaining visible signs of colony structure) was used as the response variable and time (difference in months between last time seen alive and the end of the study or when the colony was undetectable, planar area = 0), exposure level and their interaction were treated as predictors. Transect identity was included as a random effect to account for the lack of spatial independence in the sampling design. The model was based on 3 chains with 5000 iterations, including 3000 iterations to warm-up and a thinning interval of 2, with weakly informative priors. Model fit and assumptions were evaluated using residual and autocorrelation

plots, accompanied by metrics of sampling efficiency (rhat) and effective sample size (neff) scores, all of which were satisfactory and suggested that the MCMC chains were well mixed and converged. All Bayesian models were performed in Stan (Stan Development Team, 2020) via the 'rstan' interface using the package "rstanarm" (Goodrich *et al.* 2020) in R (R Core Team, 2020).

We tested the hypothesis that parrotfish erosion, level of wave exposure, and coral growth form influenced the rates of calcium carbonate loss in coral colonies at Lizard Island using a Bayesian generalized linear mixed effects model with a gamma distribution and a log link function. Loss of calcium carbonate (erosion metric #3) was the response variable, while estimated parrotfish erosion, wave exposure, and growth form were used as predictor variables. Potential geometric and environmental factors, such as: skeleton density, local coral cover, colony size (planar area), colony volume, and colony density (number of colonies per transect) were also included as control for potential morphological and environmental variation in our model. Again, we included transect as a random effect to account for the lack of spatial independence. The model fit and assumptions were as above.

4.4 Results

4.4.1 Rates of colony loss

After 24 months, 42% of the initial 143 colonies were completely eroded. After 48 months, this stood at 103 colonies, or 72%. By the end of the study, 60 months after first sampling, a total of 114 colonies or 79.7% of all colonies had been totally eroded. Thus, from the initial 143 colonies, only 29 maintained some visually discernible evidence of physical structure at the end of the study period. Our model suggested that the predicted 'half-life' of coral colonies as a recognisable physical structure following mortality at Lizard Island was on average 3.3 years (or 40 months), ranging from 2.6 years (31.3 months) in the exposed locations to 4.1 (50 months) in the deep lagoon (**Fig. 4.3**).

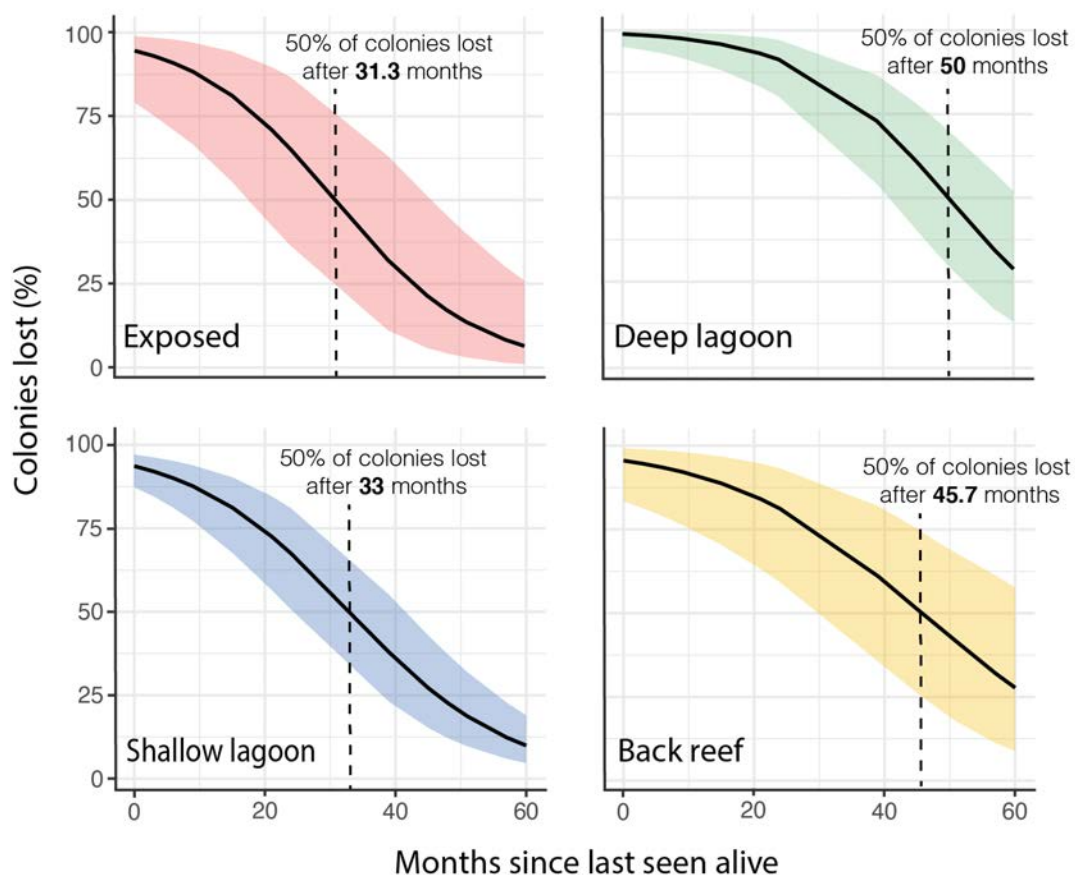


Figure 4.3 | Predicted rate of coral structure loss at each exposure level following bleaching-induced mortality at Lizard Island, northern Great Barrier Reef. A generalized linear mixed model was used to estimate the logistic regression line (black line) and 95% high posterior density intervals (coloured ribbons).

Furthermore, there was little variation in colony disappearance rates across exposure levels, with almost no effect on differences across habitats (except between deep lagoon vs. exposed, and deep lagoon vs. shallow lagoon, Supplementary Table 4.1). Indeed, locations in all exposure types presented relatively similar rates of colony disappearance based on volume (erosion metric #1) over the 60 months of the study, ranging from over 80% in the shallow lagoon and exposed locations to around 64% in the back reef and 61% in the deeper part of the lagoon (**Fig. 4.4**).

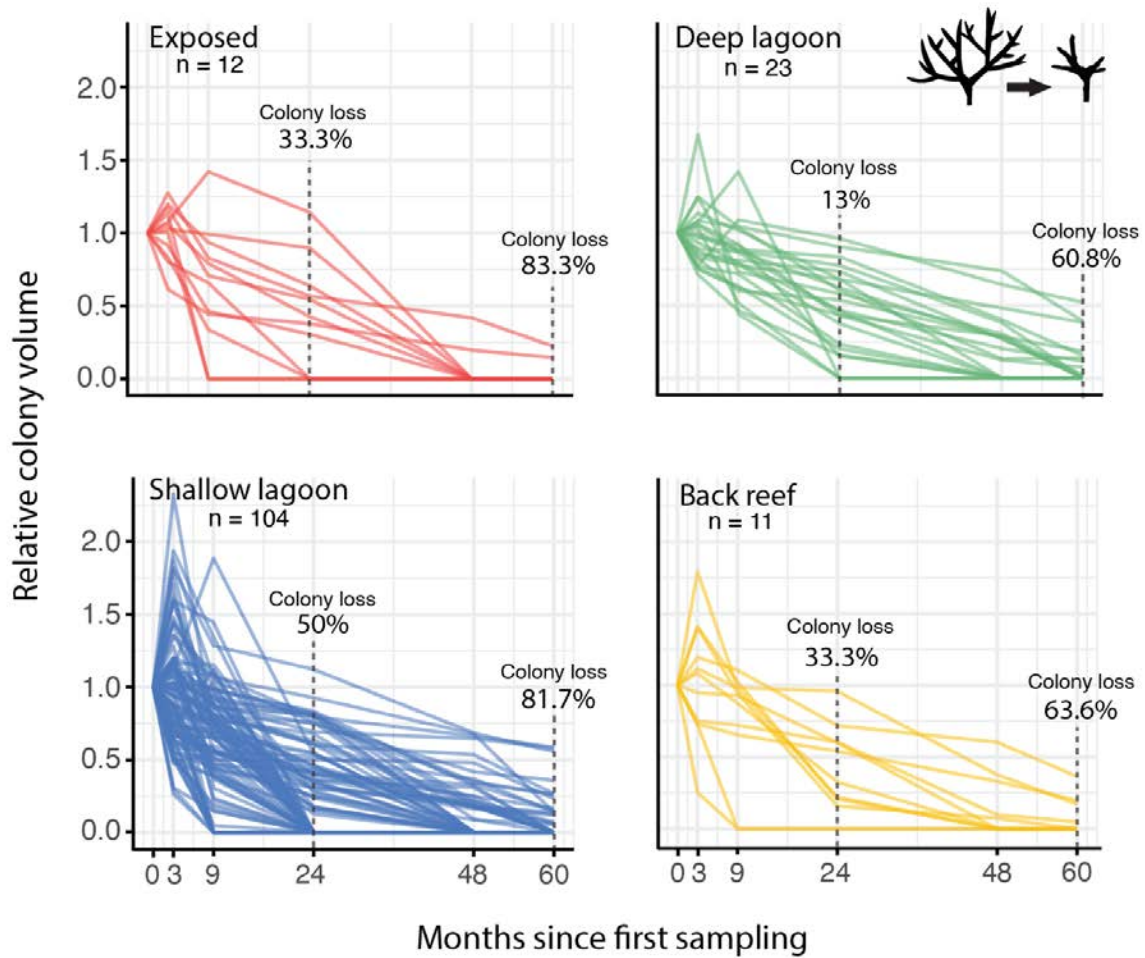


Figure 4.4 | Relative volume of complex growth form coral colonies tracked over 60 months. Each line represents a single colony, with colors representing the wave exposure categories from Figure 1. Relative volume (cm^3) is the predicted volume based on the planar area of the colony relative to the value at first detection. Vertical dashed lines represent the proportion of colonies that completely disappeared at that point in time.

4.4.2 Explanatory variables

To investigate the likely drivers of dead coral erosion at Lizard Island, we compared observed coral erosion in each transect (erosion metric #4) to the predicted erosion caused by parrotfishes

estimated from fish counts at the same sites. If parrotfishes are the main source of bioerosion of dead corals, we would expect to find a clear match between observed coral erosion and predicted parrotfish erosion. Instead, there was a clear spatial mismatch between the two rates. Only four transects were estimated to experience sufficient parrotfish-driven bioerosion to explain coral erosion, with the majority of the transects having little or no predicted parrotfish erosion. Interestingly, in the shallow lagoon, which had both the highest number of colonies tracked and the highest rates of coral colony loss (Fig. 4.4), parrotfish erosion was estimated to be close to zero (Fig. 4.5). The same pattern was observed for both transect level erosion (metric #4) and colony level erosion (metric #2) (Fig. 4.5). This was also reflected in our model, which showed no effect of predicted parrotfish erosion at the quadrat level or for coral colony estimated erosion (Fig. 4.6). This suggests that other factors may be driving dead coral colony erosion at Lizard Island.

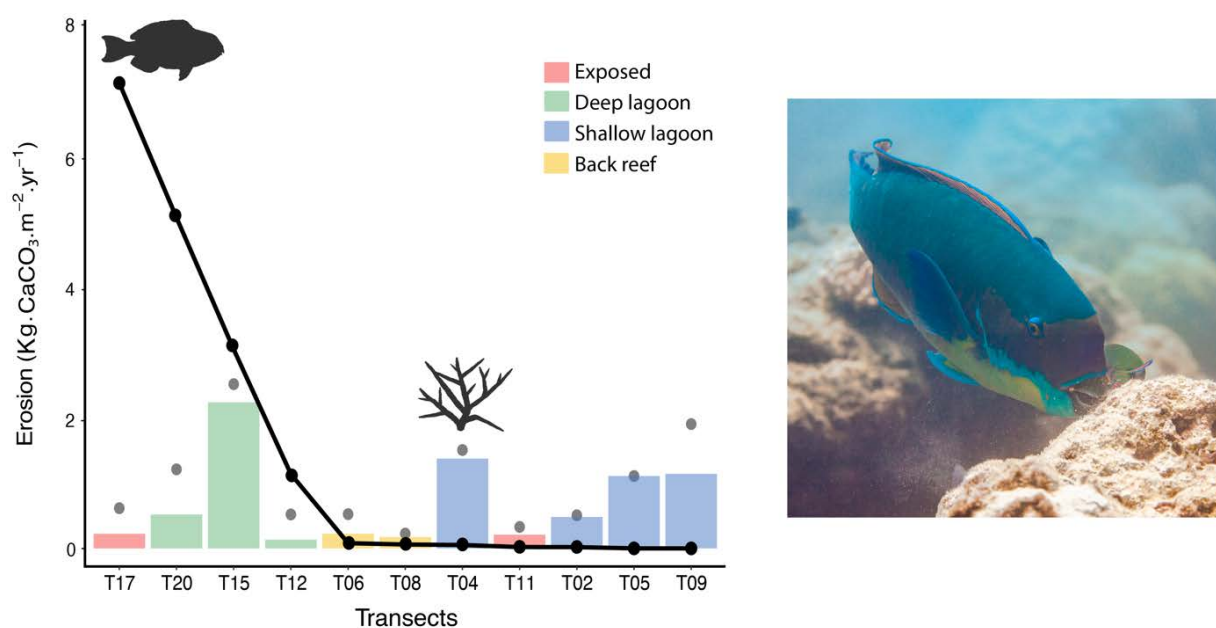


Figure 4.5 | Dead coral colony erosion and estimated parrotfish erosion on 11 transects around Lizard Island. Y-axis applies to the bars, which indicate total estimated coral erosion with colours showing exposure levels, to the black dots and line which represent predicted parrotfish erosion on each transect, and to the gray dots (erosion metric #2) which represent overall carbonate lost per colony (Kg.CaCO₃.colony.yr⁻¹). On average, coral

erosion was $0.6 \text{ kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ [metric #5]. Note that this figure is used exclusively to illustrate the distinct spatial patterns of these variables. Photograph: Victor Huertas.

After this preliminary investigation, we looked more broadly at other potential explanatory variables. Surprisingly, we found that erosion (per colony, standardized, metric #3) was constant across wave exposures levels, with no effect on erosion rates across habitats (Supplementary Table 4.1). The same was observed for growth forms, where erosion was constant across all categories (Fig. 4.6).

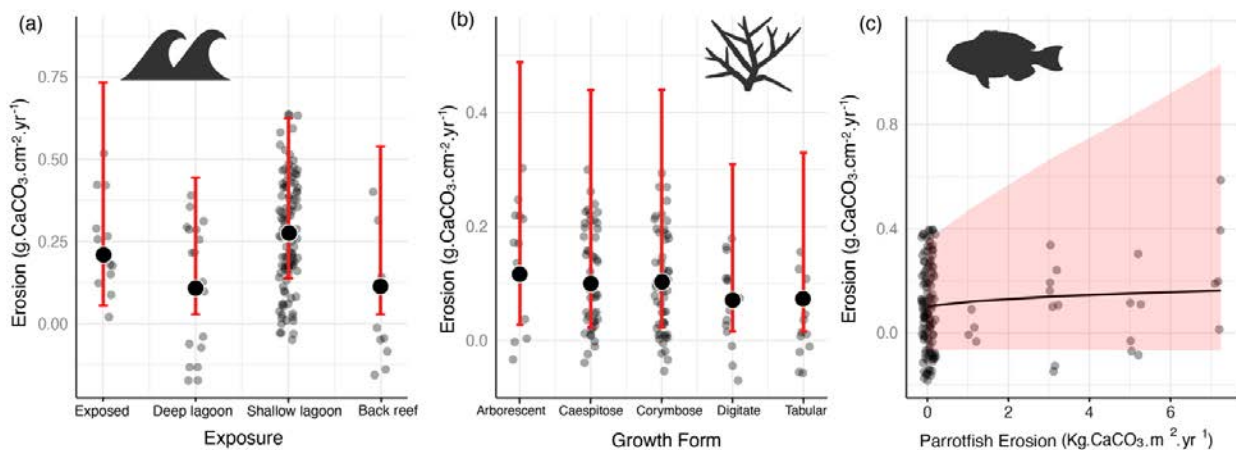


Figure 4.6 | Effects and partial residual plots of the relationship between erosion of individual coral colonies and the response variables: (a) exposure level, (b) coral colony growth form, and (c) predicted parrotfish erosion. Model fits pertain to a gamma Bayesian generalized linear mixed model (with transect as a random effect). The erosion on the y-axis is the differences in the mass of calcium carbonate (in grams) between the largest size recorded for each colony and its size at the last sampling per year (expressed as a rate per cm^2 of initial colony area, to account for variation in initial colony sizes). Black point represents estimated marginal means and red lines and ribbon represents 95% high posterior density intervals (HPD).

4.5 Discussion

The potential impacts of global climate change on carbonate accretion on coral reefs has been widely reported (Bozec *et al.* 2015; Cornwall *et al.* 2021), largely because of widespread coral bleaching and mortality events triggered by severe heatwaves. While coral mortality during and after bleaching events is well documented (Hughes *et al.*, 2017; Madin *et al.*, 2018; Morais *et al.*, 2021; Sully, Burkepile, Donovan, Hodgson, & van Woesik, 2019), the fate of coral colonies after their death, including their rates of erosion, has received limited attention (but see Kuffner *et al.*, 2019; Roff, Zhao, & Mumby, 2015). We addressed this knowledge gap by using a novel dataset that allowed us to track the fate of dead coral colonies over five years. This enabled us to investigate dead coral colonies individually and thus examine a range of environmental factors that have been hypothesized to drive their erosion, including their growth form and exposure to waves (Madin & Connolly 2006) and parrotfish erosion (Bellwood, 1995; Morgan & Kench, 2016; Perry *et al.*, 2013). Importantly, it is believed that dead coral colonies are an integral component in the formation of the reef matrix (Stanley 1981; Cornwall 2019). However, contrary to these expectations, we found intense dead coral colony erosion with an average of 79.7% of dead colonies completely disintegrating within 60 months. Furthermore, the predicted half-life of a dead coral colony was on average only 40 months, ranging from 31 to 50 months among wave exposure levels (**Fig. 4.3**). We also found that neither estimated parrotfish erosion nor exposure level or coral growth form, were capable of explaining observed variation in coral erosion rates. These results suggest we may need to reevaluate the role of corals in reef building and associated processes.

4.5.1 Coral structure loss

Our study revealed that even relatively large colonies (up to 40 cm wide) were completely eroded within just 9 months (**Fig. 4.4**). Indeed, regardless of the location, after 5 years, between 60.8 and 83.3% of all dead coral colonies were completely eroded (**Fig. 4.4**). This is a relatively fast rate of

disappearance and raises questions about the contributions of complex growth form corals to reef growth. If corals are an integral part of reef matrix growth, we would have expected a considerable degree of coral colony structure to remain. However, the loss of a relatively high number of coral colonies in only a few months suggests that corals with branching or tabular growth forms may play a limited role in reef growth. This phenomenon may be particularly important in the absence of coral recovery after a mortality event. If high rates of coral erosion are a widespread phenomenon in complex growth form corals on Indo-Pacific coral reefs, then it is possible that the major role of these corals may lay in rubble formation (Hughes, 1999) and reef infilling (Perry et al., 2013) rather than growth via the deposition of in situ coral skeletons.

Coral rubble is generated and further broken down through a variety of biological, chemical and mechanical processes such as bioerosion and storms that deposit fragmented dead coral skeletons onto the fore-reef slope (Rasser & Riegl 2002). Hughes (1999) documented a high rate of coral fragment export at Lizard Island from the reef slope down to the reef base, with an average of 132 fragments, weighing 1.87 kg, per horizontal meter of slope-base interface per year, or $\sim 0.2 \text{ kg.m}^{-2}.\text{yr}^{-1}$ if divided by the slope depth (8-12 m). However, this is still far from the observed erosion rates of dead coral colonies in our study. Hughes' values of $\sim 0.2 \text{ kg.m}^{-2}.\text{yr}^{-1}$ are approximately 3-fold lower than the $\sim 0.6 \text{ kg.m}^{-2}.\text{yr}^{-1}$ erosion rates herein (erosion metric #5). Additionally, there was limited evidence of fallen coral branches among the remaining colonies, suggesting that the branches are being broken into finer sediment fractions (see Supplementary Figure 4.4 for coral rubble cover). Clearly a large proportion of the dead coral colony structure is 'disappearing'.

4.5.2 Drivers of coral erosion - Physical

Coral loss is not just about the loss of colony structure and the services it provides to fishes and invertebrates. Coral loss also represents a major loss of calcium carbonate from the reef

structure (Gvirtzman 1994; Bozec *et al.* 2015). Therefore, it needs to be interpreted from a functional perspective, which requires knowledge of both rates of material movement and potential drivers. The primary potential drivers of erosion tested herein included the location (as a proxy for wave energy), and the morphology of the coral colony (i.e., growth form). While estimated bioerosion has been found to correlate with exposure (i.e., higher bioerosion in exposed compared to lagoonal habitats; Hoey & Bellwood, 2008; Hutchings, Kiene, Cunningham, & Donnelly, 1992), these patterns were linked with biological agents (parrotfishes or sponges etc.) not the physical action of waves. Waves could be a direct primary driver of erosion, particularly in the face of severe storms (Puotinen *et al.* 2020). However, if wave energy was important, we would expect that exposure levels would have shaped the erosion rates in our study, with more exposed habitats exhibiting higher erosion than more sheltered ones. Similarly, the vulnerability of colonies to physical erosion will likely depend on their size, shape and growth form (Madin & Connolly 2006; Madin *et al.* 2014), which are highly variable at very local scales. However, we found no clear effects of either exposure or coral morphology/growth form in our analyses. Given the absence of major storms and cyclones during the study period, there is, thus, limited evidence to support the suggestion that physical disturbance was a key driver of coral erosion of complex growth forms at Lizard Island during our study period (during which no major storms occurred) (**Fig. 4.6**).

4.5.3 Drivers of coral erosion – Internal Bioerosion

Internal bioerosion is a process which can substantially remove calcium carbonate from recently dead coral colonies (Glynn 1997; Tribollet & Golubic 2011). This process comprises microbioerosion, which is often caused by chemical dissolution driven by microborers (Garcia-Pichel 2006; Grange *et al.* 2015), and macrobioerosion, caused most by polychaetes, bivalves, and sponges (Schönberg *et al.* 2017b, a). Despite being a natural process on coral reefs, future scenarios of ocean

warming and acidification are predicted to cause an increase in internal erosion rates by accelerating CaCO_3 dissolution (Reyes-Nivia *et al.* 2013; Leggat *et al.* 2019; Cornwall *et al.* 2021). However, internal bioerosion has relatively low rates of CaCO_3 removal if compared to external bioerosion. Indeed, extensive studies of the process of erosion at our study location (Lizard Island) have suggested that this process is relatively minor compared to erosion by parrotfishes. For example, Kiene & Hutchings (1994) found internal erosion rates ranging from 0.058 to 0.2 $\text{kg m}^{-2}\cdot\text{yr}^{-1}$ while the average rates of grazing erosion ranged from 0.30 to 1.96 $\text{kg m}^{-2}\cdot\text{yr}^{-1}$. Similarly, Osorno, Peyrot-Clausade, & Hutchings, (2005) showed internal erosion (by macrobores, sponges, polychaetes, and molluscs) accounted for just 0.035 $\text{kg m}^{-2}\cdot\text{yr}^{-1}$. These examples from Lizard Island also appear to be mirrored in other studies in other areas. For example, Yeung *et al.* (2021) found that in Hong Kong, total internal erosion ranged from 0.02 to 0.36 $\text{kg}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, while total erosion (i.e. internal and external) ranged from 0.72 to 3.09 $\text{kg}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. Similarly, Kuffner *et al.*, (2019) found that in the Florida Keys the average contributions of sponge erosion and microbioerosion was up to 0.1 and 0.2 $\text{kg m}^{-2}\cdot\text{yr}^{-1}$, respectively, while parrotfish bioerosion represented 1.6 $\text{kg m}^{-2}\cdot\text{yr}^{-1}$. Taken together, these results all suggest that, internal erosion is likely to account for only a small fraction of the total loss of calcium carbonate observed in our study.

It should be noted, however, that different kinds of erosion are not isolated and may interact with each other (Grange *et al.* 2015; Schönberg *et al.* 2017b). Internal erosion can weaken the structure of dead corals, particularly complex growth form colonies, by rapidly increasing its porosity and making them more susceptible to wave action or biological activity (Leggat *et al.* 2019). Internal erosion may also make corals more susceptible to external erosion (Chazottes *et al.* 1995; Tribollet & Golubic 2005). However, the lack of an effect of location or estimated external erosion on coral loss, suggests that internal erosion, if present, had only a limited impact, directly or indirectly.

4.5.4 Drivers of coral erosion – External Bioerosion

There is an extensive body of literature that identifies parrotfishes as the primary reef bioeroders (Bruggemann, van Kessel, van Rooij, & Breeman, 1996; Gygi, 1969; Kuffner et al., 2019; Morgan & Kench, 2016; Ong & Holland, 2010; Perry et al., 2012; Scoffin et al., 1977). Indeed, one of the key locations for the development of this work was Lizard Island, where the role of excavating parrotfish were first documented in the Indo-Pacific (Bellwood & Choat 1990; Bellwood 1995, 1996). However, our analyses did not find a clear correlation between predicted parrotfish erosion and the rates of coral colony erosion. This raises the question: why do our observations contrast so markedly with these past studies?

One of the first factors to consider in explaining our results is the context of the reef in question. Our study examined coral erosion on a heavily disturbed reef system where the selected habitats had significant coral cover (>10%), due to past cyclones (Madin *et al.* 2018) and crown-of-thorns starfish outbreaks (Pratchett, 2010) prior to our study beginning in 2016. These altered conditions may not be comparable to the relatively high coral cover reefs of the past, although they may be more representative of, and particularly relevant to, the frequently disturbed reefs of the future.

In addition, in terms of context, it is important to discount the role of sea urchins at our location as these are the other primary external bio-eroding organism on coral reefs (Glynn 1988; Griffin *et al.* 2003). While these organisms may contribute substantially to this process in some areas (Peyrot-Clausade *et al.* 2000; Dumont *et al.* 2013), the role of sea urchins in bioerosion at Lizard Island is extremely limited ($\sim 0.011 \text{ kg m}^{-2} \text{ year}^{-1}$) as their abundances are low (Young & Bellwood 2011; Tebbett & Bellwood 2018). Therefore, parrotfishes are the chief external bioeroders in this location (Kiene & Hutchings 1994; Bellwood 1995; Tebbett & Bellwood 2018).

After this process of elimination, which suggests other factors only have a limited capacity to account for the coral colony erosion rates in our study, this leaves parrotfish bioerosion as the chief

explanatory factor with the capacity to account for the observed erosion rates. Therefore, the most parsimonious explanation for the mismatch in parrotfish erosion versus coral colony erosion herein, could be that the most common current approach used to quantify parrotfish bioerosion on coral reefs are inadequate. Below we detail several potential limitations that could shape our understanding of parrotfish bioerosion. Importantly, we followed methods that aligned closely with those commonly used in this research field, therefore, these limitations may apply beyond our study. They suggest that our current understanding of parrotfish bioerosion is incomplete.

The first issue is that most estimates of parrotfish bioerosion are based on static, one-off surveys of fish abundance to calculate a dynamic process (bioerosion). In other words, these estimates are underpinned by the assumption that “presence = function”, with estimated functions assumed to occur homogeneously through space and time (discussed in (Bellwood *et al.* 2019b). While such a simplifying assumption may offer insights into the potential for functions to be delivered, it does not provide any information on the actual delivery of function by fishes. This point was previously highlighted as a major limitation in our understanding reef functions more generally (Bellwood *et al.* 2019b) and a growing number of studies are now documenting a substantial disconnect between fish presence and their capacity to deliver functions (Welsh & Bellwood 2012; Longo *et al.* 2014; Carlson *et al.* 2017; Streit *et al.* 2019; Tebbett *et al.* 2020). The results of our study support this earlier work. Our estimates of coral colony erosion represents the measurement of an actual process, accounting for variation in space and time, while the estimates of parrotfish bioerosion merely represents an estimate of a potential process. As there was no clear alignment between the two, this suggests that current approaches to estimating parrotfish bioerosion may not accurately reflect ecosystem processes documented herein.

One of the primary reasons why the assumption that presence = function may not apply to parrotfish bioerosion is the fact that one-off surveys do not account for temporal variation in parrotfish presence, i.e., in movement. As bioeroding parrotfishes such as *Chlorurus microrhinos*

have home ranges in the order of nearly 8000 m², and use space within this home range in a heterogenous manner (Welsh & Bellwood 2012), the abundance of parrotfishes at the spatial scale of our surveys per site (i.e., 500 m²) could vary over relatively short temporal scales. Indeed, parrotfish home-range can vary considerably depending on the spatial and temporal scales of measurement (Davis *et al.* 2017), with these patterns being tightly connected to different aspects of their life history and ecology (Afonso *et al.* 2008). Therefore, one-off surveys may not accurately capture temporal variability (although how many times surveys would have to be replicated to capture this variability is currently unclear). It is important to note, however, that while parrotfish presence may vary over short temporal scales, average parrotfish abundance at this location has remained relatively consistent across years despite major disturbances (Huertas, Morais, Bonaldo, & Bellwood, 2021; Morais *et al.*, 2020).

Given the size of parrotfish home ranges compared to the size of the surveys used in our study, and in most other studies on parrotfish bioerosion around the world, there is also the potential that we could have underestimated the abundance of key parrotfishes. In this respect, the size of surveys commonly used are unlikely to have captured the effect of the largest of all bioeroding parrotfishes, *Bolbometopon muricatum* (Bellwood, 1994). Rarely seen on, or recorded in, short transects, this rare species feeds on erect coral growth forms (Bellwood *et al.*, 2003), removing corals at the rate of 5 tonnes per individual fish per year. On the crests of outer reefs of the GBR, they can remove nearly 30 kg m⁻² yr⁻¹ of carbonate (Bellwood *et al.* 2003). Thus, only a few individuals would be required to completely clear the study sites and account for the erosion rates documented herein. While not observed in our surveys, *B. muricatum* have been seen in small groups at all our study locations around Lizard Island (on multiple occasions from 2016-2021) and are probably part of a larger group of ~50 individuals that roves around the Lizard Island complex (authors pers. obs. Supplementary Figure 4.3). However, given their rarity, and very large home ranges (with individuals like to roam over several kilometers in a day (Hamilton 2005), *B. muricatum* are highly unlikely to be detected in small-scale transects. Indeed, specific survey designs (that cover

4000-5000 m²) per site are required to have a good chance of documenting *B. muricatum* abundances (Bellwood *et al.* 2003). Therefore, the traditional transects used to study parrotfish bioerosion may overlook one of the most relevant bioeroders in the Indo-Pacific.

It must be noted, however, that Lizard Island may be atypical relative to many other modern reefs in the Indo-Pacific, as relatively healthy *Bolbometopon muricatum* populations are still present (Bellwood, Hoey, & Hughes, 2012). Across the Indo-Pacific, from Mauritius to French Polynesia, where *Bolbometopon*, in particular, have been heavily fished, external bioerosion by parrotfishes is now negligible (Bellwood, Hoey, & Hughes, 2012). Moreover, in other coral reef realms such as the Western Atlantic, there are no bioeroding parrotfishes comparable to *B. muricatum*, with reefs in this realm functioning in a different manner to Indo-Pacific reefs (Siqueira *et al.* 2019). Therefore, the rapid loss of coral colonies recorded on Lizard Island may represent an anomaly for most Anthropocene coral reefs. On reefs where *Bolbometopon* have been severely overfished, erosion rates of coral colonies may be far lower, warranting attention in future research.

Overall, it appears that the most parsimonious explanation for the mismatch between predicted parrotfish erosion and coral colony erosion is a combination of a spatial mismatch in functions and limitations with the current method of estimating parrotfish erosion, which may not effectively account for the largest of all bioeroders, *Bolbometopon muricatum*. Indeed, while frequently used, current methods for estimating parrotfish bioerosion had not previously been 'ground-truthed' against actual measurements of coral colony erosion on the reef. Given the mismatch we documented, and the fact that similar methods for estimating parrotfish erosion are widely applied across this entire research field, this suggests our current understanding of parrotfish bioerosion on coral reefs could be severely limited, especially in terms of the erosion of recently killed complex coral colonies.

4.5.5 Conclusion

By individually tracking the fate of dead coral colonies around Lizard Island, we revealed that corals with complex growth forms rapidly erode and, in most cases, completely disappear within 5 years. Such rapid erosion rates suggest that the calcium carbonate laid down by these corals may not be incorporated into the reef matrix. At most, these corals are likely to perform a role in reef growth that is more aligned to rubble or sand formation and infilling. Furthermore, among the potential physical and biological drivers investigated, we found no clear explanation for the rapid erosion observed, including no correlation with estimated rates of parrotfish erosion, the major reported bioeroders. This suggests that there is a gap in our understanding of how bioerosion of dead corals occurs on coral reefs. We hypothesise that, at Lizard Island, this may be accounted for by roving schools of *Bolbometopon*, but the evidence is circumstantial. Clearly, our understanding of reef growth and erosion is far from complete, especially under intensifying drivers of coral mortality from global climate change.

Chapter 5.

Natural recovery of corals after severe disturbance

This chapter is published as:

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5.1 Abstract

Ecosystem recovery from human-induced disturbances, whether through natural processes or restoration, is occurring worldwide. Yet, recovery dynamics, and their implications for broader ecosystem management, remain unclear. We explored recovery dynamics using coral reefs as a case study. We tracked the fate of 809 individual coral recruits that settled after a severe bleaching event at Lizard Island, Great Barrier Reef. Recruited *Acropora* corals, first detected in 2020, grew to coral cover levels that were equivalent to global average coral cover within just two years. Furthermore, we found that just 11.5 *Acropora* recruits per square meter were sufficient to reach this cover within two years. However, wave exposure, growth form, and colony density had a marked effect on recovery rates. Our results underscore the importance of considering natural recovery in management and restoration, and highlight how lessons learnt from reef recovery can inform our understanding of recovery dynamics in high-diversity climate-disturbed ecosystems.

5.2 Introduction

Human-induced ecosystem stressors, such as climate change, are intensifying, and reconfiguring ecosystems globally (Betts *et al.* 2017; Pecl *et al.* 2017; Arrigo *et al.* 2020). These stressors have affected almost all ecosystems, including those in terrestrial (Field *et al.* 2007; Mason *et al.* 2022), freshwater (O'Reilly *et al.* 2003), and marine realms (Hoegh-Guldberg & Bruno 2010), via their impacts on plant, faunal, and microbial biodiversity and abundance, across all trophic levels (van Moorsel *et al.* 2023). In turn, these stressors are compromising the capacity of ecosystems to sustain functions and services, and to resist future global changes (Dakos *et al.* 2015). However, ecosystems are inherently self-regulating systems that have developed mechanisms for self-repair (Holling 1973; Jones & Schmitz 2009). After a disturbance, or upon the removal of human-induced pressures, natural processes often bring the system back to a near-equilibrium state, if given enough time (O'Neill 1998; Arnoldi *et al.* 2018). However, as the temporal (shortening) and spatial (growing) scales of climate change-induced stress changes rapidly, the capacity of ecosystems to recover is becoming increasingly limited (Trisos *et al.* 2020; Vercelloni *et al.* 2020). Therefore, a better understanding of ecosystem recovery processes in the context of climate change is increasingly important for implementing relevant management strategies to enhance natural recovery and establishing priorities for ecosystem restoration efforts (Clewell & McDonald 2009; Jones *et al.* 2018; Montoya 2021).

Of all the world's ecosystems being impacted by climate change, coral reefs provide one of the most iconic examples (Graham *et al.* 2015; Hughes *et al.* 2017a; Sully *et al.* 2019). Indeed, bleaching-induced coral mortality has resulted in widespread concerns, with changes in coral reef structure, biodiversity, functioning, and productivity (Graham *et al.* 2015; Hughes *et al.* 2019a; Morais *et al.* 2022). In turn, this rapidly unfolding situation has raised questions about our approach to ecosystem management on coral reefs (Hughes *et al.* 2017a; Bruno *et al.* 2019; Morrison *et al.*

2020). Traditionally, interventions aimed at mitigating climate impacts on coral reefs have focused on reducing chronic pressures, to preserve ecosystem resilience, and to enhance coral survival (Graham *et al.* 2013; Harvey *et al.* 2018; Mcleod *et al.* 2019). However, given the recent shortening of recovery periods (Sully *et al.* 2019; Vercelloni *et al.* 2020), active management interventions such as coral restoration have grown in popularity among politicians and coral reef managers (Anthony *et al.* 2017; McLeod *et al.* 2022; Quigley *et al.* 2022).

Coral reef restoration is increasingly viewed as a promising tool to enhance coral reef resilience (McLeod *et al.* 2022). However, coral restoration can be expensive (Hughes *et al.* 2023), with the median cost per hectare for coral gardening estimated to be over 60 times higher than intertidal mangrove restoration and over 90 times greater than for sea grasses (Bayraktarov *et al.* 2016). Interestingly, in the last two years since the last major coral mortality event, some regions of the Great Barrier Reef are showing signs of extensive, natural recovery of coral cover, driven primarily by *Acropora* spp. (AIMS report 2022). This increase in coral cover is likely driven by two processes: a) growth of remnant (surviving) colonies, and/or b) coral recruitment with subsequent survival and growth (Pearson 1981; Graham *et al.* 2011; Linares *et al.* 2011).

Coral colony growth can drive rapid increases in coral cover (Diaz-Pulido *et al.* 2009; Kayal *et al.* 2018), yet this process depends on colony survival. Unfortunately, survivors are often scarce following coral bleaching mass-mortality events (Gilmour *et al.* 2013; Hughes *et al.* 2019a; Morais *et al.* 2021). In these cases, recruitment, survival, and growth of new corals are the main processes underpinning coral cover recovery (Gilmour *et al.* 2013; Gouezo *et al.* 2019; Evans *et al.* 2020; Edmunds 2023). In Moorea, for example, multiple studies have shown that fast coral cover recovery after disturbances largely depends on the successful growth and survival of new recruits, with recruitment in this location being predominantly driven by *Pocillopora* spp. (Bramanti & Edmunds 2016; Holbrook *et al.* 2018; Kayal *et al.* 2018). Similarly, in Palau, dormant recruits from before a typhoon disturbance that killed almost 100% of adult corals have been identified as the drivers of

subsequent fast recovery to pre-disturbance coral cover levels (Doropoulos *et al.* 2022). Thus, the rapid increase in coral cover, from 13% in 2017 to 36% in 2022, in the northern region of the GBR, (AIMS report 2022) seems to be at odds with the reported failure of coral recruitment (Hughes *et al.* 2019a) following the regional collapse of coral cover (Hughes *et al.* 2017b). Given this apparent mismatch, the challenge now is to understand the capacity of local reefs to support natural short-term coral recovery following widespread thermal disturbances. Against the backdrop of continued global coral demise, with contemporary global average coral cover sitting at just 25% (Tebbett *et al.* 2023), it is important to understand, and to quantify, the potential for natural recovery processes in order to inform ecosystem management and to place multimillion dollar restoration projects in context.

In this study, we take advantage of a unique opportunity in a GBR location where there was local extirpation of fast-growing *Acropora* corals after the back-to-back bleaching events in 2016 and 2017 (i.e. a 95% decline in *Acropora* cover at the scale of the whole island (Madin *et al.* 2018), and 100% mortality of branching and tabular *Acropora* colonies in our study area (Morais *et al.* 2021)). Following this extirpation, we were able to closely track the natural recovery of the reef system, which appears to have been tightly linked to recruitment in 2018/2019 (Tebbett *et al.* 2022a). Specifically, by using an extensive spatial design of fixed photo-quadrats, we were able to record and track the growth of 809 individual *Acropora* recruits over 2 years across the 16 km² wide Lizard Island reef complex on the GBR (**Fig. 5.1**, Supplementary Figure 5.1). Our goal was to evaluate the potential for natural coral recovery driven by fast-growing *Acropora* spp. and to examine how the physical setting (wave exposure), traits (growth form), and colony density affected the growth of recently-settled recruits. In quantifying this process our study provides insights into the potential of *Acropora* to increase coral cover after bleaching events.

5.3 Methods

5.3.1 Study area and sampling

Tracking of individual coral recruits was based on a widespread photo-quadrat census at Lizard Island (14°40' S, 145°28'E), a mid-shelf island in the northern region of the GBR. In recent years this region was impacted by two prolonged thermal events. First from February to April 2016, leading to the most severe coral bleaching recorded on the GBR, and second from January to March 2017, leading to additional bleaching-induced coral mortality (Madin *et al.* 2018; Richards *et al.* 2021; Tebbett *et al.* 2022a). In February 2016, immediately before the onset of major bleaching, a series of 19 permanent transects (between 50 – 210 m in length, as constrained by reef morphology) along the reef crest/edge (at 0-4 m below chart-datum) were established around Lizard Island (Supplementary Figure 5.1). Along each transect, between 12 and 38 quadrats (1 m² area), approximately 5 m apart, were photographed. For the present study, these transects were photographed: in January 2018 (24 months after the 2016 bleaching event); January 2020 (after 48 months), January/February 2021 (after 60 months) and January/February 2022 (after 72 months). Photo-quadrat methods follow (Wismer *et al.* 2019a) (see Text S1 for a full description).

In the photo-quadrats, we considered recruits to be all *Acropora* colonies that were first seen in photographs from the 2020 sampling campaign (i.e. they were not visually detectable in the photographs from the previous sampling in 2018). Recruits were defined as new colonies in our photographs that were larger than 3 cm² (~2 cm in diameter). The mean size of *Acropora* recruits at the first detection in our study was ~ 70 cm². The growth form of larger recruits was apparent at first detection, however, when this was unclear, growth form was readily identified in the subsequent photographs of the same recruits in 2021 and 2022 (see Text S2 for full details of coral recruits).

Following the identification of new *Acropora* spp. recruits in the photo-quadrats, we measured the planar surface area of each colony. To do this, planar colony live tissue area was measured (in cm²) by tracing around the live coral tissue of each colony using the software ImageJ and the quadrat as a scale (Schneider *et al.* 2012). This process was repeated for each colony in each sampling period. When colonies were partially covered, we estimated their size by tracing the natural shape of the colony based on the previous sampling photograph. Coral cover of each quadrat was considered to be the sum of individual *Acropora* colony areas relative to the 1 m² area of the quadrat. However, we classified colonies as 'partially covered' if they had a major part (50% or more) of their area covered by a neighboring colony. These colonies (6% of all colonies) were excluded from our estimates of coral cover to reduce colony overlap effects. Our comparison of coral cover was solely focused on the cover of the recruits tracked within our sampling area. To contextualize our findings with recruitment levels observed across the Indo-Pacific, we utilised a large-scale dataset available from the supplementary material of Koester *et al.* (2021). This dataset comprises estimates of coral recruitment (i.e. counts of recently-settled coral colonies) on natural reef substrata across 106 reefs in 11 different locations throughout the Indo-Pacific realm.

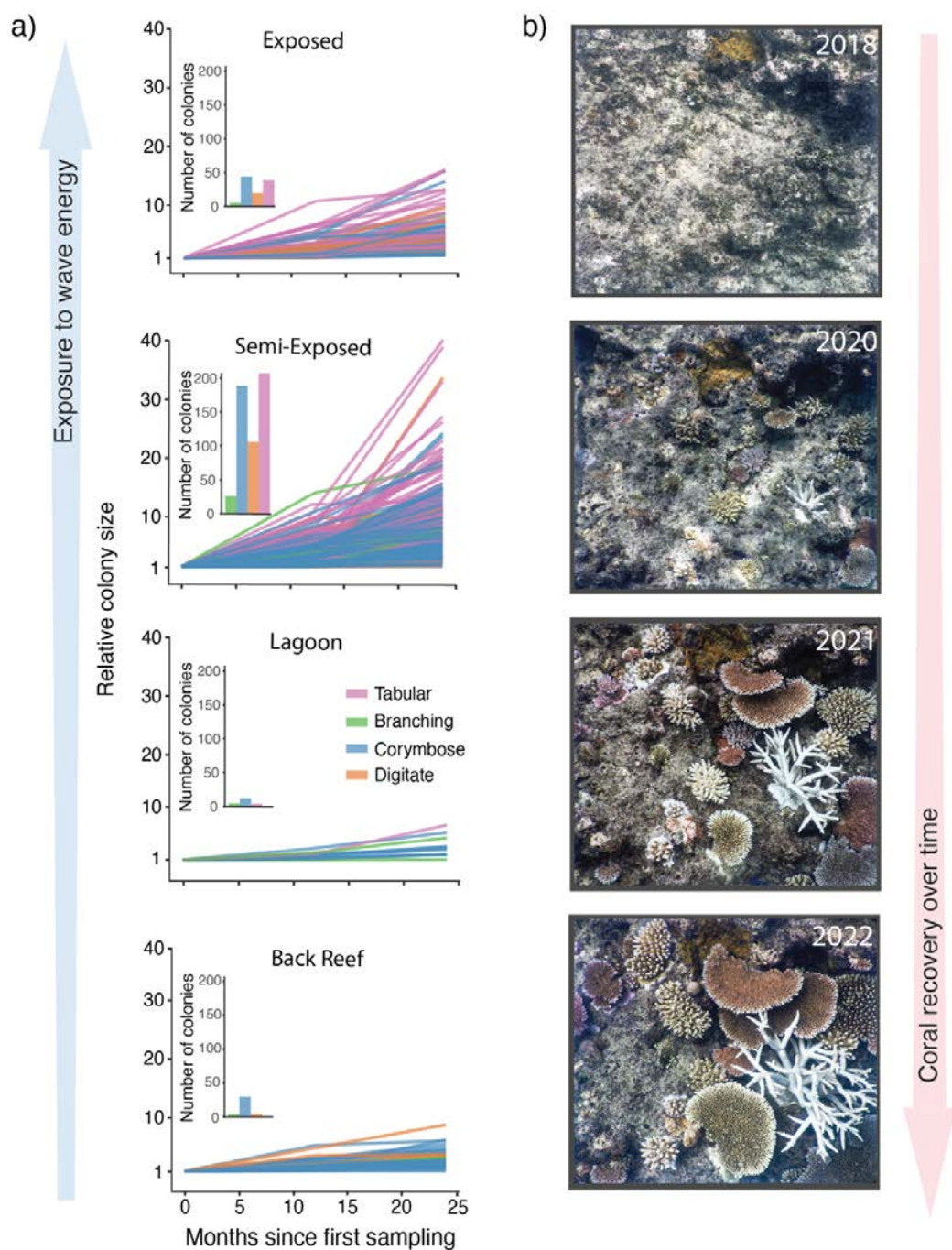


Figure 5.1 | a) Relative colony size of *Acropora* spp. coral recruits across the 24-month sampling period (2020-22). Each line represents a single colony, with colors representing the different growth forms. Relative size (cm^2) is the planar area of each colony relative to the size at first detection. The small bar graph inset in each panel represents the number of colonies from each growth form in each exposure level. **b) Example of a sequence of photo-quadrats from 2018 (before recruits were detected) to 2022 showing the growth of individual colonies and the increase of coral cover over time.**

5.3.2 Data analyses

Initially, we examined the relationship between *Acropora* coral cover change and recruit density to determine the minimum number of recruits needed to reach global average coral cover (i.e. 25%; cf. Tebbett *et al.* 2023) within 24 months (note all mentions of ‘global average coral cover’ refer to this level of 25% hereafter). To do this, we utilised a Bayesian generalized linear mixed-effects model (GLMM) with a gaussian distribution. In this model the change in *Acropora* cover (i.e. final – initial planar surface area per quadrat) during the 24 month period was treated as the response variable, while recruit density (individuals m⁻²) was fitted as a continuous fixed effect. Transect identity was also incorporated as a random effect in the model to account for any lack of spatial independence in the data. In addition to this model, we also wanted to examine how a range of factors were related to the growth rates of individual colonies. To do this, we used a second Bayesian GLMM. In this second model, we considered the growth rate of individual *Acropora* colonies as the difference in live tissue area between the first time each colony (recruit) was seen (2020) and subsequent observations (i.e. in 2021 and 2022). Note, data were only derived from recruits first detected in 2020 and all growth data were based on repeated measures of the exact same individual colonies. We then divided this difference by the sampling period (years) to obtain individual coral colony growth rate in cm² yr⁻¹. We then tested if the density of recruits (number of recruits m⁻²), level of wave exposure (see Supplementary Figure 5.1), coral growth form, and initial colony size (recruit size when first recorded in our sampling) influenced the subsequent growth rates of coral recruits at Lizard Island. This second GLMM was based on a Gamma distribution with a log-link function. Growth rate of individual coral colonies was the response variable, while recruit density, wave exposure, and the interaction between growth form and initial colony size were fitted as fixed effects. We also fitted quadrat identity, nested in transect identity, as a random effect to account for any lack of spatial independence. In both cases, the models were based on three MCMC

chains with 5000 iterations, including 1000 iterations to warm-up and a thinning interval of 5, to avoid within-chain autocorrelation, with weakly informative priors. Model fit and assumptions were evaluated using residual and auto-correlation plots, supplemented by metrics of sampling efficiency (\hat{r}) and effective sample size (neff) scores, all of which were satisfactory and suggested that the MCMC chains were well mixed and converged in both models. All Bayesian models were performed in Stan (Stan Development Team 2021) via the *brms* package (Bürkner 2017) in the software R (R Core Team 2020).

5.4 Results

By tracking the growth of 809 *Acropora* colonies that settled after severe back-to-back bleaching events in 2016 and 2017, we were able to examine the capacity of these corals to lead ecosystem recovery as they quickly drive coral cover increases (**Fig. 5.1**). Remarkably, *Acropora* corals have the potential to increase coral cover to levels that reach, or even exceed, the global average coral cover in coral reef habitats (25%) in just two years. However, this ability was strongly dependent on the number of recruits that had successfully settled, and survived, on the benthos. In this respect, we observed very low mortality rates. Only 18 of the 809 (2.2%) initial colonies died, while 114 (14.1%) were completely covered by neighbouring colonies. We found a strong positive relationship between recruit density and changes in coral cover over the subsequent two-year period (**Fig. 5.2**, Supplementary Figure 5.2, Supplementary Table 5.1). Based on this relationship, our model suggests that, on average, a density of just 11.5 *Acropora* recruits m^{-2} will yield 25% coral cover after two years (**Fig. 5.2a**, Supplementary Table 5.1). However, in areas with recruit densities lower than 11.5 individuals m^{-2} coral cover increase was slow and is likely to remain low (<10 %) even after two years (**Fig. 5.2b**).

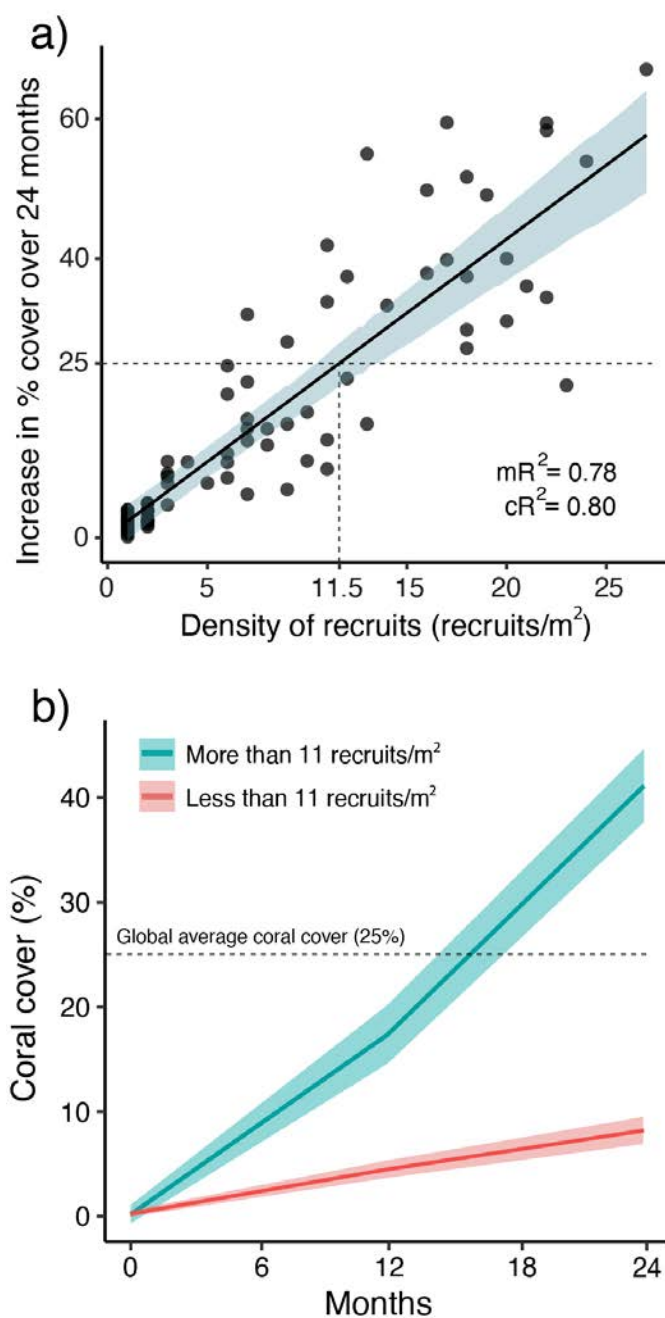


Figure 5.2 | a) The relationship between *Acropora* recruit density (individuals m⁻²) and the change in *Acropora* coral cover (%) in each quadrat over the 24-month study period. The black line and coloured ribbon denote the mean predicted fit and 95% credibility intervals of a Bayesian GLMM, while the dots show raw data points. The dashed lines represent the global average coral cover of 25% on coral reefs (cf. Tebbett et al. 2023) and the recruit density of 11.5 m⁻² that is the minimum density required, on average, to reach average global coral cover within two years. mR^2 = marginal R^2 and

The recovery of coral cover in areas with high *Acropora* recruitment appears to be strongly location dependent. In our study area, semi-exposed sites not only supported most of the recruits (78%; **Fig. 5.1**), but also recruits that grew approximately twice as fast as on lagoonal and back reefs, and about 30% faster than exposed sites (**Fig. 5.3a, b**, Supplementary Table 5.2). This was mediated by species traits (**Fig. 5.3c**) since our model detected an interaction between coral growth form and initial colony size (**Fig. 5.3c**, Supplementary Table 5.2). In general, tabular corals had the highest growth rates, followed by branching forms, while digitate forms had the slowest growth rates (**Fig. 5.3c**, Supplementary Figure 5.3). However, only exposed, and semi-exposed sites had *Acropora* recruits from all four growth forms: back reefs lacked tabular forms; lagoonal sites lacked digitate corals. Finally, our model also revealed a location-independent negative effect of recruit density on the growth rate of individual colonies (**Fig. 5.3d**, Supplementary Table 5.2). Specifically, within localities with relatively high recruitment, coral colonies grew less, on average, than colonies in less occupied areas (**Fig. 5.3d**, Supplementary Table 5.2).

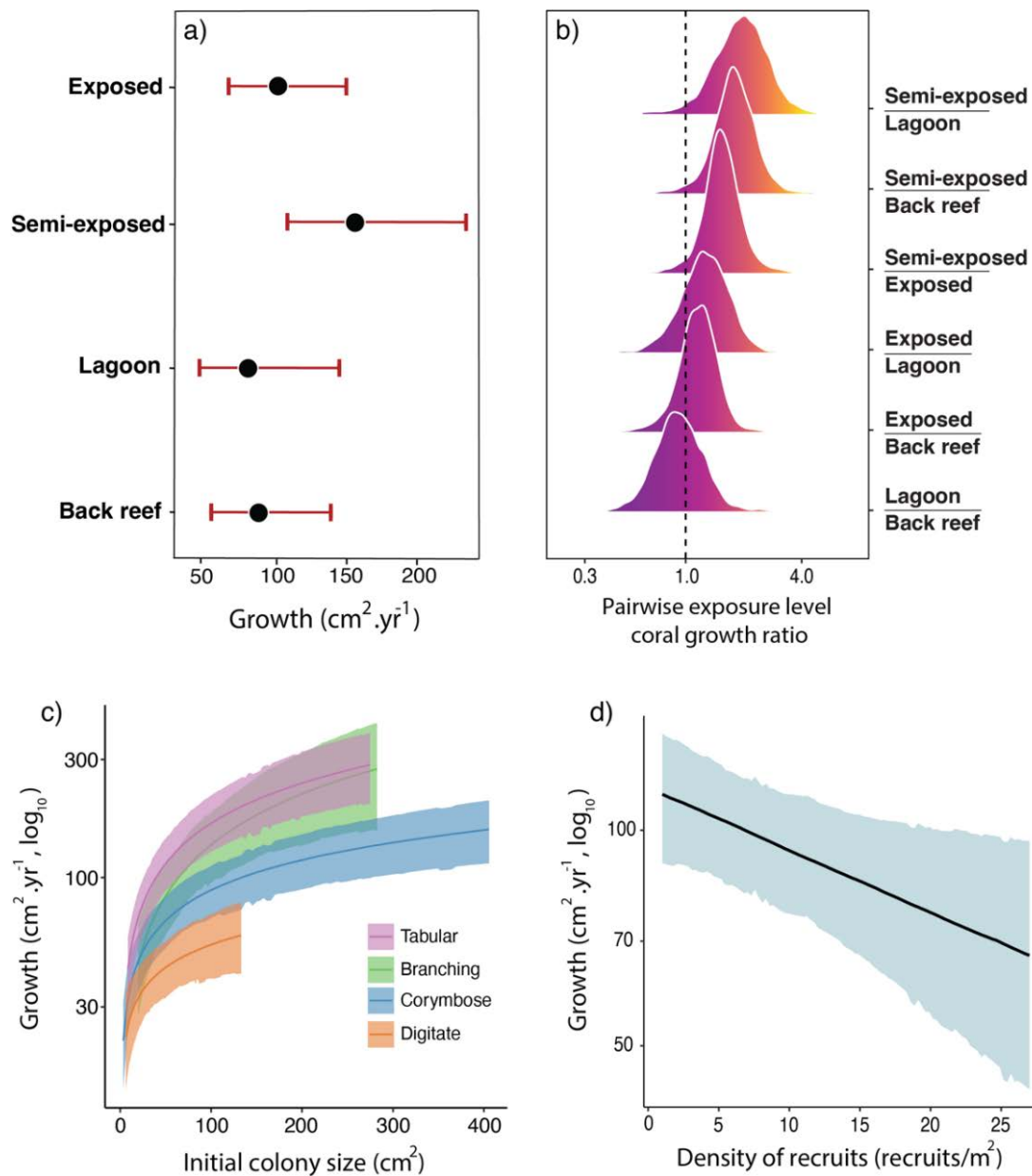


Figure 5.3 | Effect plots of the relationship between growth rates of individual *Acropora* colonies and the response variables based on a Bayesian generalised linear mixed effects model: a) model predicted colony growth rates for the different exposure levels; b) pairwise comparisons (ratio) of coral growth rates between the different exposure levels. Ratios were obtained using the draw values from our Bayesian generalised linear mixed effects model. Distributions with values predominantly exceeding 1 indicate that the exposure level in the numerator had higher colony growth rates, while distributions with values predominantly lower than 1 indicate that the exposure level in the numerator had lower colony growth rates; c) the interaction between initial colony size and coral growth form in

Throughout our study area, only 7.2% of the 428 quadrats (including those that did not have any coral recruits) had more recruits than the identified threshold for rapid coral cover recovery (i.e. 11 recruits m^{-2}) (**Fig. 5.4a**). Indeed, average recruit density across all quadrats was just 1.5 recruits m^{-2} . The proportion of quadrats with high recovery capacity herein (> 11 recruits m^{-2}) was virtually identical to values in an Indo-Pacific wide dataset of post-bleached reefs (**Fig. 5.4b**), showing that high post-bleaching coral recruitment is relatively rare. This observation contrasts starkly with recruitment rates in the same Indo-Pacific dataset for pre-bleached reefs, where 27% of transects had at least 11 recruits m^{-2} . The average recruit density for pre-bleached reefs was 9.96 recruits m^{-2} . This represents a more than three-fold decline, from 27 to 7.4%, in the proportion of samples featuring recruitment rates sufficient for rapid short-term coral recovery following bleaching events (**Fig. 5.4b**).

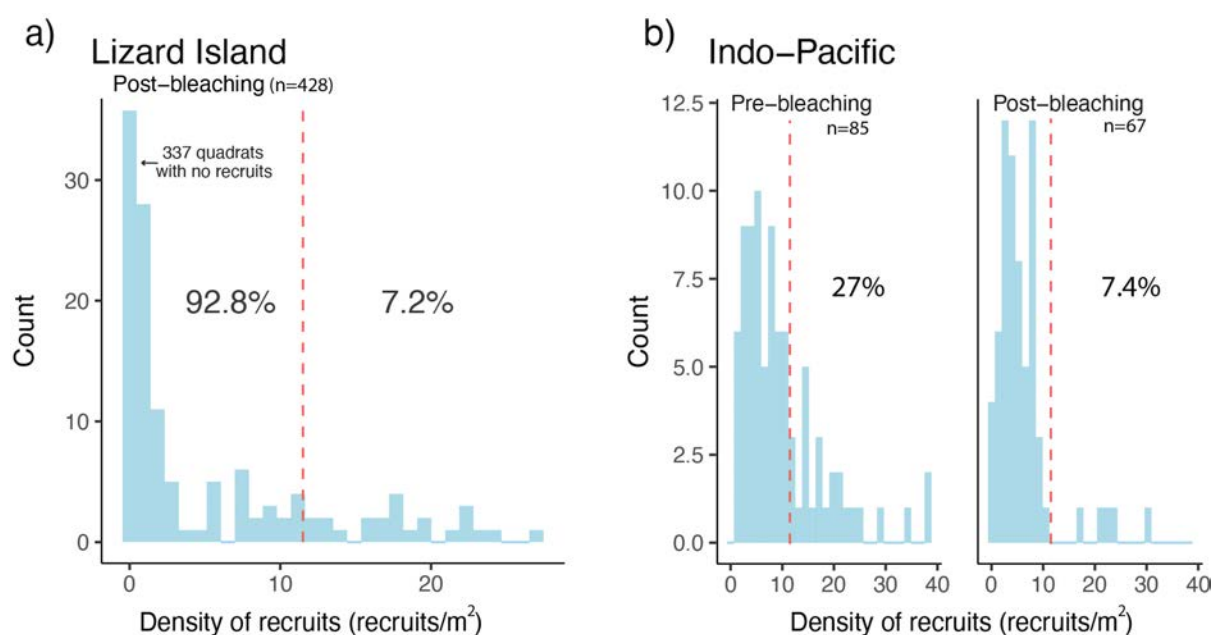


Figure 5.4 | Histograms showing frequency distributions of recruit density and the proportion of locations with more than 11 recruits per m^2 (percent values and the red dashed lines). a) Histogram with data from our study, which includes all quadrats from our sampling area, including those without colonies ($n = 428$). Note that to enhance visibility, given the zero-inflated nature of the data, we limited the y-axis. b) Histograms with data from 106 reefs at 11 Indo-Pacific locations, before and after local bleaching events (locations in which there

was no mention of bleaching events were assumed to represent pre-bleaching conditions). For panel (b) we used data compiled in Koester et al. (2021).

5.5 Discussion

5.5.1 Rapid recovery driven by early-successional species

Globally, disturbed ecosystems show inherent self-repair mechanisms, often with a recovery trajectory driven by early-successional species (Connell & Slatyer 1977; O'Neill 1998; Arnoldi *et al.* 2018). While these abundant species with high growth and colonization rates typically drive short-term recovery, such early-successional species are generally less prominent over longer-term recovery trajectories (Connell 1978; Arnoldi *et al.* 2018; Jentsch & White 2019). Thus, species-specific traits, combined with location contexts, significantly influence temporal and spatial recovery scales (Hewitt *et al.* 2022). In the Amazon rainforest, for example, early-successional species play a pivotal role in early recovery due to their fast growth and ability to establish in direct sunlight. Later, 'intermediate' species grow underneath early-successional species and eventually pave the way for 'climax' species in the final recovery stages (Uhl *et al.* 1981; Mausel *et al.* 1993). In the context of coral reefs, we quantified and highlighted the capacity of the early-successional *Acropora* to generate coral cover in a high-diversity tropical system (i.e. coral reefs around Lizard Island, Great Barrier Reef), following their local extirpation after back-to-back bleaching events in 2016 and 2017 (Madin *et al.* 2018; Morais *et al.* 2021). This marked recovery capacity was clearly dependent on the density of *Acropora* colonies that successfully settled to, and survived on, the benthos. These densities correlated strongly with coral cover in subsequent years. Indeed, we found that, on average, 11.5 or more recruits per m² were sufficient to recover coral cover to levels that are equivalent to the global average for coral reefs, in just two years. Importantly, our results from Lizard Island strongly align with those from a recent long-term monitoring report from the Australian

Institute of Marine Science (AIMS) which showed that for the entire northern GBR coral cover rapidly rose from a record low level (following the 2016 bleaching event) to its highest level (>75% coral cover on some reefs) since the beginning of the monitoring program (AIMS report 2022). This rapid recovery aligns with past research which has suggested that recovery in marine benthic systems can outpace recovery rates of other ecosystems (Jones & Schmitz 2009), although as recovery was heavily driven by one group of corals (*Acropora*) it also has implications for our understanding of ecosystem restoration and recovery debts (e.g. Moreno-Mateos *et al.* 2017).

The capacity for marine benthic systems to recover rapidly is underpinned by the demographic processes regulating the organisms that comprise these ecosystems (Carpenter & Turner 2000; Thrush & Whitlatch 2001). In this respect, the capacity for rapid coral cover recovery described in our study aligns with the results of a number of previous studies which have examined the links between demographic processes (i.e. recruitment, growth, and survival) of corals and the rapid recovery of coral cover (e.g. Bramanti & Edmunds 2016; Holbrook *et al.* 2018; Kayal *et al.* 2018; Edmunds 2021). For example, on reefs around Moorea, Holbrook *et al.* (2018) highlighted substantial variation in the rate and extent of recovery across different sites following disturbances, with some locations not only regaining their pre-disturbance coral cover but even surpassing it within five years. However, it should be noted that in this case, coral cover recovery was driven by *Pocillopora* spp. recruitment (i.e. brooding corals) rather than *Acropora* spp. (i.e. broadcast spawners) (Holbrook *et al.* 2018). In addition, another study in the same region examining coral demographic rates revealed that rapid recovery of coral cover is not solely dependent on recruitment, but also on the growth and survival of these recruits (Kayal *et al.* 2018). Such processes also appear to be important in our study system, as mortality rate of the colonies we tracked was very low (just 2.2% of colonies died during the study period). While this apparent coral recovery on the GBR appears to be positive, and contrary to some previous predictions, it raises a number of concerns.

One of the primary concerns has to do with the use of ‘coral cover’ as the metric of interest. This metric, analogous to commonly used forest metrics such as ‘canopy cover’, is broadly used to quantify coral reef declines (e.g. Gardner *et al.* 2003; Bellwood *et al.* 2004), yet it provides limited information concerning key aspects of ecosystem recovery (Connell 1973; Hughes 1984; Edmunds & Riegl 2020) and can mask recovery debts (see below). This information includes recruitment, size structure, and community composition, all of which are critical if one wishes to determine the demographic drivers underpinning coral cover changes and, most importantly, their functional implications (Edmunds & Riegl 2020; McWilliam *et al.* 2020; Dietzel *et al.* 2021a; González-Barrios *et al.* 2021). For example, it is well known that most of the early recovery of hard coral cover reported on Indo-Pacific reefs is mainly driven by one group of corals, fast-growing *Acropora* (Tanner *et al.* 1996; Emslie *et al.* 2008; Gilmour *et al.* 2013; Johns *et al.* 2014; Roff 2020). Here, we specifically focused on this group of corals to quantify the extent to which this group alone can increase coral cover. In doing so, we revealed that *Acropora* has the capacity to rapidly drive marked increases in coral cover in just two years, potentially underpinning the apparent ‘recovery’ in coral cover on the northern GBR.

5.5.2 Instability and potential for boom-and-bust dynamics

It is important to note that the ‘recovery window’ between disturbances is expected to shrink in the near future because of the intensification of human-induced impacts (Trisos *et al.* 2020; Vercelloni *et al.* 2020). Consequently, only short term-recovery will be possible in the new Anthropocene configuration. Thus, our results, in terms of coral reefs, are key to understanding how these short-term recovery dynamics may play out. Furthermore, it is also critical to place our findings of rapid coral cover recovery in a broader spatial context. Notably, only 7.2% of investigated quadrats in our study, including those with no recruits, had over 11 *Acropora* recruits per m², and thus the potential to reach 25% coral cover within two years. Indeed, the mean recruit density

herein, across all quadrats, was just 1.5 recruits per m², meaning it would take at least a decade to achieve the same 25% coral cover. This situation is very similar to data derived from 106 post-bleached reefs at 11 reef locations across the Indo-Pacific (see Table S5 in Koester *et al.* 2021), where only 7.4% of surveyed transects had the potential for rapid recovery (i.e. >11 recruits m⁻²) (**Fig. 5.4**). Thus, nearly 93% of the impacted sites will take more – and often much more – than two years to display the same degree of coral cover recovery after bleaching-induced mortality. A period of time that these coral reefs may not have as the median return time between severe bleaching events is already only 6 years, with this time forecast to become increasingly shorter (Hughes *et al.* 2018a; Vercelloni *et al.* 2020). Consequently, only a limited number of locations may have the opportunity for effective recovery, and these areas that do undergo recovery are expected to be subject to a cycle of rapid growth followed by disturbance-induced declines (Wilson *et al.* 2019; Pratchett *et al.* 2020; Morais *et al.* 2021). As such, these increases in coral cover may be the beginning of regional-scale boom-and-bust coral dynamics.

Importantly, the potential for boom-and-bust dynamics of *Acropora* colonies is also likely to be embedded in a distinct spatial context that is delineated by environmental variation; the recovery process was not evenly spread across coral growth forms nor exposure. Indeed, as for recruitment rates (cf. Tebbett *et al.* 2022a), there was distinct spatial patchiness in the growth rates of individual colonies across exposure regimes, with the rapid growth of tabular *Acropora* in semi-exposed locations being particularly notable. In this respect, our results support previous studies which suggest that tabular corals have one of the highest coral growth rates (Pratchett *et al.* 2015; Gold & Palumbi 2018) and, when combined with their shape and large size, can disproportionately enhance recovery rates of coral cover (Tanner *et al.* 1996; Ortiz *et al.* 2021). Hence, reefs dominated by tabular *Acropora* tend to recover rapidly in terms of coral cover (Linares *et al.* 2011; Osborne *et al.* 2011; Johns *et al.* 2014). However, the sensitivity of these corals to heat-induced bleaching means that these reefs also experience some of the most severe declines during marine heatwaves (Hughes *et al.* 2018b; Burn *et al.* 2023). The spatially patchy boom-and-bust coral dynamics may, therefore,

typify Anthropocene reefs, or habitats, that are dominated by tabular *Acropora* (Pratchett *et al.* 2020).

5.5.3 Restoration initiatives and recovery debt

The findings presented herein, in terms of coral recovery, also have important implications for reef restoration initiatives. Since restoration of reefs is a nascent practice, it is essential to transfer knowledge amassed in terrestrial ecosystems from decades of experience (Quigley *et al.* 2022). For example, facilitation of natural recovery is widely recognized as a key factor determining the success, or failure, of forest restoration initiatives (Shono *et al.* 2007; Clewell & McDonald 2009; Higgs *et al.* 2018). Thus, careful consideration of the appropriate scales of the interventions, as well as their location, has been identified as crucial for effective restoration efforts on coral reefs (Vardi *et al.* 2021; Quigley *et al.* 2022; Hughes *et al.* 2023; Madin *et al.* 2023). Indeed, in many cases, a spatial-temporal mismatch exists between the stressors acting on coral reef ecosystems that reduce coral cover (e.g. marine heatwaves, crown of thorns starfish outbreaks, cyclones) and restoration actions (Bellwood *et al.* 2019a). It is often not logistically or economically feasible to restore corals at large scales, although restoration could make a contribution at small scales, especially on high-value reefs (Hughes *et al.* 2023). In this endeavour, quantitative criteria may be important in determining the suitability of restoration interventions in different areas. This may include factors such as the likelihood of coral colony survival under future climate change conditions (Beyer *et al.* 2018), target coral density, and the growth rates of the selected coral species (Ladd *et al.* 2018; Edmunds & Putnam 2020; Madin *et al.* 2023).

As in forest restoration initiatives (Stanturf *et al.* 2014), coral restoration often prioritises fast-growing coral species which may enhance the rapid recovery of coral cover and re-establish some reef functions and structures (Kayal *et al.* 2015; Bramanti & Edmunds 2016; Ortiz *et al.* 2021). In this respect, our results provide invaluable guidance, as they suggest that if densities of just 11-12

Acropora recruits are established m^{-2} this can yield 25% coral cover after two years. A coral colony target that appears to also represent a good middle-ground when density dependent effects are fully considered (see Text S3 for a full discussion). Nevertheless, any intervention needs to be placed in the context of natural recovery phenomena and the existing cover of corals (Clewell & McDonald 2009). Indeed, when considering the extent and speed of natural recovery the question may shift from 'how to restore' to 'if to restore', especially as the primary cause of declines (i.e. climate change), has yet to be addressed. In this respect, it is valuable to consider what prioritising fast growing early-successional species can mean for the recovery debts that ecosystems experience during disturbance.

Species that are rare and exhibit slow growth and low colonization rates tend to face a greater risk of local or even global extirpation after disturbance due to insufficient time for recovery (Leão *et al.* 2014; Morais *et al.* 2021). For example, while marine ecosystems have one of the quickest recovery rates among six major ecosystem categories (i.e. forests, grasslands, wetlands, rivers, lakes, and marine), they also incur a substantial recovery debt in terms of reduced biodiversity and functions during the recovery process (Moreno-Mateos *et al.* 2017). Coral reefs may be at the forefront in facing this issue, with most of the short-term recovery driven by fast growing early-successional *Acropora* corals, which are also the primary corals replanted in coral restoration (Boström-Einarsson *et al.* 2020). Meanwhile, species with slower growth and lower colonization rates are experiencing protracted population declines (Pratchett *et al.* 2020; Morais *et al.* 2021) and are rarely prioritised in restoration initiatives (Boström-Einarsson *et al.* 2020). Therefore, the combined influence of rapid natural recovery in fast growing species and the enhanced recovery of such species via restoration, may accentuate recovery debts as slower-growing rare species are increasingly overlooked. This could indicate the future trajectory for numerous other ecosystems, aligning with a broad new framework of high turnover recovery dynamics in climate-disturbed systems (e.g. Jones & Schmitz 2009; Donohue *et al.* 2010; Wilcox *et al.* 2020; Yim *et al.* 2020). Therefore, the fast, yet potentially unstable, recovery reported herein, driven by abundant and fast-

growing species, may become progressively more common among climate-disturbed ecosystems, making coral reefs a perfect case study for the understanding of recovery dynamics in high diversity systems.

5.5.4 Conclusions

Overall, our data revealed the marked capacity of *Acropora* corals to recolonise reefs following severe mortality, with reefs regaining high coral cover within a few years. While such a result may offer grounds for optimism, we must be cautious when interpreting reef recovery based solely on coral cover. Furthermore, it is critical to note that *Acropora* are highly vulnerable to disturbances, which may lead to boom-and-bust dynamics; an emerging phenomenon in disturbed ecosystems globally. Coral reefs have remarkable natural recovery potential, drawing a strong parallel with forests that quickly recover canopy cover as a result of fast-growing trees. However, there are concerns pertaining to recovery debts and the logistics of restoration in both systems, especially as restoration projects often focus on species that already exhibit a high potential for natural recovery. Going forward, reef management, like management in terrestrial systems, may need to operate within an increasingly dynamic framework. Rapid recovery on coral reefs may not be a cause for optimism; it may simply reflect high-speed boom-and-bust dynamics.

Chapter 6. Concluding Discussion

The early research into coral population dynamics shed light on the distinct life histories of individual coral colonies (Connell 1973; Hughes & Jackson 1980, 1985; Hughes 1984). Since that time, the world's coral reefs have undergone significant changes. Coral abundance and diversity have been significantly declining in many parts of the world due to human-induced climate change (Hughes *et al.* 2017a, 2018b; Eakin *et al.* 2019). Coral reefs have already faced three global bleaching events (1998, 2010 and 2014-2017) (Skirving *et al.* 2019), in addition to more localised events that have occurred worldwide (Hughes *et al.* 2018a; Sully *et al.* 2019). Australia's Great Barrier Reef, the world's largest coral reef system, has experienced five mass coral bleaching events from 1998 to 2020 (Hughes *et al.* 2021; Pratchett *et al.* 2021). The cumulative impact from these repeated events has decimated many coral populations, reducing the number of adult colonies (i.e. potential sources of recruits) at a spatial scale that has likely affected the connectivity and recovery capacity of coral populations (Hughes *et al.* 2019a; Dietzel *et al.* 2021b). Due to the predicted increase in both the frequency and severity of thermal anomalies, it is expected that bleaching-induced coral mortality will significantly escalate by the century's end (Vercelloni *et al.* 2020; IPCC 2023). Such frequent and extensive disturbances present considerable challenges to the resilience of coral populations. Consequently, an unprecedented demand has emerged for comprehensive coral demographic studies that provide data beyond coral cover, aiming to obtain higher resolution when evaluating the changing trajectories of coral populations (Dietzel *et al.* 2020; Edmunds & Riegl 2020; Pratchett *et al.* 2020).

In this thesis, I explored the population dynamics and functional response of corals to disturbances, extending beyond coral cover. By incorporating analysis of individual coral colonies, the results presented here help to fill gaps in our understanding of coral demographic trends across multiple spatial and temporal scales. In **Chapter 2**, I revealed how the colony-level population

dynamics of two archetypical coral types, massive *Porites* and *Acropora*, have responded in distinctly different manners over multiple thermal disturbances events and a recovery phase (Morais *et al.* 2021). Fast-growing *Acropora* colonies, which are highly susceptible to bleaching, experienced substantial recruitment and fast growth after complete local extirpation, revealing a marked capacity for apparent 'recovery'. On the other hand, stress-tolerant colonies of massive *Porites* showed very low mortality; however, the concomitant absence of new colonies during this period implies that recruitment is rare and potentially unpredictable. These distinct colony-level population dynamics provide reasons for both hope and concern. While the resilience of individual colonies of massive *Porites* is evident, inconsistency or rarity of recruitment may negatively impact populations over longer timespans. On the other hand, although individual *Acropora* colonies are more susceptible and likely to be the most affected by subsequent bleaching events (Gilmour *et al.* 2013; Pratchett *et al.* 2020), at the level of population, these corals exhibit a notable ability to rebound after disturbances.

In **Chapter 3**, I carry an in-depth examination of the bleaching susceptibility of massive *Porites* across various hydrodynamics exposure levels (Morais *et al.* 2024), building on the foundational insights about this coral group presented in **Chapter 2**. The findings in this chapter indicate that, even on small spatial scales, massive *Porites* populations vary considerably in their bleaching prevalence and bleaching extent. This highlights the importance of considering location-specific factors when assessing coral health, also emphasising the vulnerability of corals in lagoonal habitats to rapid and/or prolonged elevated temperatures.

In **Chapter 4** I shift my attention to the colonies that died after the bleaching events (Morais *et al.* 2022). Due to the calcium carbonate skeleton, coral colonies keep providing structural complexity to the reef system even after mortality. That is why, in this chapter, I followed the fate of bleaching-induced dead colonies for up to 5 years to investigate how long the structure of coral colonies remains after mortality, and how is the loss of coral structure related to estimated erosion

rates. The results of this chapter showed that most dead colonies completely disappeared within 5 years. Moreover, there was no effect of estimated parrotfish bioerosion, wave exposure, or coral growth form, on observed erosion rates. This suggested that our understanding of the erosion of dead corals and the contribution of these colonies to reef matrix growth may be more limited than previously thought. Finally, in **Chapter 5**, I was interested in evaluating the potential for natural coral recovery driven by fast-growing *Acropora* spp. and examining how the physical characteristics (wave exposure), traits (growth form), and colony density affected the growth of recently settled recruits (Morais *et al.* 2023). The findings in this chapter offer some hope for the natural recovery of corals following thermal disturbances. However, it also showed that physical and demographic features, such as wave exposure, growth form, and colony density had a noticeable effect on these recovery rates. As a result, only a limited fraction of reefs across the Indo-Pacific region exhibited the potential for such recovery. This is reflected in the coral cover results presented in Chapter 2. In that chapter, I calculated the average coral cover by including all quadrats, even those without coral recruits. This approach revealed a remarkably low mean coral cover, indication that high recovery rates are not likely to be uniform across different reefs and are likely to be quite limited for some habitats or locations. Indeed, the likelihood of this recovery becoming a sustained, long-term process relies on effective actions being taken to tackle climate change. Lastly, this chapter also highlights the importance of considering natural recovery in coral reef management and restoration projects.

6.1 Delving into Demographics: Understanding Coral Populations Beyond Cover

This thesis underscores the critical need to delve into the demographic dynamics of coral populations, extending far beyond changes in coral cover, to fully understand the effects of disturbances (Dietzel *et al.* 2020; Edmunds & Riegl 2020). A sole focus on coral cover metrics provides an incomplete scenario, omitting crucial details of coral demography such as recruitment,

mortality, and growth—all of which are essential for a comprehensive understanding of the health and resilience of coral populations (Kayal *et al.* 2015; Pisapia *et al.* 2020; Edmunds 2021b, 2023). Specifically, in this thesis, I investigate temporal (**chapters 2, 4, 5**) and spatial (**chapters 3, 4, 5**) aspects of individual coral colonies' response to disturbance, revealing important insights into population dynamics and the functions provided by corals. The ability to measure individual colony sizes over time was pivotal to this analysis. Here, I showed that it is feasible to reassess historical datasets, acquiring valuable insights into the historical dynamics of coral populations. By using archival images from a long-term monitoring program, which was originally not designed for demographic studies (see Wismer *et al.* 2019b, a), I was able to retrospectively analyse colony sizes and other fundamental demographic features. These types of images, when scaled appropriately, enable the measurement of planar extents of dead and live coral colonies, providing a historical record from which growth rates, mortality, erosion, and recruitment can be inferred (Edmunds & Riegl 2020). There is a vast number of photographic long-term datasets around the world that were not initially intended for demographic studies, yet they possess the potential for measurement and monitoring of individual coral colonies over time. These images not only provide a snapshot of coral cover but also allow for retrospective analyses of coral colony sizes and other basic demographic properties. Therefore, mining data from existing datasets, particularly where legacy image-based data are available, offers an opportunity to enhance the accuracy of models that will predict future scenarios where no other fit for purpose, high-quality resources are available. These may complement widely available, yet limited, metrics such as coral cover in informing conservation strategies to bolster the resilience and functionality of coral in the Anthropocene.

6.2 Implications and future avenues

The findings outlined in this thesis open promising pathways for future research. For example, In **Chapter 4**, I used an innovative method that allows us to predict the colony volume,

which is a 3D metric, based only on the planar area, a 2D metric, extracted from bird's-eye-view photographs (House *et al.* 2018; Urbina-Barreto *et al.* 2021). By using this method, I was able to estimate the erosion of individual colonies over time after colony mortality. This technique opens a wide range of possibilities in investigating tri-dimensional function delivery by corals simply using planar area from photo-quadrats. Furthermore, this chapter also highlighted the notable discrepancy between the estimated bioerosion by parrotfish and the actual erosion observed in dead coral colonies. The hypothesis presented suggests that this discrepancy may stem from the shortcomings of the prevalent method used to quantify bioerosion, which predominantly relies on inferences from parrotfish abundance. This indicates that the method may not fully capture the realised functions at appropriate scale and might overlook some large home-range bioeroding agents or processes. Therefore, it is evident that there is a substantial new field ripe for exploration that will need innovative and more complete approaches to accurately estimate bioerosion.

Another example can be noted in **Chapter 5**, which outlines a range of promising directions for future research, opening avenues for in-depth exploration. This chapter showed that there is a need for dissecting the spatial and temporal scales of coral recovery, which hinge on the traits of specific species and the varying contexts of hydrodynamics conditions. It calls for a deeper evaluation of how different environmental settings can influence coral recovery potential, with a special focus on the role played by early-successional species. The results of **Chapter 5** also stress the importance of comprehending the effects of rapid coral cover recovery on the broader scope of ecosystem restoration efforts. It highlights the need for monitoring programs to focus on demographic aspects and more relevant response variables to better capture the contribution of the natural recovery process following acute disturbance (Dietzel *et al.* 2020). Consequently, it will better inform managers and policymakers about the relative practicality and scale of artificial restoration interventions, in light of the significant investment dedicated to these projects worldwide (Hughes *et al.* 2023).

An important direction for future coral reef research is the application of the metrics and ideas from this thesis across a broader array of coral groups. Although this work has centred on *Acropora* and *Porites* due to their abundance and ecological significance, there is a risk that neglecting other species in our research agendas could lead to their gradual oversight. Recognizing the rich diversity of coral genera is vital for a well-rounded understanding and effective reef management. As such, it is crucial to include these less-studied species in future studies to inform more holistic conservation strategies.

In summary, this thesis advances our understanding of demographic and functional changes in coral populations due to human-induced disturbances, analysing both spatial and temporal dimensions of bleaching, erosion, and recovery of corals. Prior research has predominantly focused on shifts in coral cover as indicators of human impact (De'ath *et al.* 2012; Tebbett *et al.* 2023). These studies often overlook the comprehensive quantitative analysis required to fully understand the demographic dynamics of coral populations and the ecological functions delivered by individual coral colonies. While some results of my chapters may offer some hope, revealing that certain coral groups may experience rapid recovery due to their specific traits, the long-term prospects for coral population viability are bleak and reefs are increasingly at risk. This is primarily because the narrowing 'recovery window' between disturbances due to the intensification of human-induced impacts (Trisos *et al.* 2020; Vercelloni *et al.* 2020). These findings underscore the critical need to address greenhouse gas emissions as a measure against anthropogenic global warming, aiming to foster the resilience and eventual recovery of coral reef ecosystems and preserve their essential functions.

References

- Abràmoff, M.D., Hospitals, I., Magalhães, P.J. & Abràmoff, M. (2004). Image Processing with ImageJ. *Biophotonics Int.*
- Afonso, P., Fontes, J., Holland, K.N. & Santos, R.S. (2008). Social status determines behaviour and habitat usage in a temperate parrotfish: Implications for marine reserve design. *Mar. Ecol. Prog. Ser.*, 359, 215–227.
- Ainsworth, T.D., Heron, S.F., Ortiz, J.C., Mumby, P.J., Grech, A., Ogawa, D., *et al.* (2016). Climate change disables coral bleaching protection on the Great Barrier Reef. *Science (80-.)*, 352, 338–342.
- Alvarez-Filip, L., Dulvy, N.K., Côte, I.M., Watkinson, A.R. & Gill, J.A. (2011). Coral identity underpins architectural complexity on Caribbean reefs. *Ecol. Appl.*, 21, 2223–2231.
- Alwany, M.A., Thaler, E. & Stachowitsch, M. (2009). Parrotfish bioerosion on Egyptian Red Sea reefs. *J. Exp. Mar. Bio. Ecol.*, 371, 170–176.
- Anthony, K., Bay, L.K., Costanza, R., Firn, J., Gunn, J., Harrison, P., *et al.* (2017). New interventions are needed to save coral reefs. *Nat. Ecol. Evol.*, 1, 1420–1422.
- Arnoldi, J.-F., Bideault, A., Loreau, M. & Haegeman, B. (2018). How ecosystems recover from pulse perturbations: A theory of short- to long-term responses. *J. Theor. Biol.*, 436, 79–92.
- Arrigo, K.R., van Dijken, G.L., Cameron, M.A., van der Grient, J., Wedding, L.M., Hazen, L., *et al.* (2020). Synergistic interactions among growing stressors increase risk to an Arctic ecosystem. *Nat. Commun.*, 11, 6255.
- Aston, E.A., Duce, S., Hoey, A.S. & Ferrari, R. (2022). A Protocol for Extracting Structural Metrics From 3D Reconstructions of Corals. *Front. Mar. Sci.*, 9, 1–14.
- Bainbridge, S.J. (2017). Temperature and light patterns at four reefs along the Great Barrier Reef during the 2015–2016 austral summer: understanding patterns of observed coral bleaching. *J. Oper. Oceanogr.*, 10, 16–29.
- Baird, A., Emslie, M. & Lewis, A. (2012). Extended periods of coral recruitment on the Great Barrier Reef. *Proc. 12th Int. Coral Reef Symp.*
- Bak, R.P.M. & Meesters, E.H. (1998). Coral population structure: the hidden information of colony

- size-frequency distributions. *Mar. Ecol. Prog. Ser.*, 162, 301–306.
- Barlow, J., França, F., Gardner, T.A., Hicks, C.C., Lennox, G.D., Berenguer, E., *et al.* (2018). The future of hyperdiverse tropical ecosystems. *Nature*, 559, 517–526.
- Barshis, D.J., Birkeland, C., Toonen, R.J., Gates, R.D. & Stillman, J.H. (2018). High-frequency temperature variability mirrors fixed differences in thermal limits of the massive coral *Porites lobata* (Dana, 1846). *J. Exp. Biol.*, 221.
- Bayley, D.T.I. & Mogg, A.O.M. (2020). A protocol for the large-scale analysis of reefs using Structure from Motion photogrammetry. *Methods Ecol. Evol.*, 11, 1410–1420.
- Bayraktarov, E., Saunders, M.I., Abdullah, S., Mills, M., Beher, J., Possingham, H.P., *et al.* (2016). The cost and feasibility of marine coastal restoration. *Ecol. Appl.*, 26, 15-1077.1.
- Bellwood, D.R. (1994). A Phylogenetic Study of the Parrotfishes Family Scaridae (Pisces: Labroidei), with a Revision of Genera. *Rec. Aust. Museum Suppl.*, 20, 1–86.
- Bellwood, D.R. (1995). Direct estimate of bioerosion by two parrotfish species, *Chlorurus gibbus* and *C. sordidus*, on the Great Barrier Reef, Australia. *Mar. Biol.*, 121, 419–429.
- Bellwood, D.R. (1996). Production and reworking of sediment by parrotfishes (family Scaridae) on the Great Barrier Reef, Australia. *Mar. Biol.*, 125, 795–800.
- Bellwood, D.R. & Choat, J.H. (1990). A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environ. Biol. Fishes*, 28, 189–214.
- Bellwood, D.R., Hoey, A.S. & Choat, J.H. (2003). Limited functional redundancy in high diversity systems: Resilience and ecosystem function on coral reefs. *Ecol. Lett.*, 6, 281–285.
- Bellwood, D.R., Hoey, A.S. & Hughes, T.P. (2012). Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proc. R. Soc. B Biol. Sci.*, 279, 1621–1629.
- Bellwood, D.R., Hughes, T.P., Folke, C. & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, 429, 827–833.
- Bellwood, D.R., Pratchett, M.S., Morrison, T.H., Gurney, G.G., Hughes, T.P., Álvarez-Romero, J.G., *et al.* (2019a). Coral reef conservation in the Anthropocene: Confronting spatial mismatches and prioritizing functions. *Biol. Conserv.*, 236, 604–615.
- Bellwood, D.R., Streit, R.P., Brandl, S.J. & Tebbett, S.B. (2019b). The meaning of the term ‘function’ in ecology: A coral reef perspective. *Funct. Ecol.*, 33, 948–961.

- Betts, M.G., Wolf, C., Ripple, W.J., Phalan, B., Millers, K.A., Duarte, A., *et al.* (2017). Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature*, 547, 441–444.
- Beyer, H.L., Kennedy, E. V., Beger, M., Chen, C.A., Cinner, J.E., Darling, E.S., *et al.* (2018). Risk-sensitive planning for conserving coral reefs under rapid climate change. *Conserv. Lett.*, 11, 1–10.
- Boström-Einarsson, L., Babcock, R.C., Bayraktarov, E., Ceccarelli, D., Cook, N., Ferse, S.C.A., *et al.* (2020). Coral restoration – A systematic review of current methods, successes, failures and future directions. *PLoS One*, 15, e0226631.
- Bozec, Y.M., Alvarez-Filip, L. & Mumby, P.J. (2015). The dynamics of architectural complexity on coral reefs under climate change. *Glob. Chang. Biol.*, 21, 223–235.
- Bramanti, L. & Edmunds, P.J. (2016). Density-associated recruitment mediates coral population dynamics on a coral reef. *Coral Reefs*, 35, 543–553.
- Brandl, S.J., Goatley, C.H.R., Bellwood, D.R. & Tornabene, L. (2018). The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs. *Biol. Rev.*, 93, 1846–1873.
- Brooks, M.E., Kristensen, K., Benthem, Koen, J., V., Magnusson, A., Berg, Casper, W., Nielsen, A., *et al.* (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *R J.*, 9, 378.
- Brown, K.T., Bender-Champ, D., Achlatis, M., van der Zande, R.M., Kubicek, A., Martin, S.B., *et al.* (2021). Habitat-specific biogenic production and erosion influences net framework and sediment coral reef carbonate budgets. *Limnol. Oceanogr.*, 66, 349–365.
- Bruggemann, J., van Kessel, A., van Rooij, J. & Breeman, A. (1996). Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: implications of fish size, feeding mode and habitat use. *Mar. Ecol. Prog. Ser.*, 134, 59–71.
- Bruno, J.F., Bates, A.E., Cacciapaglia, C., Pike, E.P., Amstrup, S.C., van Hooijdonk, R., *et al.* (2018). Climate change threatens the world's marine protected areas. *Nat. Clim. Chang.*, 8, 499–503.
- Bruno, J.F., Côté, I.M. & Toth, L.T. (2019). Climate Change, Coral Loss, and the Curious Case of the Parrotfish Paradigm: Why Don't Marine Protected Areas Improve Reef Resilience? *Ann. Rev. Mar. Sci.*, 11, 307–334.
- Bruno, J.F., Selig, E.R., Casey, K.S., Page, C.A., Willis, B.L., Harvell, C.D., *et al.* (2007). Thermal Stress and Coral Cover as Drivers of Coral Disease Outbreaks. *PLOS Biol.*, 5, e124.

- Budd, A.F. & Pandolfi, J.M. (2010). Evolutionary novelty is concentrated at the edge of coral species distributions. *Science.*, 328, 1558–1561.
- Burke, S., Pottier, P., Lagisz, M., Macartney, E.L., Ainsworth, T., Drobniak, S.M., *et al.* (2023). The impact of rising temperatures on the prevalence of coral diseases and its predictability: A global meta-analysis. *Ecol. Lett.*, 1–16.
- Bürkner, P.-C. (2017). brms : An R Package for Bayesian Multilevel Models Using Stan. *J. Stat. Softw.*, 80, 1–28.
- Burn, D., Hoey, A.S., Matthews, S., Harrison, H.B. & Pratchett, M.S. (2023). Differential bleaching susceptibility among coral taxa and colony sizes, relative to bleaching severity across Australia’s Great Barrier Reef and Coral Sea Marine Parks. *Mar. Pollut. Bull.*, 191, 114907.
- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P. & Menge, B.A. (1996). Recruitment and the Local Dynamics of Open Marine Populations. *Annu. Rev. Ecol. Syst.*, 27, 477–500.
- Cant, J., Salguero-Gómez, R. & Beger, M. (2022). Transient demographic approaches can drastically expand the toolbox of coral reef science. *Coral Reefs*, 41, 885–896.
- Cantin, N.E. & Lough, J.M. (2014). Surviving coral bleaching events: Porites growth anomalies on the great barrier reef. *PLoS One.*, 9, e88720.
- Carlot, J., Kayal, M., Lenihan, H.S., Brandl, S.J., Casey, J.M., Adjeroud, M., *et al.* (2021). Juvenile corals underpin coral reef carbonate production after disturbance. *Glob. Chang. Biol.*, 27, 2623–2632.
- Carlot, J., Vousdoukas, M., Rovere, A., Karambas, T., Lenihan, H.S., Kayal, M., *et al.* (2023). Coral reef structural complexity loss exposes coastlines to waves. *Sci. Rep.*, 13, 1683.
- Carlson, P., Davis, K., Warner, R. & Caselle, J. (2017). Fine-scale spatial patterns of parrotfish herbivory are shaped by resource availability. *Mar. Ecol. Prog. Ser.*, 577, 165–176.
- Carpenter, K.E., Abrar, M., Aeby, G., Aronson, R.B., Banks, S., Bruckner, A., *et al.* (2008). One-Third of Reef-Building Corals Face Elevated Extinction Risk from Climate Change and Local Impacts. *Science (80-)*, 321, 560–563.
- Carpenter, S.R. & Turner, M.G. (2000). Hares and Tortoises: Interactions of Fast and Slow Variables in Ecosystems. *Ecosystems*, 3, 495–497.
- Caswell, H. (2001). Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer Associates. *SERBIULA (sistema Libr. 2.0)*.

- Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci.*, 114, E6089–E6096.
- Cesar, H., Burke, L. & Pet-Soede, L. (2003). The economics of worldwide coral reef degradation. *Environ. Econ. Consult.*
- Chazottes, V., Campion-Alsumard, T.L. & Peyrot-Clausade, M. (1995). Bioerosion rates on coral reefs: interactions between macroborers, microborers and grazers (Moorea, French Polynesia). *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 113, 189–198.
- Chen, P.Y., Chen, C.C., Chu, L. & McCarl, B. (2015). Evaluating the economic damage of climate change on global coral reefs. *Glob. Environ. Chang.*, 30, 12–20.
- Chow, M.H., Tsang, R.H.L., Lam, E.K.Y. & Ang, P. (2016). Quantifying the degree of coral bleaching using digital photographic technique. *J. Exp. Mar. Bio. Ecol.*, 479, 60–68.
- Claar, D.C. & Baum, J.K. (2019). Timing matters: survey timing during extended heat stress can influence perceptions of coral susceptibility to bleaching. *Coral Reefs*, 38, 559–565.
- Claar, D.C., Starko, S., Tietjen, K.L., Epstein, H.E., Cunning, R., Cobb, K.M., *et al.* (2020). Dynamic symbioses reveal pathways to coral survival through prolonged heatwaves. *Nat. Commun.*, 11, 1–10.
- Clewell, A. & McDonald, T. (2009). Relevance of Natural Recovery to Ecological Restoration. *Ecol. Restor.*, 27, 122–124.
- Coker, D.J., Wilson, S.K. & Pratchett, M.S. (2014). Importance of live coral habitat for reef fishes. *Rev. Fish Biol. Fish.*, 24, 89–126.
- Connell, J.H. (1973). Population ecology of reef-building corals. In: *Biology and Geology of Coral Reefs*. Elsevier, pp. 205–245.
- Connell, J.H. (1978). Diversity in Tropical Rain Forests and Coral Reefs. *Science.*, 199, 1302 LP – 1310.
- Connell, J.H., Hughes, T.P. & Wallace, C.C. (1997). A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol. Monogr.*, 67, 461–488.
- Connell, J.H. & Slatyer, R.O. (1977). Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. *Am. Nat.*, 111, 1119–1144.
- Cornwall, C.E., Comeau, S., Kornder, N.A., Perry, C.T., van Hoodonk, R., DeCarlo, T.M., *et al.* (2021).

- Global declines in coral reef calcium carbonate production under ocean acidification and warming. *Proc. Natl. Acad. Sci.*, 118, e2015265118.
- Cornwall, W. (2019). The reef builders. *Science.*, 363, 1264–1269.
- Costanza, R., D'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., *et al.* (1998). The value of the world's ecosystem services and natural capital. *Nature*, 387, 253–260.
- Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., *et al.* (2014). Changes in the global value of ecosystem services. *Glob. Environ. Chang.*, 26, 152–158.
- Dakos, V., Carpenter, S.R., van Nes, E.H. & Scheffer, M. (2015). Resilience indicators: prospects and limitations for early warnings of regime shifts. *Philos. Trans. R. Soc. B Biol. Sci.*, 370, 20130263.
- Darling, E.S., Graham, N.A.J., Januchowski-hartley, F.A., Nash, K.L., Pratchett, M.S. & Wilson, S.K. (2017). Relationships between structural complexity , coral traits , and reef fish assemblages. *Coral Reefs*, 36, 561–575.
- Davis, K., Carlson, P.M., Lowe, C.G., Warner, R.R. & Caselle, J.E. (2017). Parrotfish movement patterns vary with spatiotemporal scale. *Mar. Ecol. Prog. Ser.*, 577, 149–164.
- De'ath, G., Fabricius, K.E., Sweatman, H. & Puotinen, M. (2012a). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc. Natl. Acad. Sci.*, 109, 17995 LP – 17999.
- DeCarlo, T.M., Cohen, A.L., Wong, G.T.F., Davis, K.A., Lohmann, P. & Soong, K. (2017). Mass coral mortality under local amplification of 2 °C ocean warming. *Sci. Rep.*, 7, 44586.
- Diaz-Pulido, G., McCook, L.J., Dove, S., Berkelmans, R., Roff, G., Kline, D.I., *et al.* (2009). Doom and Boom on a Resilient Reef: Climate Change, Algal Overgrowth and Coral Recovery. *PLoS One*, 4, e5239.
- Diedrich, A. (2007). The impacts of tourism on coral reef conservation awareness and support in coastal communities in Belize. *Coral Reefs*, 26, 985–996.
- Dietzel, A., Bode, M., Connolly, S.R. & Hughes, T.P. (2020). Long-term shifts in the colony size structure of coral populations along the Great Barrier Reef: Demographic change in Australia's corals. *Proc. R. Soc. B Biol. Sci.*, 287.
- Dietzel, A., Bode, M., Connolly, S.R. & Hughes, T.P. (2021a). The population sizes and global extinction risk of reef-building coral species at biogeographic scales. *Nat. Ecol. Evol.*, 5, 663–669.

- Dietzel, A., Connolly, S.R., Hughes, T.P. & Bode, M. (2021b). The spatial footprint and patchiness of large-scale disturbances on coral reefs. *Glob. Chang. Biol.*, 27, 4825–4838.
- Dixon, A.M., Puotinen, M., Ramsay, H.A. & Beger, M. (2022). Coral Reef Exposure to Damaging Tropical Cyclone Waves in a Warming Climate. *Earth's Futur.*, 10.
- Donohue, I., Leira, M., Hobbs, W., León-vintró, L., O'Reilly, J. & Irvine, K. (2010). Rapid ecosystem recovery from diffuse pollution after the Great Irish Famine. *Ecol. Appl.*, 20, 1733–1743.
- Doropoulos, C., Bozec, Y., Gouezo, M., Priest, M.A., Thomson, D.P., Mumby, P.J., *et al.* (2022). Cryptic coral recruits as dormant “seed banks”: An unrecognized mechanism of rapid reef recovery. *Ecology*, 103, 1–6.
- Duarte, C.M., Agusti, S., Barbier, E., Britten, G.L., Castilla, J.C., Gattuso, J.P., *et al.* (2020). Rebuilding marine life. *Nature*, 580, 39–51.
- Dumont, C.P., Lau, D.C.C., Astudillo, J.C., Fong, K.F., Chak, S.T.C. & Qiu, J.-W. (2013). Coral bioerosion by the sea urchin *Diadema setosum* in Hong Kong: Susceptibility of different coral species. *J. Exp. Mar. Bio. Ecol.*, 441, 71–79.
- Eakin, C.M., Morgan, J.A., Heron, S.F., Smith, T.B., Liu, G., Alvarez-Filip, L., *et al.* (2010). Caribbean Corals in Crisis: Record Thermal Stress, Bleaching, and Mortality in 2005. *PLoS One*, 5, e13969.
- Eakin, C.M., Sweatman, H.P.A. & Brainard, R.E. (2019). The 2014–2017 global-scale coral bleaching event: insights and impacts. *Coral Reefs*, 38, 539–545.
- Eddy, T.D., Lam, V.W.Y., Reygondeau, G., Cisneros-Montemayor, A.M., Greer, K., Palomares, M.L.D., *et al.* (2021). Global decline in capacity of coral reefs to provide ecosystem services. *One Earth*, 4, 1278–1285.
- Edmunds, P. (2015). A quarter-century demographic analysis of the Caribbean coral, *Orbicella annularis*, and projections of population size over the next century: Population resilience in *Orbicella*. *Limnol. Oceanogr.*, 60.
- Edmunds, P.J. (2000). Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. *Mar. Ecol. Prog. Ser.*, 202, 113–124.
- Edmunds, P.J. (2005). The effect of sub-lethal increases in temperature on the growth and population trajectories of three scleractinian corals on the southern Great Barrier Reef. *Oecologia*, 146, 350–364.
- Edmunds, P.J. (2021a). Spatiotemporal variation in coral recruitment and its association with

- seawater temperature. *Limnol. Oceanogr.*, 66, 1394–1408.
- Edmunds, P.J. (2021b). Vital rates of small reef corals are associated with variation in climate. *Limnol. Oceanogr.*, 66, 901–913.
- Edmunds, P.J. (2023). Coral recruitment: patterns and processes determining the dynamics of coral populations. *Biol. Rev.*
- Edmunds, P.J., Burgess, S.C., Putnam, H.M., Baskett, M.L., Bramanti, L., Fabina, N.S., *et al.* (2014). Evaluating the causal basis of ecological success within the scleractinia: an integral projection model approach. *Mar. Biol.*, 161, 2719–2734.
- Edmunds, P.J. & Putnam, H.M. (2020). Science-based approach to using growth rate to assess coral performance and restoration outcomes. *Biol. Lett.*, 16, 20200227.
- Edmunds, P.J. & Riegl, B. (2020). Urgent need for coral demography in a world where corals are disappearing. *Mar. Ecol. Prog. Ser.*, 635, 233–242.
- Elliff, C.I. & Silva, I.R. (2017). Coral reefs as the first line of defense: Shoreline protection in face of climate change. *Mar. Environ. Res.*, 127, 148–154.
- Emslie, M., Cheal, A., Sweatman, H. & Delean, S. (2008). Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. *Mar. Ecol. Prog. Ser.*, 371, 177–190.
- English, S., Clive, W. & Baker, V. (1997). Survey manual for tropical marine resources. Australian Institute of Marine Science, Townsville., 34–49.
- Evans, R.D., Wilson, S.K., Fisher, R., Ryan, N.M., Babcock, R., Blakeway, D., *et al.* (2020). Early recovery dynamics of turbid coral reefs after recurring bleaching events. *J. Environ. Manage.*, 268, 110666.
- Eyre, B., Cyronak, T., Drupp, P., De Carlo, E., Sachs, J. & Andersson, A. (2018). Coral reefs will transition to net dissolving before end of century. *Science.*, 359, 908–911.
- Eyre, B.D., Andersson, A.J. & Cyronak, T. (2014). Benthic coral reef calcium carbonate dissolution in an acidifying ocean. *Nat. Clim. Chang.*, 4, 969–976.
- Field, C.B., Lobell, D.B., Peters, H.A. & Chiariello, N.R. (2007). Feedbacks of Terrestrial Ecosystems to Climate Change. *Annu. Rev. Environ. Resour.*, 32, 1–29.
- Fisher, R., O’Leary, R.A., Low-Choy, S., Mengersen, K., Knowlton, N., Brainard, R.E., *et al.* (2015). Species Richness on Coral Reefs and the Pursuit of Convergent Global Estimates. *Curr. Biol.*, 25,

500–505.

- Folke, C., Polasky, S., Rockström, J., Galaz, V., Westley, F., Lamont, M., *et al.* (2021). Our future in the Anthropocene biosphere. *Ambio*, 50, 834–869.
- Foster, N.L., Baums, I.B. & Mumby, P.J. (2007). Sexual vs. asexual reproduction in an ecosystem engineer: The massive coral *Montastraea annularis*. *J. Anim. Ecol.*, 76, 384–391.
- Fulton, C. & Bellwood, D.R. (2005). Wave-induced water motion and the functional implications for coral reef fish assemblages. *Limnol. Oceanogr.*, 50, 255–264.
- Garcia-Pichel, F. (2006). Plausible mechanisms for the boring on carbonates by microbial phototrophs. *Sediment. Geol.*, 185, 205–213.
- Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. (2003). Long-Term Region-Wide Declines in Caribbean Corals. *Science (80-.)*, 301, 958–960.
- Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H. & Pratchett, M.S. (2013). Recovery of an Isolated Coral Reef System Following Severe Disturbance. *Science.*, 340, 69–71.
- Glynn, P. (1988). El Niño warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. *Galaxea*, 7, 129–160.
- Glynn, P. (1997). Bioerosion and Coral Reef Growth: A Dynamic Balance. In: *Life and death of coral reefs*. Birkeland, pp. 69–98.
- Gold, Z. & Palumbi, S.R. (2018). Long-term growth rates and effects of bleaching in *Acropora hyacinthus*. *Coral Reefs*, 37, 267–277.
- González-del-Piiego, P., Freckleton, R.P., Edwards, D.P., Koo, M.S., Scheffers, B.R., Pyron, R.A., *et al.* (2019). Phylogenetic and Trait-Based Prediction of Extinction Risk for Data-Deficient Amphibians. *Curr. Biol.*, 29, 1557-1563.e3.
- González-Barrios, F.J., Cabral-Tena, R.A. & Alvarez-Filip, L. (2021). Recovery disparity between coral cover and the physical functionality of reefs with impaired coral assemblages. *Glob. Chang. Biol.*, 27, 640–651.
- Goodrich, B., Gabry, J., Ali, I. & Brilleman, S. (2020). rstanarm: Bayesian applied regression modeling via Stan. *R Packag. version*.
- Gouezo, M., Golbuu, Y., Fabricius, K., Olsudong, D., Mereb, G., Nestor, V., *et al.* (2019). Drivers of recovery and reassembly of coral reef communities. *Proc. R. Soc. B Biol. Sci.*, 286, 20182908.

- Graham, N.A.J., Bellwood, D.R., Cinner, J.E., Hughes, T.P., Norström, A. V. & Nyström, M. (2013). Managing resilience to reverse phase shifts in coral reefs. *Front. Ecol. Environ.*, 11, 541–548.
- Graham, N.A.J., Cinner, J.E., Norström, A. V. & Nyström, M. (2014). Coral reefs as novel ecosystems: EMBRACING new futures. *Curr. Opin. Environ. Sustain.*, 7, 9–14.
- Graham, N.A.J., Jennings, S., MacNeil, M.A., Mouillot, D. & Wilson, S.K. (2015). Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, 518, 94–97.
- Graham, N.A.J. & Nash, K.L. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, 32, 315–326.
- Graham, N.A.J., Nash, K.L. & Kool, J.T. (2011). Coral reef recovery dynamics in a changing world. *Coral Reefs*, 30, 283–294.
- Graham, N.A.J., Wilson, S.K., Carr, P., Hoey, A.S., Jennings, S. & MacNeil, M.A. (2018). Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature*, 559, 250–253.
- Grange, J.S., Rybarczyk, H. & Tribollet, A. (2015). The three steps of the carbonate biogenic dissolution process by microborers in coral reefs (New Caledonia). *Environ. Sci. Pollut. Res.*, 22, 13625–13637.
- Green, R.H., Lowe, R.J., Buckley, M.L., Foster, T. & Gilmour, J.P. (2019). Physical mechanisms influencing localized patterns of temperature variability and coral bleaching within a system of reef atolls. *Coral Reefs*, 38, 759–771.
- Griffin, S.P., Garcia, R.P. & Weil, E. (2003). Bioerosion in coral reef communities in southwest Puerto Rico by the sea urchin *Echinometra viridis*. *Mar. Biol.*, 143, 79–84.
- Grimaldi, C.M., Lowe, R.J., Benthuyzen, J.A., Cuttler, M.V.W., Green, R.H. & Gilmour, J.P. (2023). Hydrodynamic and atmospheric drivers create distinct thermal environments within a coral reef atoll. *Coral Reefs*, 42, 693–706.
- Grottoli, A.G., Rodrigues, L.J. & Palardy, J.E. (2006). Heterotrophic plasticity and resilience in bleached corals. *Nature*, 440, 1186–1189.
- Gvirtzman, G. (1994). Fluctuations of sea level during the past 400 000 years: the record of Sinai, Egypt (northern Red Sea). *Coral Reefs*, 13, 203–214.
- Gygi, R.A. (1969). An estimate of the erosional effect of *Sparisoma viride* (Bonnaterre), the green parrotfish, on some Bermuda reefs. In: *Reports of Research: 1968 Seminar on Organism–*

Sediment Interrelationships, Bermuda Biological Station for Research. pp. 137–143.

- Hall, T.E., Freedman, A.S., de Roos, A.M., Edmunds, P.J., Carpenter, R.C. & Gross, K. (2021). Stony coral populations are more sensitive to changes in vital rates in disturbed environments. *Ecol. Appl.*, 31, 1–11.
- Hamilton, R. (2005). The demographics of Bumphead Parrotfish (*Bolbometopon muricatum*) in lightly and heavily fished regions of the Western Solomon Islands. University of Otago, Dunedin, New Zealand.
- Harrison, H.B., Álvarez-Noriega, M., Baird, A.H., Heron, S.F., MacDonald, C. & Hughes, T.P. (2019). Back-to-back coral bleaching events on isolated atolls in the Coral Sea. *Coral Reefs*, 38, 713–719.
- Harvey, B.J., Nash, K.L., Blanchard, J.L. & Edwards, D.P. (2018). Ecosystem-based management of coral reefs under climate change. *Ecol. Evol.*, 8, 6354–6368.
- Hewitt, J., Gladstone-Gallagher, R. & Thrush, S. (2022). Disturbance–recovery dynamics inform seafloor management for recovery. *Front. Ecol. Environ.*, 20, 564–572.
- Higgs, E., Harris, J., Murphy, S., Bowers, K., Hobbs, R., Jenkins, W., *et al.* (2018). On principles and standards in ecological restoration. *Restor. Ecol.*, 26, 399–403.
- Hoegh-Guldberg, O. & Bruno, J.F. (2010). The Impact of Climate Change on the World’s Marine Ecosystems. *Science (80-)*, 328, 1523–1528.
- Hoegh-Guldberg, O., Jacob, D., Taylor, M., Guillén Bolaños, T., Bindi, M., Brown, S., *et al.* (2019). The human imperative of stabilizing global climate change at 1.5°C. *Science.*, 365, eaaw6974.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., *et al.* (2007). Coral reefs under rapid climate change and ocean acidification. *Science*.
- Hoey, A.S. (2018). Feeding in Parrotfishes: The Influence of Species, Body Size, and Temperature. In: *Biology of Parrotfishes*. CRC Press, Boca Raton, FL: CRC Press, Taylor & Francis Group, [2018] | “A Science Publishers book.” | Include bibliographical references and index., pp. 119–133.
- Hoey, A.S. & Bellwood, D.R. (2008). Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs*, 27, 37–47.
- Holbrook, S.J., Adam, T.C., Edmunds, P.J., Schmitt, R.J., Carpenter, R.C., Brooks, A.J., *et al.* (2018). Recruitment Drives Spatial Variation in Recovery Rates of Resilient Coral Reefs. *Sci. Rep.*, 8, 7338.

- Holling, C.S. (1973). Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.*, 4, 1–23.
- House, J.E., Brambilla, V., Bidaut, L.M., Christie, A.P., Pizarro, O., Madin, J.S., *et al.* (2018). Moving to 3D: relationships between coral planar area, surface area and volume. *PeerJ*, 6, e4280.
- Huertas, V., Morais, R.A., Bonaldo, R.M. & Bellwood, D.R. (2021). Parrotfish corallivory on stress-tolerant corals in the Anthropocene. *PLoS One*, 16, e0250725.
- Hughes, R.N., Hughes, D.J., Smith, I.P. & Dale, A.C. (2015). Oceanography and marine biology: An annual review. In: *Oceanography and Marine Biology: An Annual Review* (eds. Hughes, R.N., Hughes, D.J., Smith, I.P. & Dale, A.C.). pp. 1–295.
- Hughes, T. (1999). Off-reef transport of coral fragments at Lizard Island, Australia. *Mar. Geol.*, 157, 1–6.
- Hughes, T.P. (1984). Population Dynamics Based on Individual Size Rather than Age: A General Model with a Reef Coral Example. *Am. Nat.*, 123, 778–795.
- Hughes, T.P. (1994). Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. *Science (80-)*, 265, 1547 LP – 1551.
- Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., *et al.* (2018a). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* ., 359, 80–83.
- Hughes, T.P., Baird, A.H., Morrison, T.H. & Torda, G. (2023). Principles for coral reef restoration in the anthropocene. *One Earth*, 6, 656–665.
- Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B.C., *et al.* (2017a). Coral reefs in the Anthropocene. *Nature*, 546, 82–90.
- Hughes, T.P. & Jackson, J.B.C. (1980). Do Corals Lie About Their Age? Some Demographic Consequences of Partial Mortality, Fission, and Fusion. *Science (80-)*, 209, 713–715.
- Hughes, T.P. & Jackson, J.B.C. (1985). Population Dynamics and Life Histories of Foliose Corals. *Ecol. Monogr.*, 55, 141–166.
- Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H., *et al.* (2017b). Global warming and recurrent mass bleaching of corals. *Nature*, 543, 373–377.
- Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Chase, T.J., Dietzel, A., *et al.* (2019a). Global warming impairs stock–recruitment dynamics of corals. *Nature*, 568, 387–390.
- Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M., *et al.* (2018b). Global

- warming transforms coral reef assemblages. *Nature*, 556, 492–496.
- Hughes, T.P., Kerry, J.T., Connolly, S.R., Álvarez-Romero, J.G., Eakin, C.M., Heron, S.F., *et al.* (2021). Emergent properties in the responses of tropical corals to recurrent climate extremes. *Curr. Biol.*, 31, 5393-5399.e3.
- Hughes, T.P., Kerry, J.T., Connolly, S.R., Baird, A.H., Eakin, C.M., Heron, S.F., *et al.* (2019b). Ecological memory modifies the cumulative impact of recurrent climate extremes. *Nat. Clim. Chang.*, 9, 40–43.
- Hughes, T.P., Linares, C., Dakos, V., van de Leemput, I.A. & van Nes, E.H. (2013). Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends Ecol. Evol.*, 28, 149–155.
- Hughes, T.P. & Tanner, J.E. (2000). Recruitment Failure, Life Histories, and Long-Term Decline of Caribbean Corals. *Ecology*, 81, 2250–2263.
- Husband, E., Perry, C.T. & Lange, I.D. (2022). Estimating rates of coral carbonate production from aerial and archive imagery by applying colony scale conversion metrics. *Coral Reefs*, 41, 1199-1209.
- Hutchings, P.A., Kiene, W.E., Cunningham, R.B. & Donnelly, C. (1992). Spatial and temporal patterns of non-colonial boring organisms (polychaetes, sipunculans and bivalve molluscs) in *Porites* at Lizard Island, Great Barrier Reef. *Coral Reefs*, 11, 23–31.
- Hutchings, P.A., Peyrot-Clausade, M. & Osnorno, A. (2005). Influence of land runoff on rates and agents of bioerosion of coral substrates. *Mar. Pollut. Bull.*, 51, 438–447.
- IPCC. (2023). *IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland.*
- Jentsch, A. & White, P. (2019). A theory of pulse dynamics and disturbance in ecology. *Ecology*, 100, 1–15.
- Johns, K.A., Osborne, K.O. & Logan, M. (2014). Contrasting rates of coral recovery and reassembly in coral communities on the Great Barrier Reef. *Coral Reefs*, 33, 553–563.
- Jones, H.P., Jones, P.C., Barbier, E.B., Blackburn, R.C., Rey Benayas, J.M., Holl, K.D., *et al.* (2018). Restoration and repair of Earth’s damaged ecosystems. *Proc. R. Soc. B Biol. Sci.*, 285, 20172577.
- Jones, H.P. & Schmitz, O.J. (2009). Rapid Recovery of Damaged Ecosystems. *PLoS One*, 4, e5653.

- Kalacska, M., Lucanus, O., Sousa, L., Vieira, T. & Arroyo-Mora, J.P. (2018). Freshwater Fish Habitat Complexity Mapping Using Above and Underwater Structure-From-Motion Photogrammetry. *Remote Sens.* .
- Kayal, M., Lenihan, H.S., Brooks, A.J., Holbrook, S.J., Schmitt, R.J. & Kendall, B.E. (2018). Predicting coral community recovery using multi-species population dynamics models. *Ecol. Lett.*, 21, 1790–1799.
- Kayal, M., Vercelloni, J., Wand, M.P. & Adjeroud, M. (2015). Searching for the best bet in life-strategy: A quantitative approach to individual performance and population dynamics in reef-building corals. *Ecol. Complex.*, 23, 73–84.
- Kerry, J.T. & Bellwood, D.R. (2015). Do tabular corals constitute keystone structures for fishes on coral reefs? *Coral Reefs*, 34, 41–50.
- Kiene, W.E. & Hutchings, P.A. (1994). Bioerosion experiments at Lizard Island, Great Barrier Reef. *Coral Reefs*, 13, 91–98.
- Klepac, C.N. & Barshis, D.J. (2020). Reduced thermal tolerance of massive coral species in a highly variable environment. *Proc. R. Soc. B Biol. Sci.*, 287, 19–21.
- Klepac, C.N. & Barshis, D.J. (2022). High-resolution in situ thermal metrics coupled with acute heat stress experiments reveal differential coral bleaching susceptibility. *Coral Reefs*, 41, 1045–1057.
- Kleypas, J.A., Buddemeier, R.W. & Gattuso, J.-P. (2001). The future of coral reefs in an age of global change. *Int. J. Earth Sci.*, 90, 426–437.
- Koester, A., Ford, A.K., Ferse, S.C.A., Migani, V., Bunbury, N., Sanchez, C., *et al.* (2021). First insights into coral recruit and juvenile abundances at remote Aldabra Atoll, Seychelles. *PLoS One*, 16, e0260516.
- Kohler, K.E. & Gill, S.M. (2006). Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Comput. Geosci.*, 32, 1259–1269.
- Kuffner, I.B., Toth, L.T., Hudson, J.H., Goodwin, W.B., Stathakopoulos, A., Bartlett, L.A., *et al.* (2019). Improving estimates of coral reef construction and erosion with in situ measurements. *Limnol. Oceanogr.*, 64, 2283–2294.
- Ladd, M.C., Miller, M.W., Hunt, J.H., Sharp, W.C. & Burkepile, D.E. (2018). Harnessing ecological processes to facilitate coral restoration. *Front. Ecol. Environ.*, 16, 239–247.

- Leão, T.C., Fonseca, C.R., Peres, C.A. & Tabarelij, M. (2014). Predicting Extinction Risk of Brazilian Atlantic Forest Angiosperms. *Conserv. Biol.*, 28, 1349–1359.
- Leggat, W.P., Camp, E.F., Suggett, D.J., Heron, S.F., Fordyce, A.J., Gardner, S., *et al.* (2019). Rapid Coral Decay Is Associated with Marine Heatwave Mortality Events on Reefs. *Curr. Biol.*, 29, 2723–2730.e4.
- Lenihan, H., Adjeroud, M., Kotchen, M., Hench, J. & Nakamura, T. (2008). Reef structure regulates small-scale spatial variation in coral bleaching. *Mar. Ecol. Prog. Ser.*, 370, 127–141.
- Lewis, S.L. & Maslin, M.A. (2015). Defining the Anthropocene. *Nature*, 519, 171–180.
- Linares, C., Pratchett, M. & Coker, D. (2011). Recolonisation of *Acropora hyacinthus* following climate-induced coral bleaching on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.*, 438, 97–104.
- Longo, G.O., Ferreira, C.E.L. & Floeter, S.R. (2014). Herbivory drives large-scale spatial variation in reef fish trophic interactions. *Ecol. Evol.*, 4, 4553–4566.
- Lough, J.M. (2012). Small change , big difference : Sea surface temperature distributions for tropical coral reef ecosystems , 1950 – 2011. *J. Geophys. Res. Ocean.*, 117.
- Lough, J.M., Anderson, K.D. & Hughes, T.P. (2018). Increasing thermal stress for tropical coral reefs: 1871–2017. *Sci. Rep.*, 8, 6079.
- Loya, Y. (1978). Plotless and transect methods. In: Stoddard DR, Johannes RE (eds) Coral reefs: research methods.
- Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H. & Van Woesik, R. (2001). Coral bleaching: The winners and the losers. *Ecol. Lett.*, 4, 122–131.
- MacArthur, R.H. & MacArthur, J.W. (1961). On Bird Species Diversity. *Ecology*, 42, 594–598.
- Madin, J.S., Anderson, K.D., Andreasen, M.H., Bridge, T.C.L., Cairns, S.D., Connolly, S.R., *et al.* (2016). The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Sci. Data*, 3, 160017.
- Madin, J.S., Baird, A.H., Bridge, T.C.L., Connolly, S.R., Zawada, K.J.A. & Dornelas, M. (2018). Cumulative effects of cyclones and bleaching on coral cover and species richness at Lizard Island. *Mar. Ecol. Prog. Ser.*, 604, 263–268.
- Madin, J.S., Baird, A.H., Dornelas, M. & Connolly, S.R. (2014). Mechanical vulnerability explains size-dependent mortality of reef corals. *Ecol. Lett.*, 17, 1008–1015.

- Madin, J.S. & Connolly, S.R. (2006). Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature*, 444, 477–480.
- Madin, J.S., McWilliam, M., Quigley, K., Bay, L.K., Bellwood, D., Doropoulos, C., *et al.* (2023). Selecting coral species for reef restoration. *J. Appl. Ecol.*, 60, 1537–1544.
- Marshall, P.A. & Baird, A.H. (2000). Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs*, 19, 155–163.
- Mason, R.E., Craine, J.M., Lany, N.K., Jonard, M., Ollinger, S. V., Groffman, P.M., *et al.* (2022). Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems. *Science* (80-), 376.
- Mausel, P., Wu, Y., Li, Y., Moran, E.F. & Brondizio, E.S. (1993). Spectral identification of successional stages following deforestation in the Amazon. *Geocarto Int.*, 8, 61–71.
- McClanahan, T., Darling, E., Maina, J., Muthiga, N., D’agata, S., Leblond, J., *et al.* (2020). Highly variable taxa-specific coral bleaching responses to thermal stresses. *Mar. Ecol. Prog. Ser.*, 648, 135–151.
- McLeod, E., Anthony, K.R.N., Andersson, A., Beeden, R., Golbuu, Y., Kleypas, J., *et al.* (2013). Preparing to manage coral reefs for ocean acidification: Lessons from coral bleaching. *Front. Ecol. Environ.*, 11, 20–27.
- McLeod, E., Anthony, K.R.N., Mumby, P.J., Maynard, J., Beeden, R., Graham, N.A.J., *et al.* (2019). The future of resilience-based management in coral reef ecosystems. *J. Environ. Manage.*, 233, 291–301.
- McLeod, I.M., Hein, M.Y., Babcock, R., Bay, L., Bourne, D.G., Cook, N., *et al.* (2022). Coral restoration and adaptation in Australia: The first five years. *PLoS One*, 17, e0273325.
- McWilliam, M., Chase, T.J. & Hoogenboom, M.O. (2018). Neighbor Diversity Regulates the Productivity of Coral Assemblages. *Curr. Biol.*, 28, 3634-3639.e3.
- McWilliam, M., Pratchett, M.S., Hoogenboom, M.O. & Hughes, T.P. (2020). Deficits in functional trait diversity following recovery on coral reefs. *Proc. R. Soc. B Biol. Sci.*, 287.
- Moberg, F.F. & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecol. Econ.*, 29, 215–233.
- Montoya, D. (2021). Challenges and directions toward a general theory of ecological recovery dynamics: A metacommunity perspective. *One Earth*, 4, 1083–1094.

- van Moorsel, S.J., Thébault, E., Radchuk, V., Narwani, A., Montoya, J.M., Dakos, V., *et al.* (2023). Predicting effects of multiple interacting global change drivers across trophic levels. *Glob. Chang. Biol.*, 29, 1223–1238.
- Morais, J., Morais, R., Tebbett, S.B. & Bellwood, D.R. (2022). On the fate of dead coral colonies. *Funct. Ecol.*, 36, 3148–3160.
- Morais, J., Morais, R.A., Tebbett, S.B., Pratchett, M.S. & Bellwood, D.R. (2021). Dangerous demographics in post-bleach corals reveal boom-bust versus protracted declines. *Sci. Rep.*, 11, 18787.
- Morais, J., Tebbett, S.B., Morais, R.A. & Bellwood, D.R. (2023). Natural recovery of corals after severe disturbance. *Ecol. Lett.*, 1–12.
- Morais, J., Tebbett, S.B., Morais, R.A. & Bellwood, D.R. (2024). Hot spots of bleaching in massive *Porites* coral colonies. *Mar. Environ. Res.*, 193, 106276.
- Morais, R.A., Depczynski, M., Fulton, C., Marnane, M., Narvaez, P., Huertas, V., *et al.* (2020). Severe coral loss shifts energetic dynamics on a coral reef. *Funct. Ecol.*, 34, 1507–1518.
- Moreno-Mateos, D., Barbier, E.B., Jones, P.C., Jones, H.P., Aronson, J., López-López, J.A., *et al.* (2017). Anthropogenic ecosystem disturbance and the recovery debt. *Nat. Commun.*, 8, 14163.
- Morgan, K.M. & Kench, P.S. (2016). Parrotfish erosion underpins reef growth, sand talus development and island building in the Maldives. *Sediment. Geol.*, 341, 50–57.
- Morrison, T.H., Adger, N., Barnett, J., Brown, K., Possingham, H. & Hughes, T. (2020). Advancing Coral Reef Governance into the Anthropocene. *One Earth*, 2, 64–74.
- Nolan, C., Overpeck, J.T., Allen, J.R.M., Anderson, P.M., Betancourt, J.L., Binney, H.A., *et al.* (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science (80-)*, 361, 920–923.
- O’Mahoney, J., Simes, R., Redhill, D., Heaton, K., Atkinson, C., Hayward, E., *et al.* (2017). At what price? The economic, social and icon value of the Great Barrier Reef.
- O’Neill, R. V. (1998). Recovery in complex ecosystems. *J. Aquat. Ecosyst. Stress Recover.*, 6, 181–187.
- O’Reilly, C.M., Alin, S.R., Plisnier, P.-D., Cohen, A.S. & McKee, B.A. (2003). Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. *Nature*, 424, 766–768.
- Ong, L. & Holland, K.N. (2010). Bioerosion of coral reefs by two Hawaiian parrotfishes: species, size

- differences and fishery implications. *Mar. Biol.*, 157, 1313–1323.
- Ortiz, J.C., Pears, R.J., Beeden, R., Dryden, J., Wolff, N.H., Gomez Cabrera, M. del C., *et al.* (2021). Important ecosystem function, low redundancy and high vulnerability: The trifacta argument for protecting the Great Barrier Reef's tabular *Acropora*. *Conserv. Lett.*, 14, 1–18.
- Osborne, K., Dolman, A.M., Burgess, S.C. & Johns, K.A. (2011). Disturbance and the Dynamics of Coral Cover on the Great Barrier Reef (1995–2009). *PLoS One*, 6, e17516.
- Osorno, A., Peyrot-Clausade, M. & Hutchings, P.A. (2005). Patterns and rates of erosion in dead Porites across the Great Barrier Reef (Australia) after 2 years and 4 years of exposure. *Coral Reefs*, 24, 292–303.
- Pearson, R. (1981). Recovery and Recolonization of Coral Reefs. *Mar. Ecol. Prog. Ser.*, 4, 105–122.
- Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., *et al.* (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* (80-.), 355, eaai9214.
- Perry, C.T., Alvarez-Filip, L., Graham, N.A.J., Mumby, P.J., Wilson, S.K., Kench, P.S., *et al.* (2018). Loss of coral reef growth capacity to track future increases in sea level. *Nature*, 558, 396–400.
- Perry, C.T., Edinger, E.N., Kench, P.S., Murphy, G.N., Smithers, S.G., Steneck, R.S., *et al.* (2012). Estimating rates of biologically driven coral reef framework production and erosion: A new census-based carbonate budget methodology and applications to the reefs of Bonaire. *Coral Reefs*, 31, 853–868.
- Perry, C.T., Kench, P.S., O'Leary, M.J., Morgan, K.M. & Januchowski-Hartley, F. (2015). Linking reef ecology to island building: Parrotfish identified as major producers of island-building sediment in the Maldives. *Geology*, 43, 503–506.
- Perry, C.T., Kench, P.S., Smithers, S.G., Yamano, H., O'Leary, M. & Gulliver, P. (2013a). Time scales and modes of reef lagoon infilling in the maldives and controls on the onset of reef island formation. *Geology*, 41, 1111–1114.
- Perry, C.T., Murphy, G.N., Kench, P.S., Smithers, S.G., Edinger, E.N., Steneck, R.S., *et al.* (2013b). Caribbean-wide decline in carbonate production threatens coral reef growth. *Nat. Commun.*, 4, 1402.
- Peyrot-Clausade, M., Chabanet, P., Conand, C., Fontaine, M.F., Letourneur, Y. & Harmelin-Vivien, M. (2000). Sea urchin and fish bioerosion on La Réunion and Moorea reefs. *Bull. Mar. Sci.*, 66, 477–

485.

- Pichon, M. (1978). Problems of measuring and mapping coral colonies. In: Stoddard DR, Johannes RE (eds) *Coral reefs: research methods*.
- Pisapia, C., Burn, D. & Pratchett, M.S. (2019). Changes in the population and community structure of corals during recent disturbances (February 2016–October 2017) on Maldivian coral reefs. *Sci. Rep.*, 9, 8402.
- Pisapia, C., Edmunds, P.J., Moeller, H. V., M. Riegl, B., McWilliam, M., Wells, C.D., *et al.* (2020). *Projected shifts in coral size structure in the Anthropocene*. *Adv. Mar. Biol.* 1st edn. Elsevier Ltd.
- Pizarro, O., Friedman, A., Bryson, M., Williams, S.B. & Madin, J. (2017). A simple, fast, and repeatable survey method for underwater visual 3D benthic mapping and monitoring. *Ecol. Evol.*, 7, 1770–1782.
- Pratchett, M., Caballes, C., Wilmes, J., Matthews, S., Mellin, C., Sweatman, H., *et al.* (2017). Thirty Years of Research on Crown-of-Thorns Starfish (1986–2016): Scientific Advances and Emerging Opportunities. *Diversity*, 9, 2–49.
- Pratchett, M.S. (2010). Changes in coral assemblages during an outbreak of *Acanthaster planci* at Lizard Island, northern Great Barrier Reef (1995–1999). *Coral Reefs*, 29, 717–725.
- Pratchett, M.S., Anderson, K.D., Hoogenboom, M.O., Widman, E., Baird, A.H., Pandolfi, J.M., *et al.* (2015). Spatial, temporal and taxonomic variation in coral growth - implications for the structure and function of coral reef ecosystems. *Oceanogr. Mar. Biol. An Annu. Rev.*, 53, 215–295.
- Pratchett, M.S., Heron, S.F., Mellin, C. & Cumming, G.S. (2021). Recurrent Mass-Bleaching and the Potential for Ecosystem Collapse on Australia’s Great Barrier Reef. In: *Ecosystem Collapse and Climate Change* (eds. Canadell, J.G. & Jackson, R.B.). Springer International Publishing, Cham, pp. 265–289.
- Pratchett, M.S., McCowan, D., Maynard, J.A. & Heron, S.F. (2013). Changes in Bleaching Susceptibility among Corals Subject to Ocean Warming and Recurrent Bleaching in Moorea, French Polynesia. *PLoS One*, 8, e70443.
- Pratchett, M.S., McWilliam, M.J. & Riegl, B. (2020). Contrasting shifts in coral assemblages with increasing disturbances. *Coral Reefs*, 39, 783–793.
- Puotinen, M., Drost, E., Lowe, R., Depczynski, M., Radford, B., Heyward, A., *et al.* (2020). Towards

- modelling the future risk of cyclone wave damage to the world's coral reefs. *Glob. Chang. Biol.*, 26, 4302–4315.
- Quigley, K.M., Hein, M. & Suggett, D.J. (2022). Translating the 10 golden rules of reforestation for coral reef restoration. *Conserv. Biol.*, 36, 1–8.
- Rasser, M. & Riegl, B. (2002). Holocene coral reef rubble and its binding agents. *Coral Reefs*, 21, 57–72.
- Reguero, B.G., Beck, M.W., Agostini, V.N., Kramer, P. & Hancock, B. (2018). Coral reefs for coastal protection: A new methodological approach and engineering case study in Grenada. *J. Environ. Manage.*, 210, 146–161.
- Reyes-Nivia, C., Diaz-Pulido, G., Kline, D., Guldberg, O.H. & Dove, S. (2013). Ocean acidification and warming scenarios increase microbioerosion of coral skeletons. *Glob. Chang. Biol.*, 19, 1919–1929.
- Richards, Z.T., Juskiewicz, D.J. & Hoggett, A. (2021). Spatio-temporal persistence of scleractinian coral species at Lizard Island, Great Barrier Reef. *Coral Reefs*, 40, 1369–1378.
- Riegl, B. & Purkis, S. (2015). Coral population dynamics across consecutive mass mortality events. *Glob. Chang. Biol.*, 21, 3995–4005.
- Roff, G. (2020). Evolutionary History Drives Biogeographic Patterns of Coral Reef Resilience. *Bioscience*, 71, 26–39.
- Roff, G., Zhao, J. & Mumby, P.J. (2015). Decadal-scale rates of reef erosion following El Niño-related mass coral mortality. *Glob. Chang. Biol.*, 21, 4415–4424.
- Rogers, J.S., Monismith, S.G., Koweeck, D.A., Torres, W.I. & Dunbar, R.B. (2016). Thermodynamics and hydrodynamics in an atoll reef system and their influence on coral cover. *Limnol. Oceanogr.*, 61, 2191–2206.
- Rosenberg, K. V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A., *et al.* (2019). Decline of the North American avifauna. *Science (80-.)*, 366, 120–124.
- Safaie, A., Silbiger, N.J., McClanahan, T.R., Pawlak, G., Barshis, D.J., Hench, J.L., *et al.* (2018). High frequency temperature variability reduces the risk of coral bleaching. *Nat. Commun.*, 9, 1671.
- Schmidt, G.M., Wall, M., Taylor, M., Jantzen, C. & Richter, C. (2016). Large-amplitude internal waves sustain coral health during thermal stress. *Coral Reefs*, 35, 869–881.

- Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods*, 9, 671–675.
- Schönberg, C.H.L., Fang, J.K.-H. & Carballo, J.L. (2017a). Bioeroding Sponges and the Future of Coral Reefs. In: *Climate Change, Ocean Acidification and Sponges*. Springer International Publishing, Cham, pp. 179–372.
- Schönberg, C.H.L., Fang, J.K.H., Carreiro-Silva, M., Tribollet, A. & Wisshak, M. (2017b). Bioerosion: the other ocean acidification problem. *ICES J. Mar. Sci.*, 74, 895–925.
- AIMS (2022). *Long-Term Monitoring Program - Annual Summary Report of Coral Reef Condition*. Townsville.
- Scoffin, T., Stearn, C., Boucher, D., Frydl, P., Hawkins, C., Hunter, I., *et al.* (1977). Calcium carbonate budget of a fringing reef on the West Coast of Barbados.
- Sévellec, F. & Drijfhout, S.S. (2018). A novel probabilistic forecast system predicting anomalously warm 2018-2022 reinforcing the long-term global warming trend. *Nat. Commun.*, 9, 3024.
- Shenkar, N., Fine, M. & Loya, Y. (2005). Size matters: bleaching dynamics of the coral *Oculina patagonica*. *Mar. Ecol. Prog. Ser.*, 294, 181–188.
- Shono, K., Cadaweng, E.A. & Durst, P.B. (2007). Application of Assisted Natural Regeneration to Restore Degraded Tropical Forestlands. *Restor. Ecol.*, 15, 620–626.
- Siqueira, A.C., Bellwood, D.R. & Cowman, P.F. (2019). The evolution of traits and functions in herbivorous coral reef fishes through space and time. *Proc. R. Soc. B Biol. Sci.*, 286, 20182672.
- Skirving, W.J., Heron, S.F., Marsh, B.L., Liu, G., De La Cour, J.L., Geiger, E.F., *et al.* (2019). The relentless march of mass coral bleaching: a global perspective of changing heat stress. *Coral Reefs*, 38, 547–557.
- Smith, K.E., Burrows, M.T., Hobday, A.J., King, N.G., Moore, P.J., Sen Gupta, A., *et al.* (2023). Biological Impacts of Marine Heatwaves. *Ann. Rev. Mar. Sci.*, 15, 119–145.
- Souter, D.W. & Lindén, O. (2000). The health and future of coral reef systems. *Ocean Coast. Manag.*, 43, 657–688.
- Spalding, M.D., Ravilious, C. & Green, E.P. (Edmund P. (2001). *World atlas of coral reefs*. University of California Press, Berkeley.
- Stanley, G.D. (1981). Early history of scleractinian corals and its geological consequences. *Geology*, 9,

507.

- Stanturf, J.A., Palik, B.J. & Dumroese, R.K. (2014). Contemporary forest restoration: A review emphasizing function. *For. Ecol. Manage.*, 331, 292–323.
- Storlazzi, C.D., Cheriton, O.M., van Hooijdonk, R., Zhao, Z. & Brainard, R. (2020). Internal tides can provide thermal refugia that will buffer some coral reefs from future global warming. *Sci. Rep.*, 10, 13435.
- Storlazzi, C.D., Dartnell, P., Hatcher, G.A. & Gibbs, A.E. (2016). End of the chain? Rugosity and fine-scale bathymetry from existing underwater digital imagery using structure-from-motion (SfM) technology. *Coral Reefs*, 35, 889–894.
- Storlazzi, C.D., Reguero, B.G., Cole, A.D., Lowe, E., Shope, J.B., Gibbs, A.E., *et al.* (2019). *Rigorously valuing the role of U.S. coral reefs in coastal hazard risk reduction*. Open-File Rep. Reston, VA.
- Streit, R.P., Cumming, G.S. & Bellwood, D.R. (2019). Patchy delivery of functions undermines functional redundancy in a high diversity system. *Funct. Ecol.*, 33, 1144–1155.
- Sully, S., Burkepile, D.E., Donovan, M.K., Hodgson, G. & van Woesik, R. (2019). A global analysis of coral bleaching over the past two decades. *Nat. Commun.*, 10, 1264.
- Summerhayes, C.P. & Zalasiewicz, J. (2018). Global warming and the Anthropocene. *Geol. Today*, 34, 194–200.
- Tanner, J.E., Hughes, T.P. & Connell, J.H. (1996). The Role of History in Community Dynamics: A Modelling Approach. *Ecology*, 77, 108–117.
- Team, R.C. (2020). R: A Language and Environment for Statistical Computing.
- Team, S.D. (2021). RStan: the R interface to Stan. R package version 2.21.2.
- Tebbett, S.B. & Bellwood, D.R. (2018). Functional links on coral reefs: Urchins and triggerfishes, a cautionary tale. *Mar. Environ. Res.*, 141, 255–263.
- Tebbett, S.B., Connolly, S.R. & Bellwood, D.R. (2023). Benthic composition changes on coral reefs at global scales. *Nat. Ecol. Evol.*, 7, 71–81.
- Tebbett, S.B., Goatley, C., Streit, R. & Bellwood, D. (2020). Algal turf sediments limit the spatial extent of function delivery on coral reefs. *Sci. Total Environ.*, 734, 139422.
- Tebbett, S.B., Morais, J. & Bellwood, D.R. (2022a). Spatial patchiness in change, recruitment, and recovery on coral reefs at Lizard Island following consecutive bleaching events. *Mar. Environ.*

Res., 173, 105537.

- Tebbett, S.B., Streit, R.P., Morais, J., Schlaefer, J.A., Swan, S. & Bellwood, D.R. (2022b). Benthic cyanobacterial mat formation during severe coral bleaching at Lizard Island: The mediating role of water currents. *Mar. Environ. Res.*, 181, 105752.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., *et al.* (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.*, 31, 79–92.
- Thrush, S.F. & Whitlatch, R.B. (2001). Recovery Dynamics in Benthic Communities: Balancing Detail with Simplification. In: *Ecological Comparisons of Sedimentary Shores* (ed. Reise, K.). Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 297–316.
- Tribollet, A. & Golubic, S. (2005). Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef, Australia. *Coral Reefs*, 24, 422–434.
- Tribollet, A. & Golubic, S. (2011). Reef Bioerosion: Agents and Processes. *Coral Reefs An Ecosyst. Transit.*, 1–552.
- Trisos, C.H., Merow, C. & Pigot, A.L. (2020). The projected timing of abrupt ecological disruption from climate change. *Nature*, 580, 496–501.
- Trygonis, V. & Sini, M. (2012). photoQuad: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. *J. Exp. Mar. Bio. Ecol.*, 424–425, 99–108.
- Uhl, C., Clark, K., Clark, H. & Murphy, P. (1981). Early Plant Succession after Cutting and Burning in the Upper Rio Negro Region of the Amazon Basin. *J. Ecol.*, 69, 631.
- Urban, M.C. (2015). Accelerating extinction risk from climate change. *Science (80-)*, 348, 571–573.
- Urbina-Barreto, I., Chiroleu, F., Pinel, R., Fréchon, L., Mahamadaly, V., Elise, S., *et al.* (2021). Quantifying the shelter capacity of coral reefs using photogrammetric 3D modeling: From colonies to reefscapes. *Ecol. Indic.*, 121, 107151.
- Vardi, T., Hoot, W.C., Levy, J., Shaver, E., Winters, R.S., Banaszak, A.T., *et al.* (2021). Six priorities to advance the science and practice of coral reef restoration worldwide. *Restor. Ecol.*, 29, 1–7.
- Vercelloni, J., Liquet, B., Kennedy, E. V., González-Rivero, M., Caley, M.J., Peterson, E.E., *et al.* (2020). Forecasting intensifying disturbance effects on coral reefs. *Glob. Chang. Biol.*, 26, 2785–2797.

- Victor, S., Golbuu, Y., Yukihiro, H. & Van Woesik, R. (2009). Acropora size-frequency distributions reflect spatially variable conditions on coral reefs of Palau. *Bull. Mar. Sci.*, 85, 149–157.
- Wagner, D.E., Kramer, P. & Woesik, R. Van. (2010). Species composition, habitat, and water quality influence coral bleaching in southern Florida. *Mar. Ecol. Prog. Ser.*, 408, 65–78.
- Welsh, J.Q. & Bellwood, D.R. (2012). Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. *Coral Reefs*, 31, 55–65.
- Wilcox, K.R., Koerner, S.E., Hoover, D.L., Borkenhagen, A.K., Burkepile, D.E., Collins, S.L., *et al.* (2020). Rapid recovery of ecosystem function following extreme drought in a South African savanna grassland. *Ecology*, 101, 1–9.
- Wilson, S.K., Robinson, J.P.W., Chong-Seng, K., Robinson, J. & Graham, N.A.J. (2019). Boom and bust of keystone structure on coral reefs. *Coral Reefs*, 38, 625–635.
- Wismer, S., Tebbett, S.B., Streit, R.P. & Bellwood, D.R. (2019a). Spatial mismatch in fish and coral loss following 2016 mass coral bleaching. *Sci. Total Environ.*, 650, 1487–1498.
- Wismer, S., Tebbett, S.B., Streit, R.P. & Bellwood, D.R. (2019b). Young fishes persist despite coral loss on the Great Barrier Reef. *Commun. Biol.*, 2, 1–7.
- Van Woesik, R., Houk, P., Isechal, A.L., Idechong, J.W., Victor, S. & Golbuu, Y. (2012a). Climate-change refugia in the sheltered bays of Palau: Analogs of future reefs. *Ecol. Evol.*, 2, 2474–2484.
- Van Woesik, R., Irikawa, A., Anzai, R. & Nakamura, T. (2012b). Effects of coral colony morphologies on mass transfer and susceptibility to thermal stress. *Coral Reefs*, 31, 633–639.
- Van Woesik, R., Sakai, K., Ganase, A. & Loya, Y. (2011). Revisiting the winners and the losers a decade after coral bleaching. *Mar. Ecol. Prog. Ser.*, 434, 67–76.
- Woodhead, A.J., Hicks, C.C., Norström, A. V., Williams, G.J. & Graham, N.A.J. (2019). Coral reef ecosystem services in the Anthropocene. *Funct. Ecol.*, 33, 1023–1034.
- Wyatt, A.S.J., Leichter, J.J., Toth, L.T., Miyajima, T., Aronson, R.B. & Nagata, T. (2020). Heat accumulation on coral reefs mitigated by internal waves. *Nat. Geosci.*, 13, 28–34.
- Yarlett, R.T., Perry, C.T., Wilson, R.W. & Harborne, A.R. (2020). Inter-habitat variability in parrotfish bioerosion rates and grazing pressure on an Indian Ocean reef platform. *Diversity*, 12, 1–17.
- Yeung, Y.H., Xie, J.Y., Zhao, Y., Yu, H.Y., Chen, C., Lu, W.W., *et al.* (2021). Rapid external erosion of coral substrate in subtropical Hong Kong waters. *Mar. Pollut. Bull.*, 169, 112495.

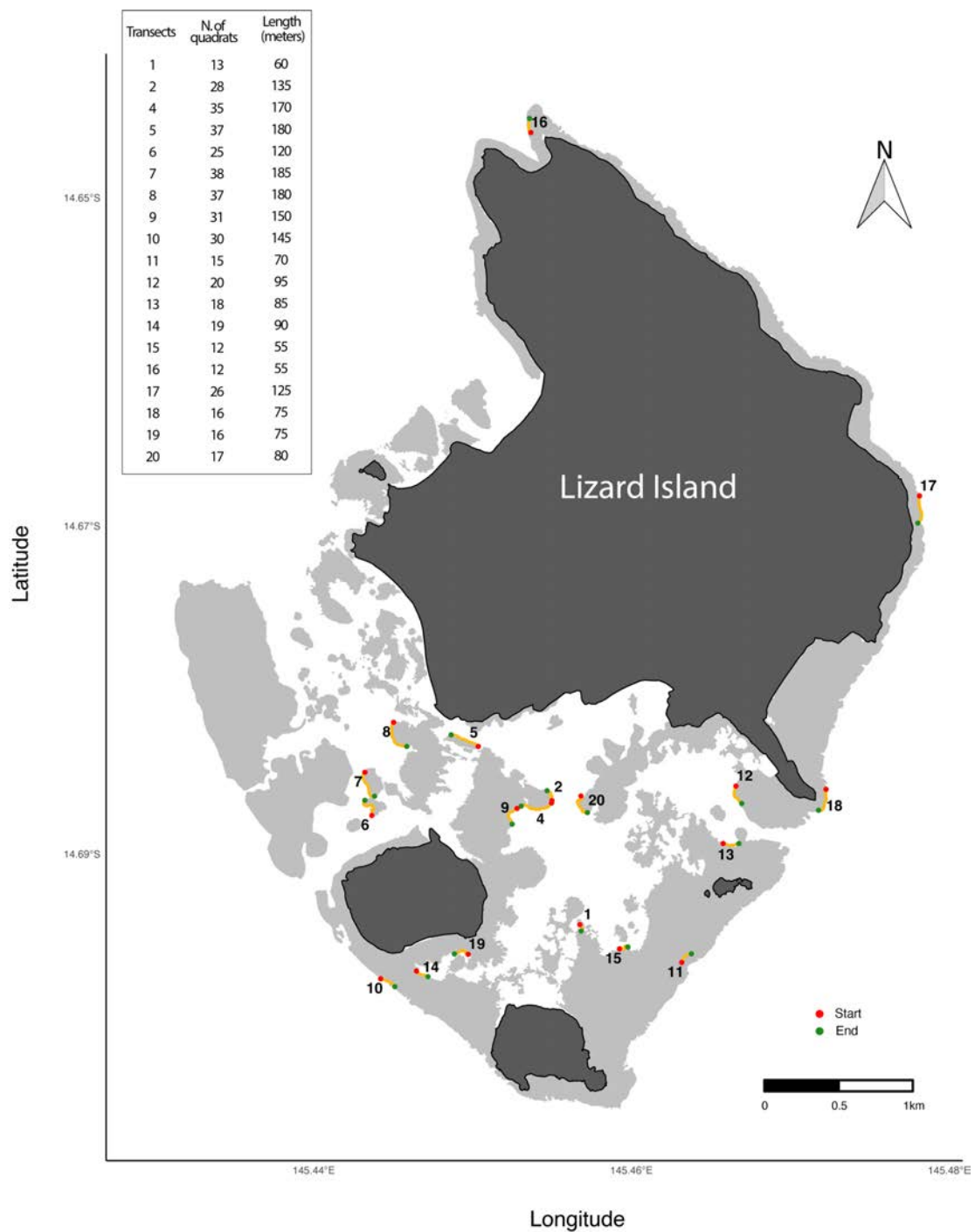
- Yim, U.H., Hong, S., Lee, C., Kim, M., Jung, J.-H., Ha, S.Y., *et al.* (2020). Rapid recovery of coastal environment and ecosystem to the Hebei Spirit oil spill's impact. *Environ. Int.*, 136, 105438.
- Young, M.A.L. & Bellwood, D.R. (2011). Diel patterns in sea urchin activity and predation on sea urchins on the Great Barrier Reef. *Coral Reefs*, 30, 729–736.
- Zaneveld, J.R., Burkepile, D.E., Shantz, A.A., Pritchard, C.E., McMinds, R., Payet, J.P., *et al.* (2016). Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nat. Commun.*, 7, 11833.

Appendix A.
Supplementary Material to Chapter 2

Supplementary Figures



Supplementary Figure 2.1 | Clear signs of bleaching in *Acropora* colonies at Lizard Island (a, b). Both photos show signs of mild bleaching in *Acropora* colonies in February 2021. **And an example of a potential source reef of coral planulae, Linnet Reef, approximately 15 km from Lizard Island (c, d).** Note the larger colonies on Linnet Reef, photographed in January 2021, which may have survived the 2016 bleaching event. All photographs SB Tebbett.



Supplementary Figure 2.2 | Map of study sites. Map of Lizard Island, located in the northern region of GBR, showing the 19 transects in our study. The start of the transects are represented by red circles while the end is represented by the green circle. The inner table shows the number of quadrats per transect and the approximate length of each transect based on the 5-meter interval between quadrats.



Supplementary Figure 2.3 | Examples of images used to count and measure recruits of *Acropora* colonies.
The sequence of images shows increasing levels of magnification of the same photograph, with close-up views of an individual coral colony recruit. All photographs taken at Lizard Island by SB Tebbett.

Supplementary Tables

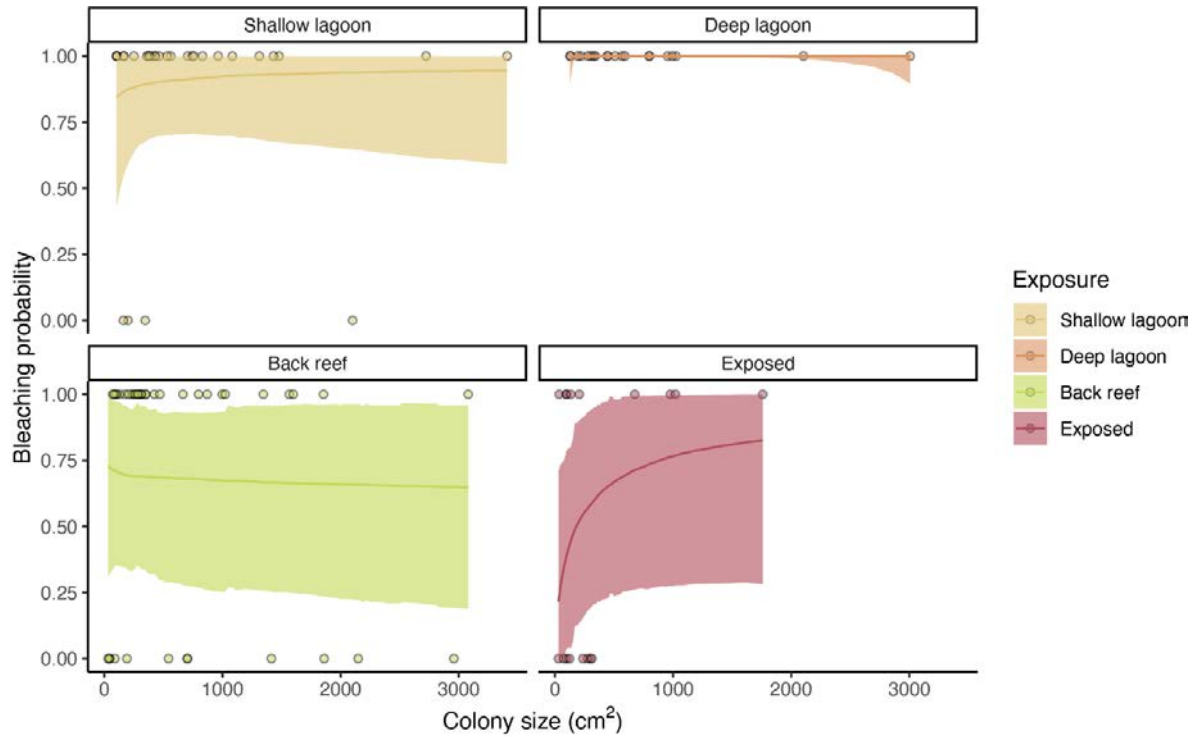
Supplementary Table 2.1 | List of likely *Acropora* species found in our sampling area. This table shows the likely *Acropora* species occurring in our sampling area based on morphological characteristics and using Lizard Island field guide (<http://lifq.australianmuseum.net.au/Hierarchy.html>) for identification.

Species
<i>Acropora carduus</i>
<i>Acropora cerealis</i>
<i>Acropora cytherea</i>
<i>Acropora divaricata</i>
<i>Acropora elseyi</i>
<i>Acropora florida</i>
<i>Acropora gemmifera</i>
<i>Acropora grandis</i>
<i>Acropora humilis</i>
<i>Acropora hyacinthus</i>
<i>Acropora intermedia</i>
<i>Acropora latistella</i>
<i>Acropora loripes</i>
<i>Acropora millepora</i>
<i>Acropora monticulosa</i>
<i>Acropora muricata</i>
<i>Acropora nasuta</i>
<i>Acropora samoensis</i>
<i>Acropora sarmentosa</i>
<i>Acropora selago</i>
<i>Acropora spathulata</i>
<i>Acropora tenuis</i>
<i>Acropora valenciennesi</i>
<i>Acropora valida</i>
<i>Acropora willisae</i>
<i>Acropora yongei</i>

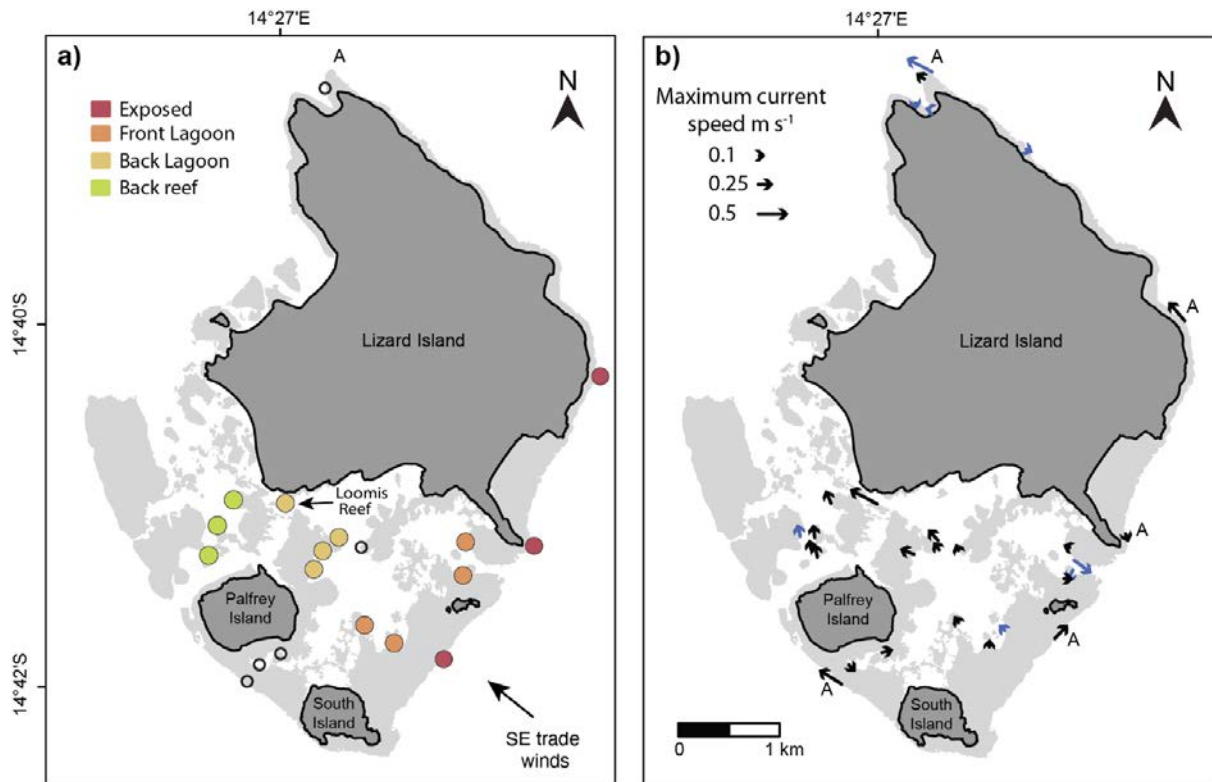
Supplementary text. Likely species of massive Porites in our sampling area. For massive Porites, the likely species occurring in our sampling area were *Porites australiensis*, *Porites lobata* and *Porites lutea*. However, it is difficult to tell these three species apart with massive Porites being one of the most difficult coral groups to separate without molecular analysis. These identifications are also based on the Lizard Island field guide.

Appendix B.
Supplementary Material to Chapter 3

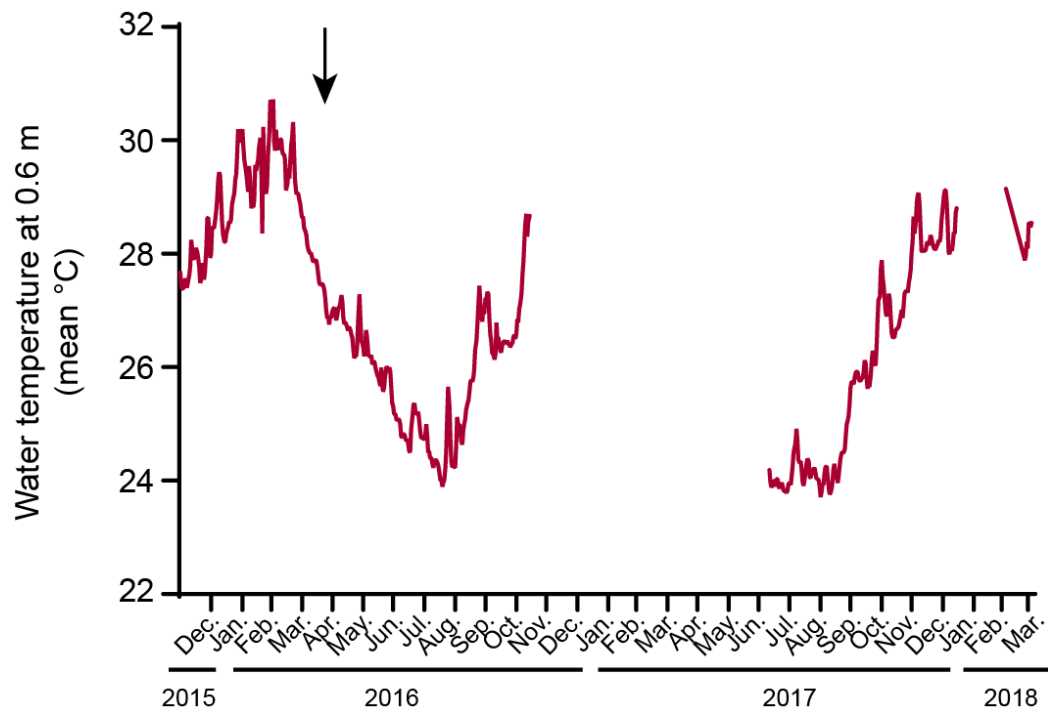
Supplementary Figures



Supplementary Figure 3.1 The relationships between colony size and the probability of an individual massive *Porites* colony being bleached across different wave exposure levels at Lizard Island. Lines represent model estimated marginal means from a Bayesian generalised linear mixed effects model (binomial family), coloured ribbons denote the 95% high posterior density intervals, and points represent bleaching status (i.e. bleached or not bleached) of individual massive *Porites* colonies.



Supplementary Figure 3.2 | a) Map of Lizard Island, showing all the 19 transect locations. Coloured points represent transects that supported massive *Porites* colonies and their exposure categories (relative to the prevailing south-east trade winds). Black circles represent transects that did not contain massive *Porites* colonies. b) Map adapted from Tebbett et al. (2022) showing the water current speeds and directions around Lizard Island. Note black arrows are current meters associated with benthic transects while blue arrows are extra current meters in strategic locations. The 'A' denotes current meters on rope arrays.



Supplementary Figure 3.3 | Mean water temperature at 0.6 m depth. The arrow indicates the timing of our sampling trip. Figure adapted from Tebbett et al. (2019) with data sourced from the Australian Institute of Marine Science (AIMS 2018).

Supplementary Tables

Supplementary Table 3.1 | Summary of the Bayesian generalized linear mixed-effects model (GLMM) with a binomial distribution and a logit link function used to test the hypothesis that the interactions between exposure and colony size influenced the prevalence of bleaching (i.e. presence or absence of any sign of bleached area) across the community of massive *Porites* colonies examined at Lizard Island. Inferences were based upon the mean slope of the predictor variable and associated 95% high posterior density intervals (HPD). If the HPDs intersected zero, no effect was inferred. L = lower, U = upper.

Variable	Estimate	L-95% HPD	U-95% HPD	Rhat	Bulk_ESS
b_Intercept	0.21484315	-8.21068	8.710295	1.000312	2350.520
b_ExposureFrontlagoon	7.59202918	-259.619	308.6127	1.003682	1838.314
b_ExposureBackreef	1.15034813	-7.91546	10.94835	1.000353	2411.813
b_ExposureExposed	-4.0349616	-14.5619	5.721970	1.000607	2211.971
b_logstLiveArea_cm2	0.30976922	-0.98668	1.74191	1.000045	2415.551
b_ExpFrontlagoon:logstLiveArea	1.46229916	-37.2105	52.83531	1.003785	1701.330
b_ExpBackreef:logstLiveArea	-0.4118304	-1.91185	1.076717	1.000113	2464.921
b_ExpExposed:logstLiveArea	0.39964892	-1.28851	2.156271	1.000500	2312.154

Supplementary Table 3.2 | Summary of the Bayesian generalized linear mixed-effects model (GLMM) with a gamma distribution and a log link function used to test the hypothesis that the interactions between exposure and colony size influenced the bleaching extent (% of bleached area per colony) in massive *Porites* colonies at Lizard Island. Inferences were based upon the mean slope of the predictor variable and associated 95% high posterior density intervals (HPD). If the HPDs intersected zero, no effect was inferred. L = lower, U = upper.

Variable	Estimate	L-95% HPD	U-95% HPD	Rhat	Bulk_ESS
b_Intercept	0.753182	-0.67369	2.16172	1.000190	3143.004
b_ExposureFrontlagoon	0.546163	-1.55331	2.687358	0.999819	3429.421
b_ExposureBackreef	-1.282033	-2.93995	0.407685	0.999993	3213.254
b_ExposureExposed	-1.534435	-3.45039	0.446122	0.999710	3338.913
b_logstLiveArea_cm2	-0.209997	-0.43245	0.005314	0.999993	3175.603
b_ExpFrontlagoon:logstLiveArea	-0.157685	-0.48529	0.175243	0.999599	3440.381
b_ExpBackreef:logstLiveArea	0.079826	-0.17760	0.346235	1.000011	3256.706
b_ExpoExposed:logstLiveArea	0.027220	-0.28630	0.355168	0.999679	3401.726

Supplementary Table 3.3 | Pairwise comparisons used to compare prevalence of bleaching in massive *Porites* colonies among wave exposure levels. Inferences were based on the associated 95% high posterior density intervals (HPD). If the HPDs intersected zero, no effect was inferred.

Contrast	Estimate	lower.HPD	upper.HPD
Back lagoon - Front lagoon	-23.767751	-116.37113	1.3863144
Back lagoon - Back reef	1.5803511	-0.8544203	4.9874095
Back lagoon - Exposed	1.4001795	-1.7854619	4.6182863
Front lagoon - Back reef	25.3991	0.3412926	117.79399
Front lagoon - Exposed	25.172589	0.9527401	118.33807
Back reef - Exposed	-0.2226226	-3.4146720	2.5882155

Supplementary Table 3.4 | Pairwise comparisons of the slopes of relationships between the bleaching status (i.e. if they were bleached or not) of massive *Porites* colonies and their size among different exposure levels. The slopes are from a Bayesian generalized linear mixed-effects model (GLMM) with a binomial distribution and a logit link function that examined the prevalence of bleaching in massive *Porites* around Lizard Island. If the HPDs intersected zero, no effect was inferred.

Contrast	Estimate	lower.HPD	upper.HPD
Back lagoon - Front lagoon	-1.280093	-48.0948	33.142533
Back lagoon - Back reef	0.375100	-1.04732	1.9949697
Back lagoon - Exposed	-0.416796	-2.30310	1.2498243
Front lagoon - Back reef	1.679120	-33.6102	47.911775
Front lagoon - Exposed	0.887787	-33.6797	47.609409
Back reef - Exposed	-0.791364	-2.14121	0.3926449

Supplementary Table 3.5 | Pairwise comparisons used to compare massive *Porites* colony bleaching extent among wave exposure levels. Inferences were based on the associated 95% high posterior density intervals (HPD). If the HPDs intersected zero, no effect was inferred.

Contrast	Estimate	lower.HPD	upper.HPD
Back lagoon - Front lagoon	0.47824148	0.0426110	0.9730125
Back lagoon - Back reef	0.76784017	0.2354252	1.2374358
Back lagoon - Exposed	1.36425398	0.7562894	1.8903461
Front lagoon - Back reef	0.28902914	-0.225800	0.7945464
Front lagoon - Exposed	0.88463603	0.2855213	1.4849068
Back reef - Exposed	0.59720449	0.0073809	1.1984957

Supplementary Table 3.6 | Pairwise comparisons of the slopes of the relationship between *Porites* colony bleaching extent and their size among all the exposure levels. Slopes are from a Bayesian generalized linear mixed-effects model (GLMM) with a gamma distribution and a log link function. If the HPDs intersected zero, no effect was inferred.

Contrast	Estimate	lower.HPD	upper.HPD
Back lagoon - Front lagoon	0.1505517	-0.186016	0.4925180
Back lagoon - Back reef	-0.0791605	-0.360652	0.1978352
Back lagoon - Exposed	-0.0336413	-0.359697	0.3115460
Front lagoon - Back reef	-0.2292252	-0.533490	0.0588759
Front lagoon - Exposed	-0.1823614	-0.514358	0.1639981
Back reef - Exposed	0.0479132	-0.253219	0.3202284

Appendix C. Supplementary Material to Chapter 4

Supplementary Methods

Model to estimate coral volume

Body size is a key trait determining ecosystem function for all organisms, including corals (Bellwood, Streit, Brandl, & Tebbett, 2019; Graham et al., 2006; Reguero, Beck, Agostini, Kramer, & Hancock, 2018). One non-destructive way of measuring body size for corals is estimating their volume from 3D models using photogrammetric approaches via Structure-from-Motion (Aston, Duce, Hoey, & Ferrari, 2022; Bayley & Mogg, 2020; Burns, Delparte, Gates, & Takabayashi, 2015; Cresswell et al., 2020; Pizarro, Friedman, Bryson, Williams, & Madin, 2017). However, this technique is relatively costly, particularly from a time perspective, as 3D models may require many hours or days to be built on average computer processors (House et al., 2018; Laforsch et al., 2008; Naumann, Niggel, Laforsch, Glaser, & Wild, 2009). As a potential solution, it has been proposed that 2D estimates of body size (planar area) may be inextricably linked to 3D volume for corals of the same morphology (House et al., 2018; Husband, Perry, & Lange, 2022; Urbina-Barreto et al., 2021). As the 2D planar area is quickly obtained by tracing coral colonies from still photographs, it significantly reduces costs and processing time, allowing hundreds of coral colonies to be measured for repeated time periods with relative ease (Morais, Morais, Tebbett, Pratchett, & Bellwood, 2021). Furthermore, for the vast libraries of still photographs (*i.e.*, photoquadrats) of benthic communities that are available online (e.g., CoralNet, <https://coralnet.ucsd.edu/>), this may be the only available form of estimating coral volume.

In this paper, the first step to calculate erosion rates after mortality for individual colonies was to use published relationships to convert estimates of coral planar area extracted from our photoquadrats to predict 3D colony volume. We used the relationships between planar area and

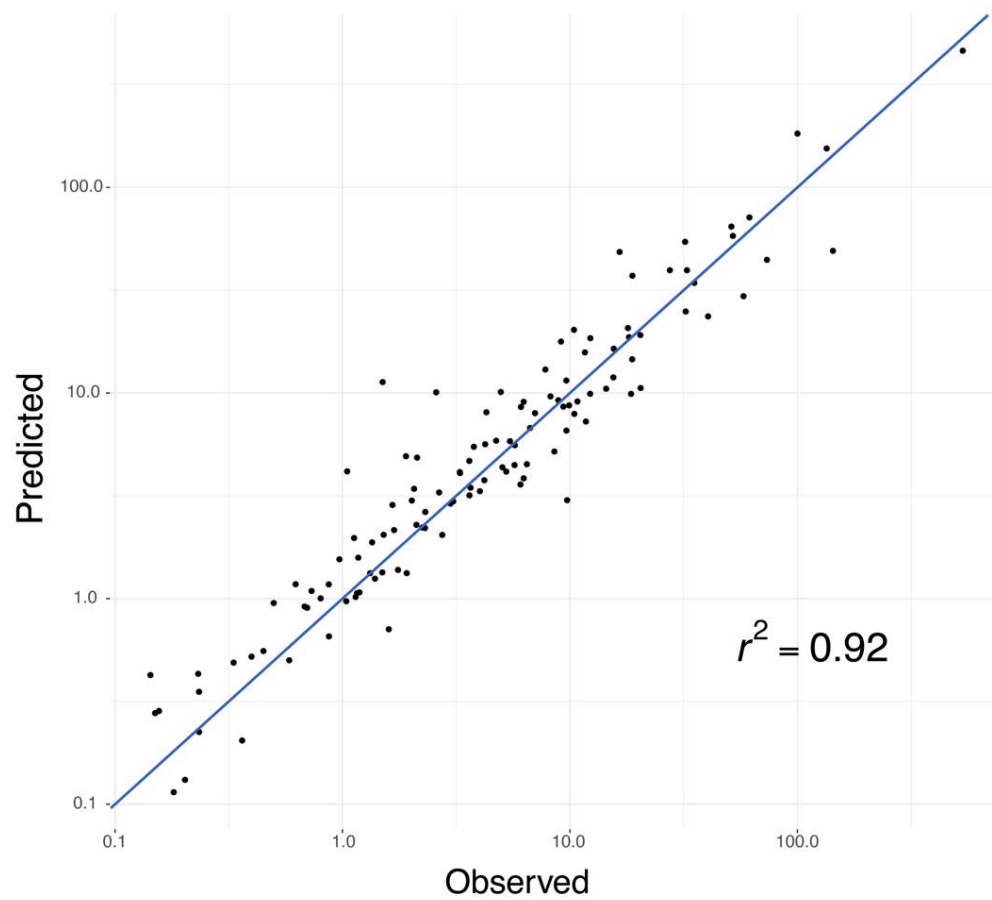
colony volume provided in Urbina-Barreto et al., (2021). In this study, the authors used underwater photogrammetry to build 3D models of 120 coral colonies across a gradient in body size and growth forms. One of their major findings was that planar area and the diameter of coral colonies can work as satisfactory proxies for estimating colony volume for the coral morphologies evaluated. Using their dataset (publically available in: <https://zenodo.org/record/4309245>), we first used a generalized linear model (GLM) with a gamma distribution and a log link to evaluate the relationship between coral colony 3D volume (response variable) and the predictor variables of coral growth form and the 2D planar surface area (logged). Model fit and assumptions were validated as in the main manuscript. We then used this model to predict the volume for all colonies measured by Urbina-Barreto et al., 2021 and used a simple linear regression to measure the predictive accuracy (as the R^2) of the log predicted values relative to the log observed values. Given the high predictive accuracy ($R^2 = 0.92$; Figure S1) of this model, we were able to use this relationship to predict the volume of all colonies in our dataset based on their planar area and growth morphology. It is important to note there are some potential limitations in this method. For example, Urbina-Barreto et al., (2021) did not work with dead and/or degraded coral colonies. They used live corals to make their 3D models while we only worked with dead colonies. However, other studies such as (House et al., 2018) used dead corals (coral skeleton) in their analyses and also obtained a strong relationship between coral planar area and volume. Thus, this is likely not to have a strong effect on your results. Also, their study focused on a new method to quantify the shelter volume provided by individual living corals colonies for fishes. The data on the relationship between colony volume and planar area that we used here was just one, albeit critical, step in their process of measuring shelter volume. However, the relationship between the observed coral 3D volume and predicted coral 3D volume, using only the 2D planar area as a predictor, clearly suggested a high predictive accuracy (Figure S1)

Supplementary References

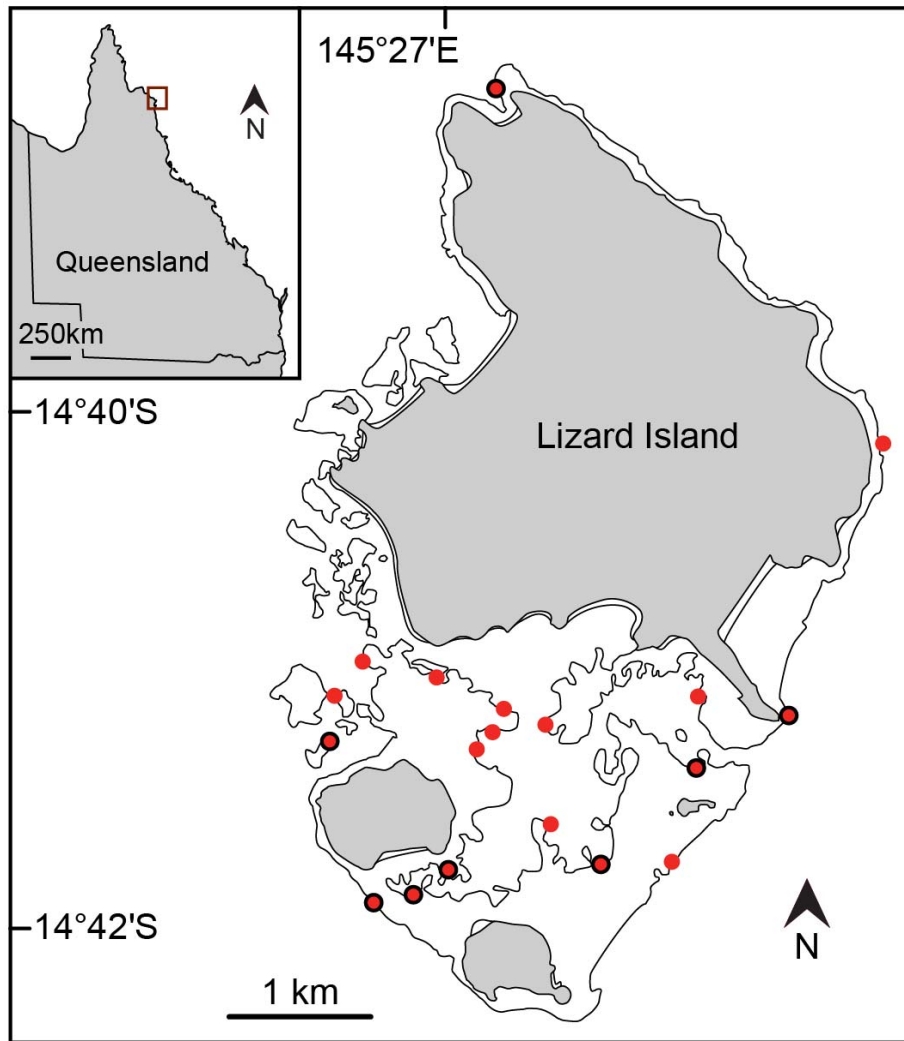
- Aston, E. A., Duce, S., Hoey, A. S., & Ferrari, R. (2022). A Protocol for Extracting Structural Metrics From 3D Reconstructions of Corals. *Frontiers in Marine Science*, 9(April), 1–14. doi: 10.3389/fmars.2022.854395
- Bayley, D. T. I., & Mogg, A. O. M. (2020). A protocol for the large-scale analysis of reefs using Structure from Motion photogrammetry. *Methods in Ecology and Evolution*, 11(11), 1410–1420. doi: 10.1111/2041-210X.13476
- Bellwood, D. R., Streit, R. P., Brandl, S. J., & Tebbett, S. B. (2019). The meaning of the term ‘function’ in ecology: A coral reef perspective. *Functional Ecology*, 33(6), 948–961. doi: 10.1111/1365-2435.13265
- Burns, J. H. R., Delparte, D., Gates, R. D., & Takabayashi, M. (2015). Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. *PeerJ*, 3, e1077. doi: 10.7717/peerj.1077
- Cresswell, A. K., Orr, M., Renton, M., Haywood, M. D. E., Giraldo, A., Slawinski, D., ... Thomson, D. P. (2020). Structure-from-motion reveals coral growth is influenced by colony size and wave energy on the reef slope at Ningaloo Reef , Western Australia. *Journal of Experimental Marine Biology and Ecology*, 530–531(December 2019), 151438. doi: 10.1016/j.jembe.2020.151438
- Graham, N. A. J., Wilson, S. K., Jennings, S., Polunin, N. V. C., Bijoux, J. P., & Robinson, J. (2006). Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences*, 103(22), 8425 LP – 8429. doi: 10.1073/pnas.0600693103
- House, J. E., Brambilla, V., Bidaut, L. M., Christie, A. P., Pizarro, O., Madin, J. S., & Dornelas, M. (2018). Moving to 3D: Relationships between coral planar area, surface area and volume. *PeerJ*, 2018(2). doi: 10.7717/peerj.4280
- Husband, E., Perry, C. T., & Lange, I. D. (2022). Estimating rates of coral carbonate production from aerial and archive imagery by applying colony scale conversion metrics. *Coral Reefs*. doi: 10.1007/s00338-022-02247-6
- Laforsch, C., Christoph, E., Glaser, C., Naumann, M., Wild, C., & Niggli, W. (2008). A precise and non-destructive method to calculate the surface area in living scleractinian corals using X-ray computed tomography and 3D modeling. *Coral Reefs*, 27(4), 811–820. doi: 10.1007/s00338-008-0405-4

- Morais, J., Morais, R. A., Tebbett, S. B., Pratchett, M. S., & Bellwood, D. R. (2021). Dangerous demographics in post-bleach corals reveal boom-bust versus protracted declines. *Scientific Reports*, *11*(1), 18787. doi: 10.1038/s41598-021-98239-7
- Naumann, M. S., Niggli, W., Laforsch, C., Glaser, C., & Wild, C. (2009). Coral surface area quantification-evaluation of established techniques by comparison with computer tomography. *Coral Reefs*, *28*(1), 109–117. doi: 10.1007/s00338-008-0459-3
- Pizarro, O., Friedman, A., Bryson, M., Williams, S. B., & Madin, J. (2017). A simple, fast, and repeatable survey method for underwater visual 3D benthic mapping and monitoring. *Ecology and Evolution*, *7*(6), 1770–1782. doi: <https://doi.org/10.1002/ece3.2701>
- Reguero, B. G., Beck, M. W., Agostini, V. N., Kramer, P., & Hancock, B. (2018). Coral reefs for coastal protection: A new methodological approach and engineering case study in Grenada. *Journal of Environmental Management*, *210*, 146–161. doi: 10.1016/j.jenvman.2018.01.024
- Tebbett, S. B., Morais, J., & Bellwood, D. R. (2022). Spatial patchiness in change, recruitment, and recovery on coral reefs at Lizard Island following consecutive bleaching events. *Marine Environmental Research*, *173*(November 2021), 105537. doi: 10.1016/j.marenvres.2021.105537
- Urbina-Barreto, I., Chiroleu, F., Pinel, R., Fréchon, L., Mahamadaly, V., Elise, S., ... Adjeroud, M. (2021). Quantifying the shelter capacity of coral reefs using photogrammetric 3D modeling: From colonies to reefscapes. *Ecological Indicators*, *121*(October), 107151. doi: 10.1016/j.ecolind.2020.107151

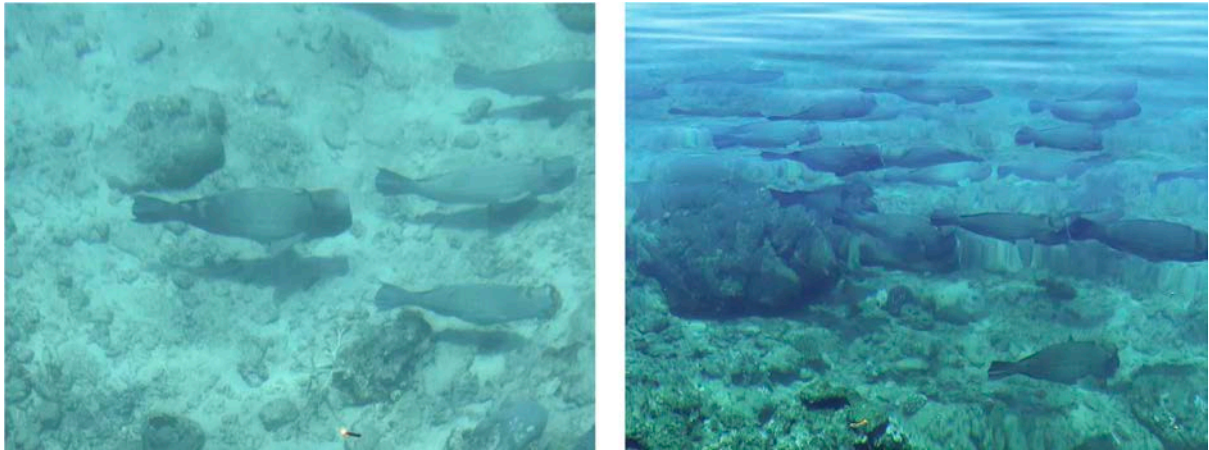
Supplementary Figures



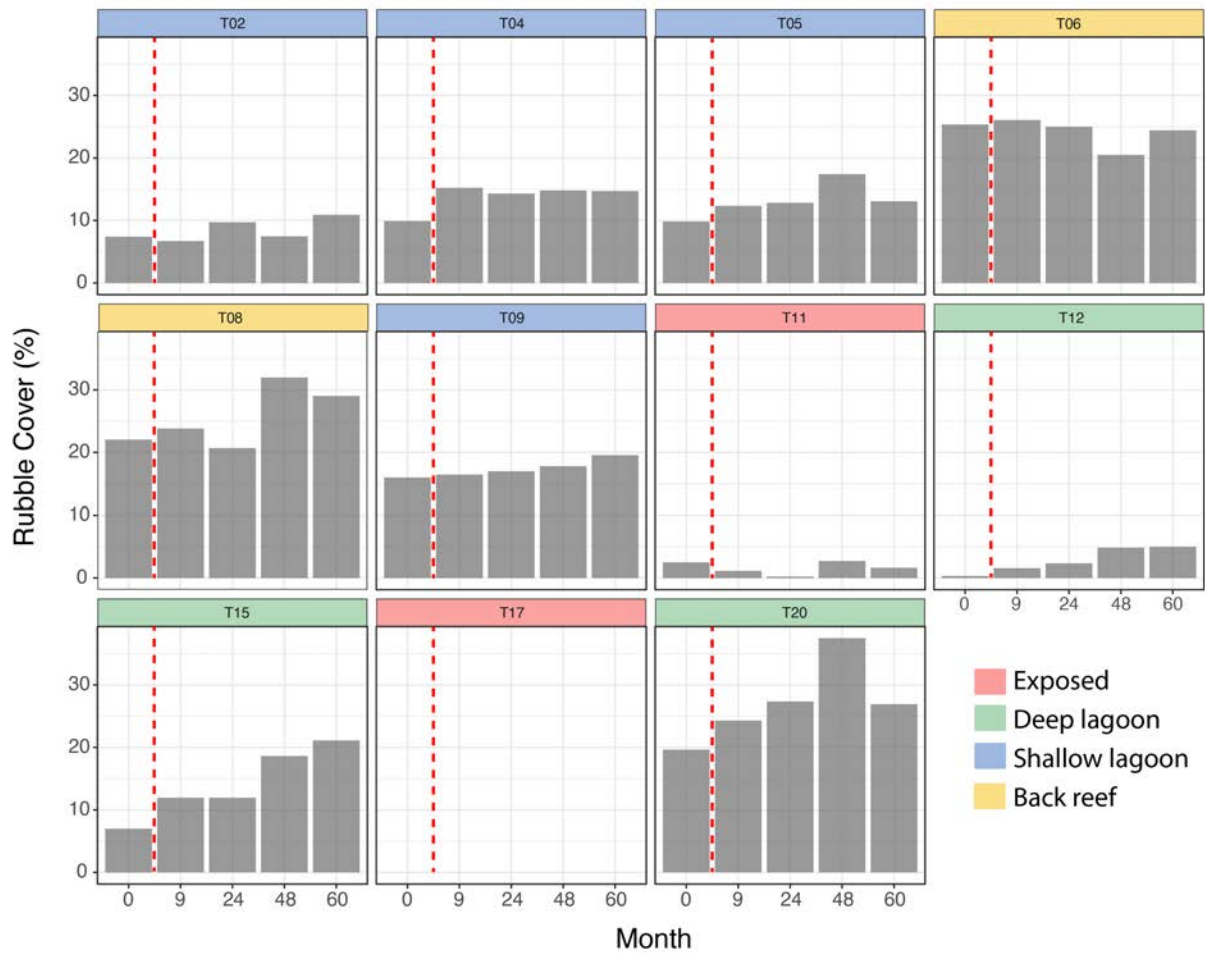
Supplementary Figure 4.1 | Relationship between the observed coral 3D volume and predicted coral 3D volume using only 2D planar area data as a predictor. Data sourced from Urbina-Barreto et al., 2021.



Supplementary Figure 4.2 | Map of Lizard Island, located in the northern region of the GBR, showing the original 19 transects in which fish counts were performed. The red circles represent the sites that were used in this study. Red circles with black rings represent fish counting sites that were not included in this study due to the absence of dead corals in these areas.



Supplementary Figure 4.3 | Photographs showing a school of *Bolbometopon muricatum* seen on Lizard Island during one of our field trips in January 2021 (photos taken from boat).



Supplementary Figure 4.4 | Coral rubble cover in each transect throughout the study period. Dashed red lines represent the 2016 bleaching event. Different colors represent the wave exposure levels and match Figure 1. Data from Tebbett, Morais, & Bellwood, (2022).

Supplementary Tables

Supplementary Table 4.1 | Summary of pairwise comparisons used to compare coral colony erosion and disappearance among categorical predictor variables. Inferences were based upon the mean slope of the predictor variable and associated 95% high posterior density intervals (HPD). If the HPDs intersected zero, no effect was inferred.

Response variable	Model used	Contrast	Estimate	Lower.HPD	Upper.HPD
Erosion (CaCO₃.cm⁻².yr⁻¹)	GLMM	Back reef - Deep lagoon	0.0376	-1.1848	1.2636
	Gamma (link='log')	Back reef – Exposed	-0.6014	-1.7662	0.5720
		Back reef - Shallow lagoon	-0.8441	-2.6597	0.9563
		Deep lagoon – Exposed	-0.6355	-1.5778	0.3100
		Deep lagoon - Shallow lagoon	-0.8840	-2.6353	0.9111
		Exposed - Shallow lagoon	-0.2458	-2.0148	1.5196
Erosion (CaCO₃.cm⁻².yr⁻¹)	GLMM Gamma (link='log')	Arborescent – Caespitose	0.1034	-0.4457	0.6801
		Arborescent – Corymbose	0.0983	-0.4423	0.6414
		Arborescent – Digitate	0.4650	-0.1105	1.1095
		Arborescent – Tabular	0.4322	-0.2265	1.1276
		Caespitose – Corymbose	-0.0052	-0.5219	0.5112
		Caespitose – Digitate	0.3675	-0.2183	0.9433
		Caespitose – Tabular	0.3238	-0.3917	1.0295
		Corymbose – Digitate	0.3759	-0.0105	0.7477
		Corymbose – Tabular	0.3325	-0.1291	0.8037
		Digitate - Tabular	-0.0404	-0.5971	0.4849
Erosion (disappearance of colonies)	GLMM binomial(link = "logit")	Back reef - Deep lagoon	0.8556	-0.4809	2.5518
		Back reef – Exposed	-0.8482	-2.4509	0.7961
		Back reef - Shallow lagoon	-0.7319	-2.1049	0.5623
		Deep lagoon – Exposed	-1.7282	-3.3498	-0.1450
		Deep lagoon - Shallow lagoon	-1.6077	-2.9147	-0.3796
		Exposed - Shallow lagoon	0.1118	-1.2620	1.4842

Appendix D.

Supplementary Material to Chapter 5

Supplementary Methods

Photo-quadrat methods and 'open space' for recruitment

In each sampling period, each quadrat was photographed (Camera: Nikon Coolpix AW130) while on SCUBA. All photographs were taken from a planar 'bird's-eye' perspective between 09:00 and 16:00 h. The quadrat frame was not fixed on the reef; instead, the same quadrat area was relocated on subsequent trips using a second underwater camera containing all previous images from each quadrat ordered from the start to the end of the transect (see Wismer et al., 2019a for a sensitivity analysis of this method). As the present study was specifically focused on *Acropora* spp. recruits, we only used quadrats with new recruits first recorded in 2020 (i.e. 91 quadrats spread across 13 of the 19 transects, Figure S1). It is important to note that 'open space' suitable for coral recruitment was widespread in our quadrats during this period. This is because two cyclones in 2014 and 2015 (i.e. prior to the bleaching event) reduced coral cover on exposed and semi-exposed reefs around Lizard Island by up to 90% (Ceccarelli *et al.* 2016; Madin *et al.* 2018). As severe tropical storms generate wave energies that result in physical damage to corals, either by breaking branches or by dislocating entire colonies, storm-induced disturbance can create optimum substrata for future recruitment (Kayal et al. 2018). Moreover, in terms of corals that were not dislodged by cyclones and died in subsequent bleaching events, we documented rapid and complete erosion of these colonies before the main recruitment event documented herein (see Morais et al. 2022). As a result, 'open space', suitable for coral recruitment, was widespread around Lizard Island soon after the bleaching events.

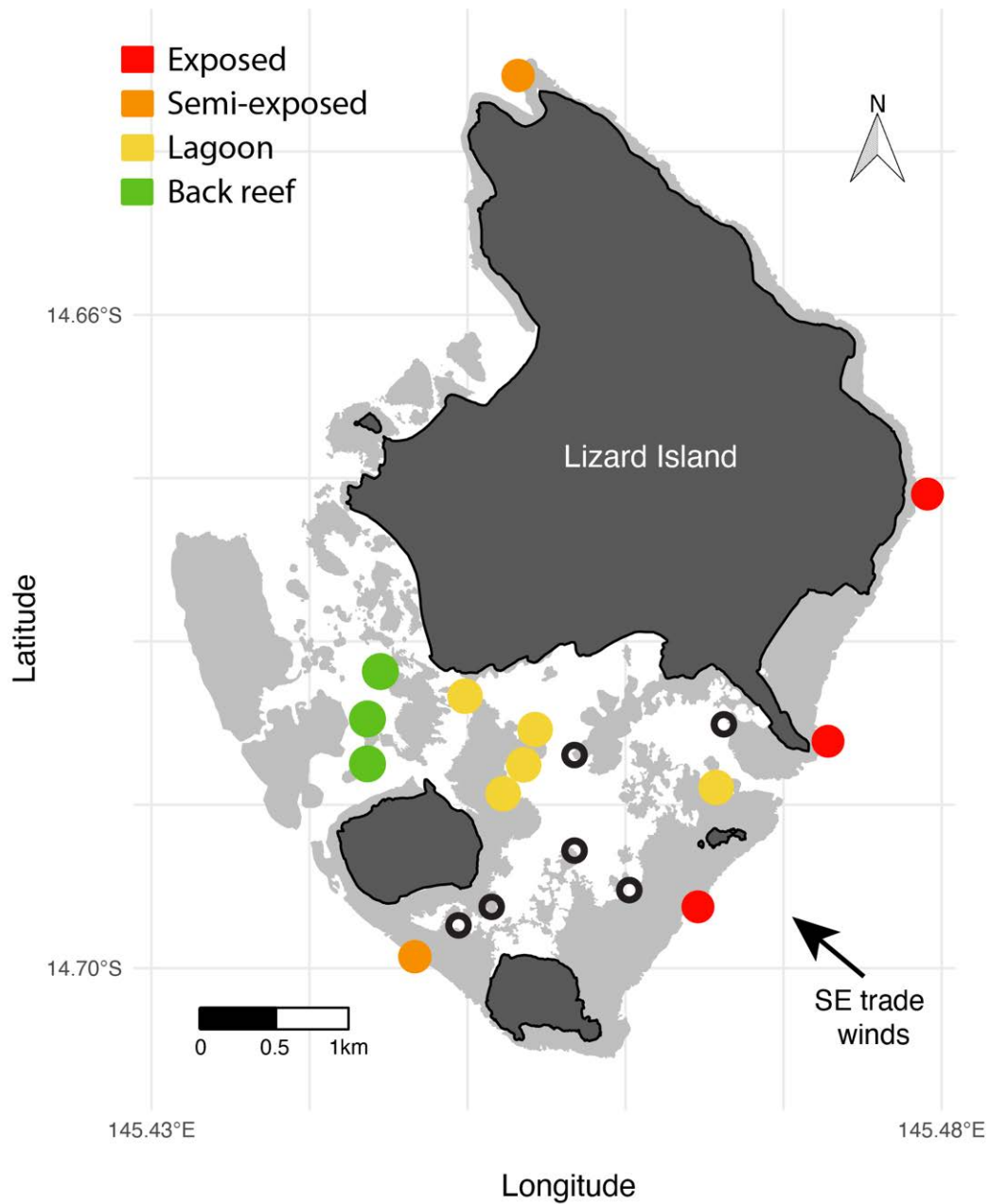
Time frame of coral recruit detection

It is important to note that very few new *Acropora* recruits were recorded in the previous (2018; n = 27 recruits detected) or subsequent (2021; n = 53 recruits detected) sampling periods. Given these low numbers, and to ensure we only focused on recruits that were likely to have settled on the substratum during a similar, narrow, recruitment window, we only considered recruits first seen in 2020. This represents 91% (n = 809) of the new recruits that settled in our study area during the sampling period (see Morais et al. 2021). The increased recruitment in 2020 can potentially be attributed to two factors: a) detection in 2020 of recruits accumulated from both the 2018 and 2019 recruitment seasons; and/or b) the potential for optimal environmental conditions in 2018 and/or 2019 to foster abnormally high recruitment rates (Edmunds 2017, 2023; Gouezo *et al.* 2020; Adjeroud *et al.* 2022). Given the lack of sampling in 2019 and the relatively large sizes of detected recruits for all growth forms (mean size of ~70 cm²; 23 times the minimum detected size), cumulative detection of recruits from 2018 and 2019 is very likely.

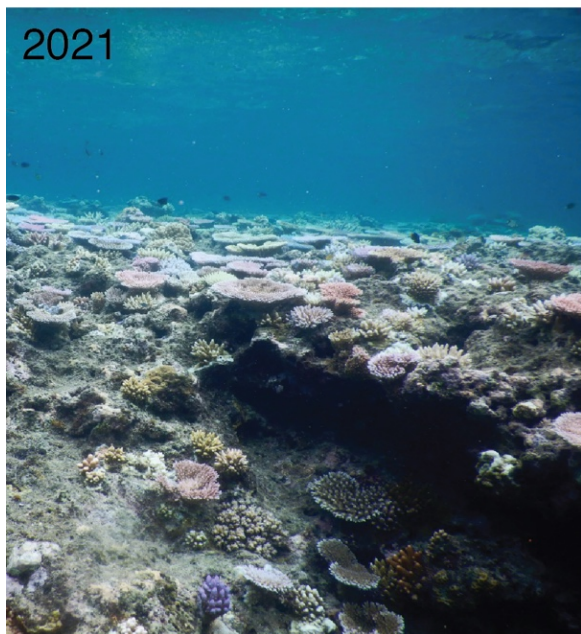
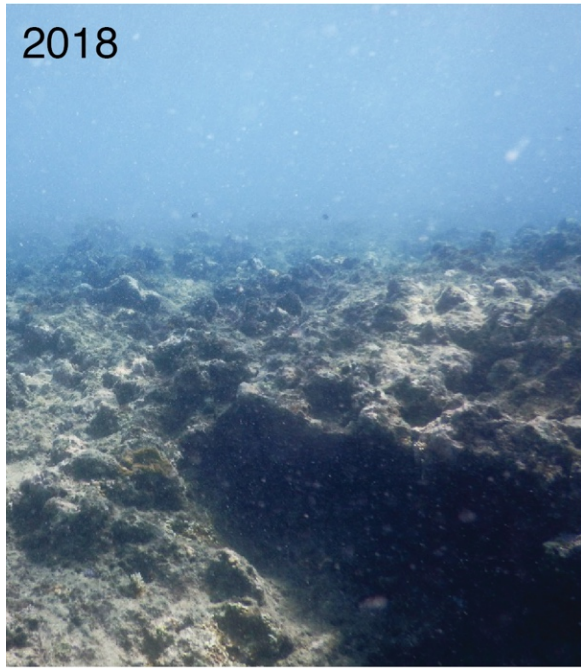
Coral colony density dependent effects and implications for restoration

Importantly, we found a negative linear density-dependent effect of coral recruit density on the growth rate of individual colonies (with recruit density spanning from 1-29 colonies m^{-2}). This aligns with past restoration studies which also showed negative linear density-dependent effects in *Acropora*, including on colony growth rates and branch numbers (Griffin et al. 2015; Ladd et al. 2016). Therefore, simply maximising the number of recruits per m^2 is not the most efficient means for generating coral cover. Nevertheless, $\sim 11-12$ recruits m^{-2} appears to be a good target density as this density of colonies can: a) rapidly produce relatively high levels of coral cover, b) represents a middle-ground (i.e. across the 1-29 colonies m^{-2} density range that we examined) in terms of minimising density dependent effects on coral growth rates, and c) represents a middle-ground for the colony densities (which range from 0.1-25 corals m^{-2}) considered in restoration projects by practitioners (reviewed in Ladd et al. 2018). However, despite the negative density-dependent effects we document on an individual colony level, it is also important to note that previous studies have demonstrated positive density-dependent effects between adult cover and recruitment rates (Kayal et al. 2015, 2018; Bramanti & Edmunds 2016). Unfortunately, we were unable to assess such effects in our study as the prior bleaching events killed 100% of *Acropora* in our sampling area, therefore, there was no established colonies during our key recruitment period.

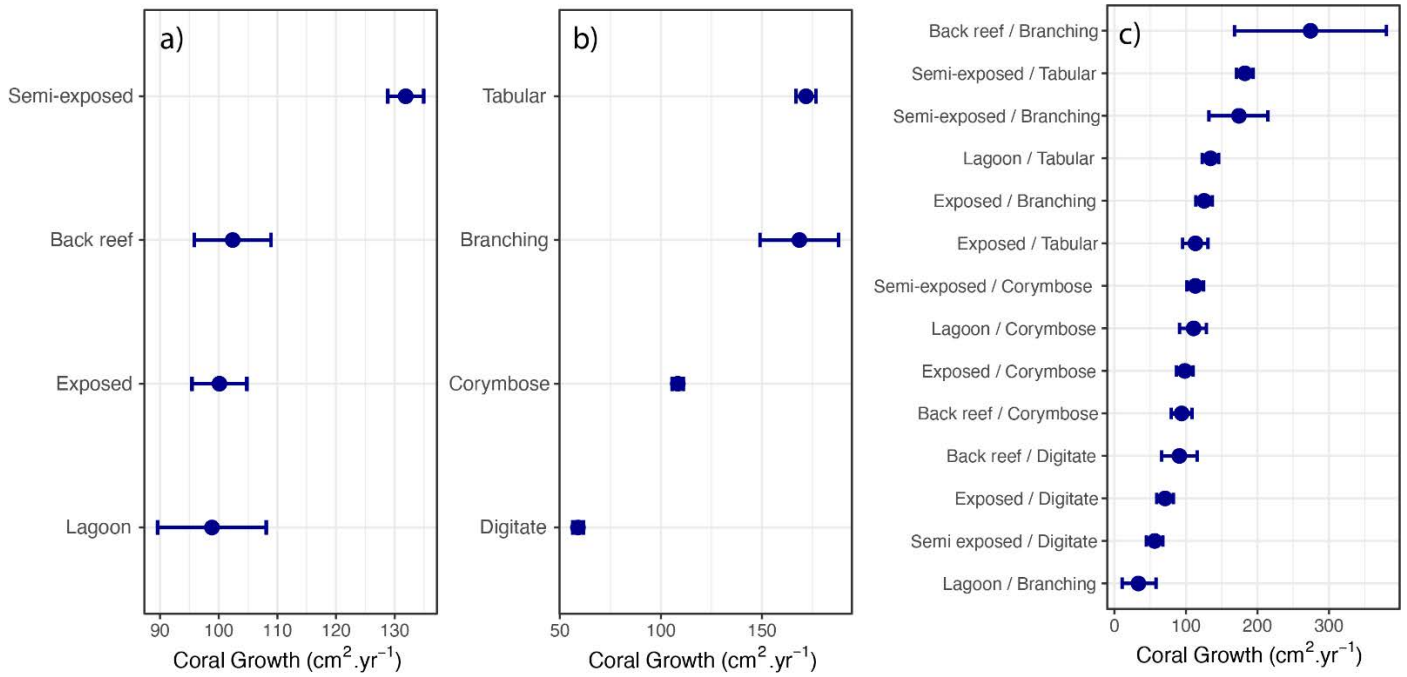
Supplementary Figures



Supplementary Figure 5.1 | A map of Lizard Island, located in the northern region of the Great Barrier Reef, showing the 19 sampling locations. Coloured points represent transects that supported *Acropora* recruits and their exposure categories (relative to the prevailing south-east trade winds). Black circles represent transects that did not support coral recruits.



Supplementary Figure 5.2 | A series of photographs taken from 2018 to 2022 showing the establishment of coral recruits and the increase in coral cover over time in the same semi-exposed reef section at Lizard Island.



Supplementary Figure 5.3 | Average (\pm SE) *Acropora* colony growth rates in cm² per year: a) among different exposure levels; b) among different growth forms; and c) among different growth forms in different exposure levels.

Supplementary Tables

Supplementary Table 5.1 | Summary of the Bayesian generalized linear mixed-effects model (GLMM) with a gaussian distribution used to examine the relationship between *Acropora* coral cover change and recruit density to determine the minimum number of recruits needed to reach global average coral cover. Inferences were based on the mean slope of the predictor variable and associated 95% high posterior density intervals

Variable	Estimate	L-95% CI	U-95% CI	Rhat	Bulk_ESS
Intercept	0.255569	-2.3720473	2.978857	1.000774	2278.750
n_recruits	2.123497	1.7868951	2.398694	1.000237	2087.460

(HPD). If the HPDs intersected zero, no effect was inferred.

Supplementary Table 5.2 | Summary of the Bayesian generalized linear mixed-effects model (GLMM) with a gamma distribution and a log link function used to test the hypothesis that density of recruits (number of recruits per m²), level of wave exposure, and the interactions between growth form and initial colony size (recruit size at the first sampling) influenced the growth rates in coral recruits at Lizard Island. Inferences were based on the mean slope of the predictor variable and associated 95% high posterior density intervals (HPD). If the HPDs intersected zero, no effect was inferred.

Variable	Estimate	L-95% CI	U-95% CI	Rhat	Bulk_ESS
Intercept	4.878513	4.5225669	5.2556655	1.0009801	2199.1838
n_recruits	-0.142584	-0.2575595	-0.0115723	1.0016151	2490.8190
growth_formCorymbose	-0.235833	-0.4717836	0.0060013	1.0007294	2270.2341
growth_formDigitate	-0.675343	-0.9507975	-0.4247386	1.0003928	2243.0437
growth_formTabular	0.295672	0.0512792	0.5288850	1.0008584	2311.9618
logInitial_Size	0.526398	0.3295796	0.7225136	1.0002009	2272.7496
ExposureExposed	-0.429558	-0.8894452	0.0454105	1.0044303	1882.5524
ExposureLagoon	-0.672220	-1.2236598	-0.0749337	1.0022916	2261.7640
ExposureBackreef	-0.577636	-1.1153273	-0.1226968	1.0020473	2183.8142
Corymbose:logInitial_Size	-0.214719	-0.4411894	-0.0247083	1.0005136	2272.0421
Digitate:logInitial_Size	-0.292639	-0.5368478	-0.0537475	1.0010912	2236.7906
Tabular:logInitial_Size	-0.108982	-0.3343906	0.0945261	1.0001651	2296.3796

Supplementary References

- Adjeroud, M., Peignon, C., Gauliard, C., Penin, L. & Kayal, M. (2022). Extremely high but localized pulses of coral recruitment in the southwestern lagoon of New Caledonia and implications for conservation. *Mar. Ecol. Prog. Ser.*, 692, 67–79.
- Bramanti, L. & Edmunds, P.J. (2016). Density-associated recruitment mediates coral population dynamics on a coral reef. *Coral Reefs*, 35, 543–553.
- Ceccarelli, D.M., Emslie, M.J. & Richards, Z.T. (2016). Post-Disturbance Stability of Fish Assemblages Measured at Coarse Taxonomic Resolution Masks Change at Finer Scales. *PLoS One*, 11, e0156232.
- Edmunds, P.J. (2017). Unusually high coral recruitment during the 2016 El Niño in Mo'orea, French Polynesia. *PLoS One*, 12, e0185167.
- Edmunds, P.J. (2023). Coral recruitment: patterns and processes determining the dynamics of coral populations. *Biol. Rev.*
- Gouezo, M., Olsudong, D., Fabricius, K., Harrison, P., Golbuu, Y. & Doropoulos, C. (2020). Relative roles of biological and physical processes influencing coral recruitment during the lag phase of reef community recovery. *Sci. Rep.*, 10, 2471.
- Griffin, J.N., Schrack, E.C., Lewis, K.A., Baums, I.B., Soomdat, N. & Silliman, B.R. (2015). Density-dependent effects on initial growth of a branching coral under restoration. *Restor. Ecol.*, 23, 197–200.
- Kayal, M., Lenihan, H.S., Brooks, A.J., Holbrook, S.J., Schmitt, R.J. & Kendall, B.E. (2018). Predicting coral community recovery using multi-species population dynamics models. *Ecol. Lett.*, 21, 1790–1799.
- Kayal, M., Vercelloni, J., Wand, M.P. & Adjeroud, M. (2015). Searching for the best bet in life-strategy: A quantitative approach to individual performance and population dynamics in reef-building corals. *Ecol. Complex.*, 23, 73–84.
- Ladd, M.C., Miller, M.W., Hunt, J.H., Sharp, W.C. & Burkepile, D.E. (2018). Harnessing ecological processes to facilitate coral restoration. *Front. Ecol. Environ.*, 16, 239–247.
- Ladd, M.C., Shantz, A.A., Nedimyer, K. & Burkepile, D.E. (2016). Density Dependence Drives Habitat Production and Survivorship of *Acropora cervicornis* Used for Restoration on a Caribbean Coral

Reef. *Front. Mar. Sci.*, 3, 1–14.

Madin, J.S., Baird, A.H., Bridge, T.C.L., Connolly, S.R., Zawada, K.J.A. & Dornelas, M. (2018). Cumulative effects of cyclones and bleaching on coral cover and species richness at Lizard Island. *Mar. Ecol. Prog. Ser.*, 604, 263–268.

Morais, J., Morais, R., Tebbett, S.B. & Bellwood, D.R. (2022). On the fate of dead coral colonies. *Funct. Ecol.*, 36, 3148–3160.

Morais, J., Morais, R.A., Tebbett, S.B., Pratchett, M.S. & Bellwood, D.R. (2021). Dangerous demographics in post-bleach corals reveal boom-bust versus protracted declines. *Sci. Rep.*, 11, 18787.

Wismer, S., Tebbett, S.B., Streit, R.P. & Bellwood, D.R. (2019). Spatial mismatch in fish and coral loss following 2016 mass coral bleaching. *Sci. Total Environ.*, 650, 1487–1498.

Appendix E.

Publications during candidature

Publications arising from thesis chapters

Morais, J., Morais, R. A., Tebbett, S. B., Pratchett, M. S., & Bellwood, D. R. (2021). Dangerous demographics in post-bleach corals reveal boom-bust versus protracted declines.

Scientific Reports, 11(1), 18787.

<https://doi.org/10.1038/s41598-021-98239-7>

(Chapter 2)

Morais, J., Tebbett, S. B., Morais, R. A., & Bellwood, D. R. (2024). Hot spots of bleaching in massive *Porites* coral colonies.

Marine Environmental Research, 193, 106276.

<https://doi.org/10.1016/j.marenvres.2023.106276>.

(Chapter 3)

Morais, J., Morais, R., Tebbett, S. B., & Bellwood, D. R. (2022). On the fate of dead coral colonies.

Functional Ecology, 36(12), 3148–3160.

<https://doi.org/10.1111/1365-2435.14182>

(Chapter 4)

Morais, J., Tebbett, S. B., Morais, R. A., & Bellwood, D. R. (2023). Natural recovery of corals after severe disturbance.

Ecology Letters, April, 1–12.

<https://doi.org/10.1111/ele.14332>

(Chapter 5)

Other peer-reviewed papers published during candidature

Morais, J., Cardoso, A.P.L. & Santos, B.A. (2022). A global synthesis of the current knowledge on the taxonomic and geographic distribution of major coral diseases. *Environ. Adv.*, 8, 100231.

Morais, J. & Santos, B.A. (2022). Prevalence and extent of coral diseases in shallow and mesophotic reefs of the Southwestern Atlantic. *Coral Reefs*, 41, 1317–1322.

Schlaefer, J.A., Tebbett, S.B., Bowden, C.L., **Morais, J.**, Collins, W.P., Duce, S., Hemingson, C.R., et al. (2022). A snapshot of sediment dynamics on an inshore coral reef. *Mar. Environ. Res.*, 181, 105763.

Tebbett, S.B., **Morais, J.** & Bellwood, D.R. (2022a). Spatial patchiness in change, recruitment, and recovery on coral reefs at Lizard Island following consecutive bleaching events. *Mar. Environ. Res.*, 173, 105537.

Tebbett, S.B., Schlaefer, J.A., Bowden, C.L., Collins, **Morais, J.**, W.P., Hemingson, C.R., Ling, S.D., et al. (2023). Bio-physical determinants of sediment accumulation on an offshore coral reef: A snapshot study. *Sci. Total Environ.*, 895, 165188.

Tebbett, S.B., Streit, R.P., **Morais, J.**, Schlaefer, J.A., Swan, S. & Bellwood, D.R. (2022b). Benthic cyanobacterial mat formation during severe coral bleaching at Lizard Island: The mediating role of water currents. *Mar. Environ. Res.*, 181, 1057