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Vulnerability of coral assemblages on isolated reefs within Australia's Coral Sea Marine Park

Thesis submitted by:

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in February 2025

For the degree of Doctor of Philosophy

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Acknowledgements

First and foremost, I would like to thank my primary supervisor, Professor Morgan Pratchett, for his unwavering dedication, exceptional academic guidance, and his amazing ability to provide extremely constructive feedback in record time. You inspired me to pursue a PhD in the first place and I wouldn't be here without the opportunities you provided me. I would also like to thank my co-supervisors, Professor Andrew Hoey and Dr. Chiara Pisapia, for their incredible support and guidance. Despite extremely busy schedules, you were always available when I asked for help, with Chiara even managing to bridge a seven-hour time difference at the drop of a hat! All of you have gone above and beyond, providing me with a very long list of field- and desk-based opportunities that broadened my understanding of coral reef ecology and management far beyond what my PhD alone could offer. I couldn't have asked for a more incredible supervisory dream-team, and I can confidently say I genuinely enjoyed undertaking my PhD because of you. I look forward to future collaborations and, hopefully, repaying you with the lightning-fast draft feedback you provided for me!

Special thanks go to Parks Australia, who provided considerable funding for the fieldwork in the Coral Sea, and to Martin Russell, for his company in the field and for providing insightful comments on published chapters in this thesis. This PhD was also supported through a JCU Postgraduate Research Scholarship, with additional funding from the ARC Centre of Excellence for Coral Reef Studies. Thank you to the support staff at James Cook University, especially those within the ARC CoE, Graduate Research School and the College of Science and Engineering.

This thesis is the product of roughly 6 months at sea, made possible by (i) months of logistical planning by Morgan Pratchett, Andrew Hoey, Hugo Harrison, and Eva McClure, and (ii) the exceptional skill of the captain and crews of MV *Iron Joy* and MV *Wild Blue*. Special thanks to Captain Rob Benn and his crew for navigating often challenging conditions in the

Coral Sea – There is nobody I would trust more at the helm in the face of an oncoming cyclone, and I'll never not be impressed when a three-course meal and a cheese board is produced from a galley in 3m swells!

Months at sea were made infinitely more enjoyable by an exceptional group of colleagues and friends. While there are far too many to name here, special mentions must go to Russell Kelley for sharing his knowledge of coral taxonomy; Andrew Baird, Mike McWilliam, Cassy Thompson, Daniella Ceccarelli, Josie Chandler, and Victor Huertas for their assistance with benthic surveys; and the core survey team - Andrew Hoey, Morgan Pratchett, Hugo Harrison, Daniella Ceccarelli, Dave Williamson, Ed Roberts, Cassy Thompson, Eva McClure, Victor Huertas, Josie Chandler, Ben Cresswell, and Gemma Galbraith - who were instrumental in every aspect of the fieldwork. Thank you to everyone for the hard work, humour, and occasional sea sickness tablet.

Likewise, months of analysis and writing were made infinitely more enjoyable by incredible office mates - Katie Sambrook, Eoghan Aston, Eoghan's coffee machine, Erika Gress, Eric Fakan, Alexia Dubuc, and Cece Martin – and the many incredible lab field trips to break up the desk work - Thanks to Cassy Thompson, Peter Doll, Kai Pacey, Bethan Lang, Sarah Kwong and Josie Chandler for being the most supportive lab-mates anyone could have wished for!

Finally, I could not have completed this thesis without the ongoing support of friends and family from all over the world. Thank you to my parents, Maria and Martin, and family in the UK for always pushing me to follow my dreams; to my 'Hale Street Family', Maren and Sarah, for reminding me to stop typing and sharing so many epic adventures, and, especially, my fiancé, Ryan Marshall. Thank you for moving countries with me, for enduring months of my absence at sea (including missing your birthday for six years in a row!), and for putting up with the late nights and office marathons. This thesis is dedicated to you.

Statement of Contribution

This thesis was conducted under the supervision of Prof. Morgan Pratchett, Prof. Andrew Hoey and Dr. Chiara Pisapia. Please see the table below for specific contributions by supervisors and other collaborators.

Chapter	Contributor	Nature of Assistance
Chapter 1: General Introduction	Morgan Pratchett[1]	Conceptualisation/ chapter preparation
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Chapter 3:	Morgan Pratchett[1]	Conceptualisation / manuscript preparation / data collection
	Andrew Hoey[1]	Conceptualisation / manuscript preparation
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	Chiara Pisapia[2]	Chapter preparation
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This thesis was also supported by Russell Kelley, who provided coral taxonomy expertise in the field; Martin Russell, Mitchell Baskys and others at Parks Australia, for their financial and field support; and Captain Rob Benn and crew at Rob Benn Holdings for logistical field support.

This thesis was funded by a JCU postgraduate research scholarship provided to Deborah Burn, with support from the Australian Research Council Centre of Excellence for Coral Reef Studies, as well as the Director of Parks Australia.

Abstract

Isolated coral reef ecosystems, far removed from direct anthropogenic pressures, are often considered to support relatively pristine, healthy coral communities. Perennial, localised pressures, such as poor water quality and resource exploitation which exacerbate coral mortality and prolong recovery, diminish with distance from continental landmass and human populations and as such their effects are negligible on isolated reefs. However, isolated coral reefs are not immune from pervasive effects of climate change and other broadscale disturbances, and there is conspicuous evidence of sustained coral loss across many remote reef systems. Limited connectivity poses additional challenges to recovery, as isolated reefs depend primarily on self-recruitment and may face prolonged recovery periods. However, logistic difficulties in monitoring isolated, remote coral reefs leave significant knowledge gaps regarding the vulnerability and recovery potential of coral assemblages, emphasizing the need for long-term research on susceptibility to disturbances and coral replenishment.

In this thesis, I aimed to advance understanding of vulnerability of isolated coral assemblages through long-term targeted research in Australia's Coral Sea Marine Park (CSMP). Complementary sampling of coral assemblages in the adjacent Great Barrier Reef Marine Park (GBRMP) also provided an opportunity to assess differences in coral cover, communities, response to disturbance, and recovery capacity between isolated reefs and more proximal reefs within the same region. Specifically, I conducted annual in-water monitoring of coral health and abundance of >40,000 colonies at 155 sites across the CSMP and GBRMP between 2018-2021, encompassing a major coral bleaching event.

To provide a contemporary baseline for the current status of CSMP coral assemblages and comparable sites within the GBRMP, **Chapter 2** explored spatial variation in coral cover and composition across 155 sites at 19 reefs throughout the CSMP and 17 reefs along the GBRMP based on sampling conducted in 2018, 2019, and 2020. This chapter revealed

significant variation among regions and habitats within and between marine parks, with the northern CSMP exhibiting high coral cover (41.53%) dominated by slow-growing taxa such as *Porites*. In contrast, the southern CSMP (31.26% cover) and central GBRMP (32.73% cover) were dominated by fast-growing taxa, including *Acropora* and *Isopora*, which are highly vulnerable to disturbances. The central CSMP and southern GBRMP had notably low coral cover, reflecting ongoing impacts from cyclones and crown-of-thorns starfish outbreaks, respectively. These findings highlighted regional differences in coral assemblages that reflect historical and contemporary disturbance regimes, and will affect vulnerability to future disturbances.

Chapter 3 explored differential recovery potential and resilience of coral assemblages across the GBRMP and CSMP by quantifying densities of juvenile corals at 124 sites across 17 reefs in the CSMP and 17 reefs in the GBRMP in 2019 and 2020. To advance understanding of stock-recruitment relationships between isolated and more proximal reefs, I also compared relationships between coral cover and juvenile densities for three common taxa (*Acropora*, *Pocillopora* and *Porites*) between marine parks. Juvenile densities were significantly lower in the CSMP (13.99 ± 0.72 SE juveniles $10m^{-2}$) compared to the GBRMP (23.72 ± 1.86 SE juveniles $10m^{-2}$), with the central CSMP having particularly low densities of fast-growing taxa such as *Acropora* and *Pocillopora*. Relationships between juvenile abundance and adult coral cover were strongest in the GBRMP, where higher coral cover likely supports greater larval recruitment. Low juvenile coral densities in the CSMP likely reflect the limited abundance of spawning corals on individual reefs, and are likely to constrain the recovery capacity of these reefs, particularly following major disturbances such as coral bleaching. Critically, there is likely to be very limited connectivity among the widely separated reefs throughout the CSMP, reflecting key constraints to coral replenishment and recovery on isolated reefs in the CSMP.

C**hapter 4** examined patterns of bleaching susceptibility among coral taxa and colony sizes during the 2020 mass bleaching event. Bleaching susceptibility of 38,414 colonies in 10 common coral taxa across two colony size classes was assessed at 33 reefs in the GBRMP and CSMP. Taxonomic identity and colony size were key determinants of bleaching susceptibility, with smaller colonies generally more resistant to bleaching. However, exceptions such as *Montipora* and *Pocillopora* juveniles were highly susceptible to bleaching, indicating taxonomic variation in size-based vulnerabilities. Reef-scale bleaching severity altered susceptibility hierarchies, with massive *Porites* shifting from among the least susceptible to the most vulnerable taxa under severe conditions. These findings reveal that colony size, taxon, and bleaching severity interact to influence impacts of thermal stress on coral assemblages, with implications for post-disturbance community composition.

Following on from Chapter 4, **Chapter 5** explored the fate of coral assemblages in the aftermath of the 2020 bleaching event; I quantified changes in coral cover and community composition at 43 sites across three latitudinal regions revisited in the CSMP in 2021. Inter-annual changes in the cover of individual coral taxa were used to estimate bleaching-induced mortality, understand taxonomic contributions to overall coral loss, and identify shifts in community composition. This chapter revealed that heat stress, measured as monthly maximum degree heating weeks (DHW), exceeded the critical threshold of 8 DHW at all sites in March 2020, ranging from 9.25 DHW to 12.83 DHW. Consequently, coral cover in the CSMP declined from 29.50% (± 0.90 SE) in 2020 to 17.99% (± 0.77) in 2021; a proportional loss of 38.9%. Significant declines in coral cover were observed across most regions and habitats, except for the northern CSMP reef crest habitats, where coral cover was already low. Declines in cover were driven by substantial mortality of traditionally susceptible coral taxa (e.g., *Acropora*, *Isopora* and *Stylophora*), but also of taxa generally considered resistant to bleaching (e.g., massive *Porites*, *Favites*), reflecting the severity of the heat stress during this

bleaching event. Disproportionate losses among common taxa (predominantly loss of *Acropora* and *Porites*) led to significant shifts in community composition across the central CSMP toward a dominance of *Pocillopora*, whilst other regions and habitats experienced either disproportionate losses of only the rarest taxa, or comprehensive loss of all taxa, with no resultant community shifts. This chapter highlights the vulnerability of CSMP coral assemblages to marine heatwaves, with important implications for structure and function of coral assemblages across the marine park.

Overall, this thesis demonstrates that isolated coral reefs of the CSMP, despite their remoteness, are highly vulnerable to climate-induced disturbances. Low coral cover in the central CSMP and northern CSMP crest habitats reflects the lasting impacts of marine heatwaves and cyclones, compounded by limited connectivity and coral recruitment that constrains recovery. Severe heat stress (>9 DHW) in 2020 resulted in widespread bleaching, where traditional hierarchies of bleaching susceptibility among coral taxa were altered when bleaching was most severe. Significant mortality followed, with disproportionate losses among certain taxa causing shifts in community composition in the central CSMP, but with relatively comprehensive declines in all taxa across other regions. Substantial coral loss, and particularly the loss of structurally complex branching taxa, will likely have significant impacts on reef structure and function, including declines in habitat complexity and associated biodiversity. Prolonged recovery times due to isolation and increased frequency of major disturbances pose significant challenges for reef resilience. These findings highlight the vulnerability of coral assemblages in the CSMP and urgent need for continued monitoring and targeted research on connectivity, recruitment, and recovery processes that underpin the long-term persistence of isolated coral reef ecosystems.

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Chapter 1. General Introduction

1.1 Vulnerability of isolated coral reefs

Coral reefs are among the most threatened ecosystems on the planet, owing to the increasing incidence and severity of natural and anthropogenic disturbances (Gardner et al. 2003; Pandolfi et al. 2003; Riegl et al. 2009; Burt et al. 2013; Cheal et al. 2017; Duran et al. 2018; Hughes et al. 2018a; Oliver et al. 2018; Mellin et al. 2019a). Whilst climate change is emerging as the foremost threat to coral reefs (Hughes et al. 2017), perennial anthropogenic pressures cause chronic degradation of coral reef communities and disproportionately affect reefs located in close proximity to urban centres and landmasses (Jupiter et al. 2008; Heery et al. 2018). Increasing anthropogenic pressures, including physical damage (Davis 1977; Hawkins and Roberts 1992; Dinsdale and Harriott 2004; Lirman et al. 2010), declining water quality (Dubinsky and Stambler 1996; Erftemeijer et al. 2012; Ennis et al. 2016; Cramer et al. 2020), and destructive fishing practices (McManus et al. 1997; Zaneveld et al. 2016), have contributed greatly to the sustained degradation of coral reefs over several centuries (Pandolfi et al. 2003). Remote coral reefs, which are relatively isolated from these direct anthropogenic impacts, are often considered to be relatively 'pristine' environments (Sandin et al. 2008; Riegl et al. 2010). Coral cover (e.g., Barott et al. 2010) as well as abundance and diversity of fishes (DeMartini et al. 2008; Cresswell et al. 2023), for example, are often higher on remote coral reefs.

While isolation affords protection from many direct anthropogenic pressures, there is conspicuous and increasing evidence of degradation of remote coral reefs, largely attributed to pervasive effects of anthropogenic climate change and fisheries exploitation. In particular, widespread and severe coral bleaching events have resulted in significant loss of hard coral populations on reefs regardless of proximity to humans or land (Wilkinson and Souter 2008; Obura and Mangubhai 2011; Depczynski et al. 2013; Sheppard et al. 2017; Brainard et al. 2018;

Hédouin et al. 2020). Similarly, isolated coral reefs are susceptible to severe tropical storms (cyclones, hurricanes, typhoons), which can not only cause extensive disturbance, but inhibit recovery of coral populations (Oxley et al. 2003; Gilmour et al. 2019a). Moreover, crown-of-thorns starfish population irruptions (Birkeland 1982; Brodie et al. 2005; Fabricius et al. 2010), which cause significant coral loss, have also been reported from remote and isolated coral reefs (Timmers et al. 2012; Roche et al. 2015). Importantly, severe large-scale disturbances have the potential to effectively suppress coral populations at the entire scale of some small, isolated reef systems, which will greatly impede capacity for subsequent recovery (Gilmour et al. 2013).

Many of the world's most remote coral reefs are not only located far from major urban centres and sources of local anthropogenic pressures, but widely separated from other coral reefs. For example, Mellish Reef in Australia's Coral Sea Marine Park (CSMP), is over 300km away from the closest reef. In the Indian Ocean, the Cocos (Keeling) Islands are > 900km from the next nearest reef (Christmas Island). Large and/ or highly connected coral reef systems may be highly resilient to major large-scale disturbances (Macarthur and Wilson 1967), whereby there is increased likelihood that at least some proportion of the population is unaffected and represents source populations for replenishment and recovery of depleted populations (Schoener and Schoener 1983). In contrast, small and isolated reef systems may be particularly vulnerable to disturbances owing to the potential localised loss of brood-stock (Lande 1988; Kattan et al. 1994; Gilmour et al. 2013). Poor connectivity among widely separated or fragmented habitats, such as remote and isolated coral reefs, increases reliance on self-recruitment, such that large-scale disturbances which cause significant losses across the entire extent of individual habitat patches, may limit population replenishment and recovery (Ayre and Hughes 2004; Graham et al. 2006; Underwood et al. 2006; Gilmour et al. 2013). Given the increasing incidence, severity and extent of major disturbances (e.g., Oliver et al. 2018),

understanding the capacity of isolated coral reefs to recover will be fundamental in determining the vulnerability of coral communities on remote, isolated coral reefs.

To explore the vulnerability of coral communities on remote, isolated coral reefs, data was compiled on the disturbance history, and corresponding effects on coral abundance, at six isolated Indo-Pacific coral reef complexes: Australia's CSMP, the Chagos Archipelago, Australia's eastern Indian Ocean reefs, the Gilbert Islands (Kiribati), the Line Islands (Kiribati), and the Phoenix Islands (Kiribati) (Fig. 1.1). Herein, isolated reefs are defined as individual coral reefs, singular atolls, or small groups of < 5 reefs which are > 160km from large, inhabited landmasses, and have ≤ 3 other reefs or atolls within a 50km radius. While there are considerable challenges to undertaking recurrent monitoring, especially at isolated reefs (Burn et al. 2022), there has been relatively frequent and extensive sampling undertaken at each of the aforementioned locations. Data on disturbance history, coral cover and coral recruitment was collected from relevant literature (peer reviewed journal articles and reports), the Australian Government's Bureau of Meteorology (for cyclones) and NOAA's Coral Reef Watch tool (for bleaching). Where data was not freely available in the text, the Web Plot Digitizer online tool was used to extract data from figures.

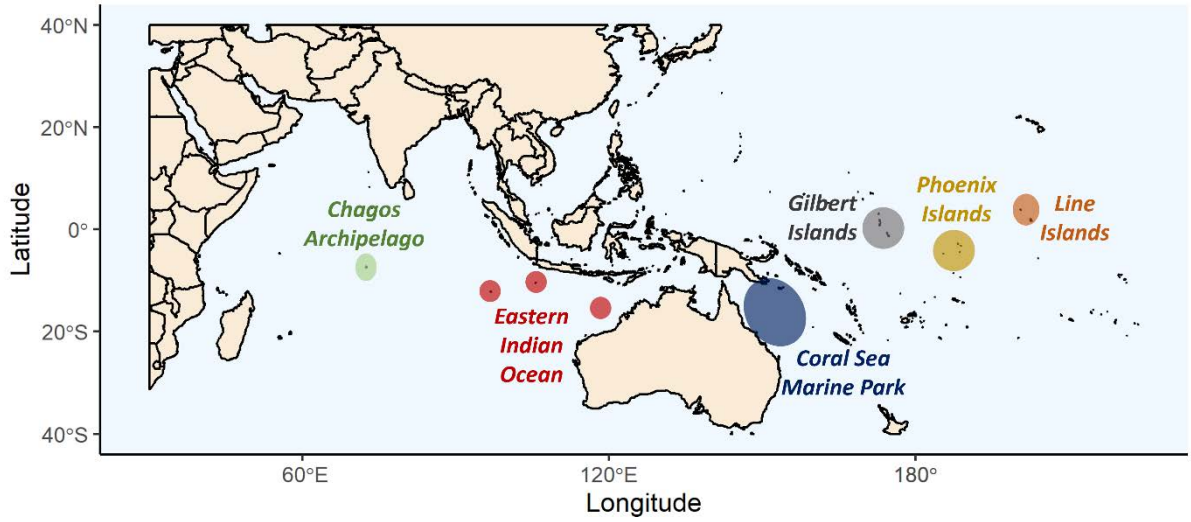


Figure 1.1: Map of remote, isolated reef complexes in the Indo-Pacific that are considered in this chapter.

1.2 Disturbances and their effects on isolated coral communities

Coral reefs are subject to a range of natural and anthropogenic disturbances, which are increasing in frequency and intensity (Hughes et al. 2003; Hoegh-Guldberg et al. 2007; Oliver et al. 2018), and thereby contributing to sustained (and in some cases accelerated) coral loss and reef degradation (De'ath et al. 2012). Sustained declines in the abundance of corals are attributed to concurrent punctuated disturbances (e.g., severe tropical storms or population irruptions of corallivores), chronic increases in environmental pressures (e.g., declining water quality or ocean acidification) or the culmination of these disturbances and pressures (Gardner et al. 2005; De'ath et al. 2012; Ortiz et al. 2018; Gilmour et al. 2019a; Mellin et al. 2019a; Cramer et al. 2020; Vercelloni et al. 2020). Given that many perennial pressures, including overfishing and poor water quality, attenuate with distance from major landmasses and urban centres (Jupiter et al. 2008; Sandin et al. 2008; Heery et al. 2018; McClanahan et al. 2019b), isolated oceanic coral reefs provide an important opportunity to assess the relative importance of acute disturbances versus chronic pressures in driving coral reef degradation (McCauley et al. 2010; Baumann et al. 2022). Critically, isolated reef systems are often subject to severe, large-scale disturbances, such as severe storms (e.g., cyclones), population irruptions of crown-of-thorns starfish, and marine heatwaves, which will be discussed in turn. In particular, it is clear that isolated reef systems are increasingly exposed to the highly pervasive effects of abnormally high sea surface temperatures that lead to coral bleaching (Brainard et al. 2018; Harrison et al. 2019; Head et al. 2019; Magel et al. 2019).

1.2.1 Cyclones and Storms

Tropical cyclones commonly occur in warm, tropical waters either side of the equator, affecting many of the world's coral reefs (Studholme et al. 2022). The effects of these tropical cyclones and severe storms on coral reef communities have been well documented and include lethal and sub-lethal effects on coral, loss of 3-dimensional reef complexity and subsequent

decline in fish abundance and diversity (Lassig 1983; Massel and Done 1993; Harmelin-Vivien 1994; Madin and Connolly 2006; Gouezo et al. 2015; Baird et al. 2018a). The incidence of tropical cyclones is strongly related to latitude and bioregion (Puotinen et al. 2020), where some remote reefs, such as those in Australia's CSMP experience a much higher cyclonic frequency and intensity than others in different regions (Brewer et al. 2007; Table 1.1). For example, only one cyclone (Linda) passed directly over Ashmore Reef in the Eastern Indian Ocean between 1976 and 2020 (Somaweera et al. 2021), and cyclones are also extremely rare over the equatorial reefs of Kiribati (Saverimuttu 2020).

Studies on the direct impacts of cyclones at isolated coral reefs are scarce (Gilmour and Smith 2006), partly due to difficulties in completing timely surveys in such locations. The majority of information available on the effects of cyclones on coral reef assemblages is for coastal, well-connected, and more easily accessible coral reefs. But it is possible that the unique bathymetry, structural framework, and level of exposure of isolated oceanic reefs may incur different effects from cyclones on their coral communities than their coastal counterparts (Fabricius et al. 2008). Indeed, remote oceanic reefs have a stronger reef framework than inshore coastal reefs (Fabricius et al. 2008), with high skeletal density of corals (Risk and Sammarco 1991), and substrate consolidated by a high abundance of crustose coralline algae (Littler and Doty 1975; Dean et al. 2015). It is possible that these traits could mitigate the flattening effects of cyclones. However, the negative effects of cyclones are highly site specific and dependent on the relative exposure of a site (Gilmour and Smith 2006; Gilmour et al. 2019a; Puotinen et al. 2020), suggesting that the smallest oceanic reefs could be highly vulnerable to cyclonic activity.

Regular surveys at Scott Reef in the Eastern Indian Ocean (Gilmour et al. 2019b) have provided some understanding of the effects of cyclones in isolated, remote locations. In 2004, category 5 cyclone Fay tracked over Scott Reef, causing thousands of massive coral colonies

to be pushed up onto the reef flat (Gilmour and Smith 2006). In this instance there was only a 4% decline in coral cover, as catastrophic bleaching in 1998 had already removed many of the most susceptible corals (Gilmour and Smith 2006). It was noted, though, that recovery from the bleaching was greatly impeded as a consequence, with many juvenile corals killed (Gilmour and Smith 2006). The destruction witnessed suggested the potential for such cyclones to cause massive declines in coral cover. In 2013, following significant recovery of coral cover at Scott Reef, the exposed, westerly sites experienced 65% declines in coral cover due to three concurrent cyclones (Vince [2011], Iggy [2012], and Lua [2012]), which was the largest decline since the mass bleaching in 1998 (Gilmour et al. 2019b; Fig. 1.3). Isolated reefs are particularly vulnerable to the effects of severe cyclones, owing to their exposure to oceanic conditions. However, effects are nonetheless very patchy at the scale of individual reefs, with disproportionate impacts among directly exposed habitats (Gilmour et al. 2019b).

Whilst severe tropical storms rarely cause large scale and comprehensive coral loss (Fabricius et al. 2008), they can directly inhibit coral recovery through the loss of both gravid and juvenile corals, and the destabilisation of substrate (Gilmour and Smith 2006; Chong-Seng et al. 2014; Yadav et al. 2016; Fig. 1.2, 1.3). This persistent inhibition of recovery could explain the persistently low coral cover at some locations in Australia's CSMP, where cyclonic activity is high (Oxley et al. 2003; Brewer et al. 2007). But since regular monitoring/surveys have not historically taken place at reefs in the CSMP, and recent annual surveys are confounded by bleaching events, it is impossible to determine the independent and direct effects of cyclones on these coral communities. Rather, there is evidence that cyclones are compounding upon other disturbances, whereby low coral cover at the Herald Cays and Chilcott Reef in the central CSMP in 2003 was attributed to a combination of bleaching in 2002 and a category 3 cyclone (Katrina; category 2 as it passed the reefs; Table 1.1) occurring in 1998 (Oxley et al. 2003). The historically low (persistently <20% prior to 2019; Fig. 1.2) coral cover of the remote reefs

of the central CSMP, and the low abundance of branching corals in the central and northern CSMP are also generally attributed to the combination of cyclones and coral bleaching, combined with constraints on coral recruitment and recovery (Oxley et al. 2003, 2005; Ceccarelli et al. 2008; Edgar et al. 2015; Fig. 1.2).

Table 1.1: Cyclones passing over isolated reefs between 1984-2021. Dates and categories are presented for the day the cyclones passed over the reefs. Only Lihou Reef and the Herald Cays are represented for the Coral Sea Marine Park due to the high frequency of cyclones in the region.

Date	Cyclone Name	Category	Notes
31/12/1988	Delilah	1	Passed directly over Lihou
03/04/1989	Aivu	4	Passed directly over Herald
26/02/1991	Kelvin	2	Passed directly over Lihou
08/03/1997	Justin	2	Passed directly over Lihou
11/02/1997	Gillian	1	Passed Northwest of Herald
18/01/1998	Katrina	2	Passed over both Herald Cays and Lihou
21/03/2004	Grace	1	Passed over both Herald Cays and Lihou
28/01/2006	Jim	2	Passed close to both Herald Cays and Lihou
19/03/2006	Larry	3	Passed directly over Lihou, and 70km South of Herald
23/01/2010	Olga	1	Passed ~50km north of Herald
02/02/2011	Yasi	4	Passed directly over Herald
30/01/2011	Anthony	Tropical low	Passed directly over Lihou
04/02/2012	Jasmine	1	Passed directly over both Herald and Lihou
05/03/2013	Sandra	1	Passed directly over Lihou
11/03/2014	Hadi	Tropical low	Passed directly over Lihou
29/01/2014	Dylan	Tropical low	Passed ~30km South of Herald
02/02/2014	Edna	Tropical low	Passed mid-way between Herald Cays and Lihou
25/03/2017	Debbie	1	Passed directly over Lihou
03/04/2018	Iris	Tropical low - 1	Tropical low over Lihou on 30th march, intensifying to Category 1 over Herald Cays on 3rd April
19/12/2018	Owen	Tropical low	Passed ~40km Southwest of Lihou on December 19th
01/04/2008	Rosie	1	Christmas Island
22/03/2014	Gillian	1-4	Category 1 over Christmas Island, intensifying to a 4 south of Christmas the following day
25/12/2014	Kate	1-4	Category 1 over Cocos Keeling, intensifying to a 4 2 days later south of Cocos Keeling
23/03/2004	Fay	5	over Scott Reef
30/04/2017	Frances	2 - low	Dissipated on approach to Scott Reef

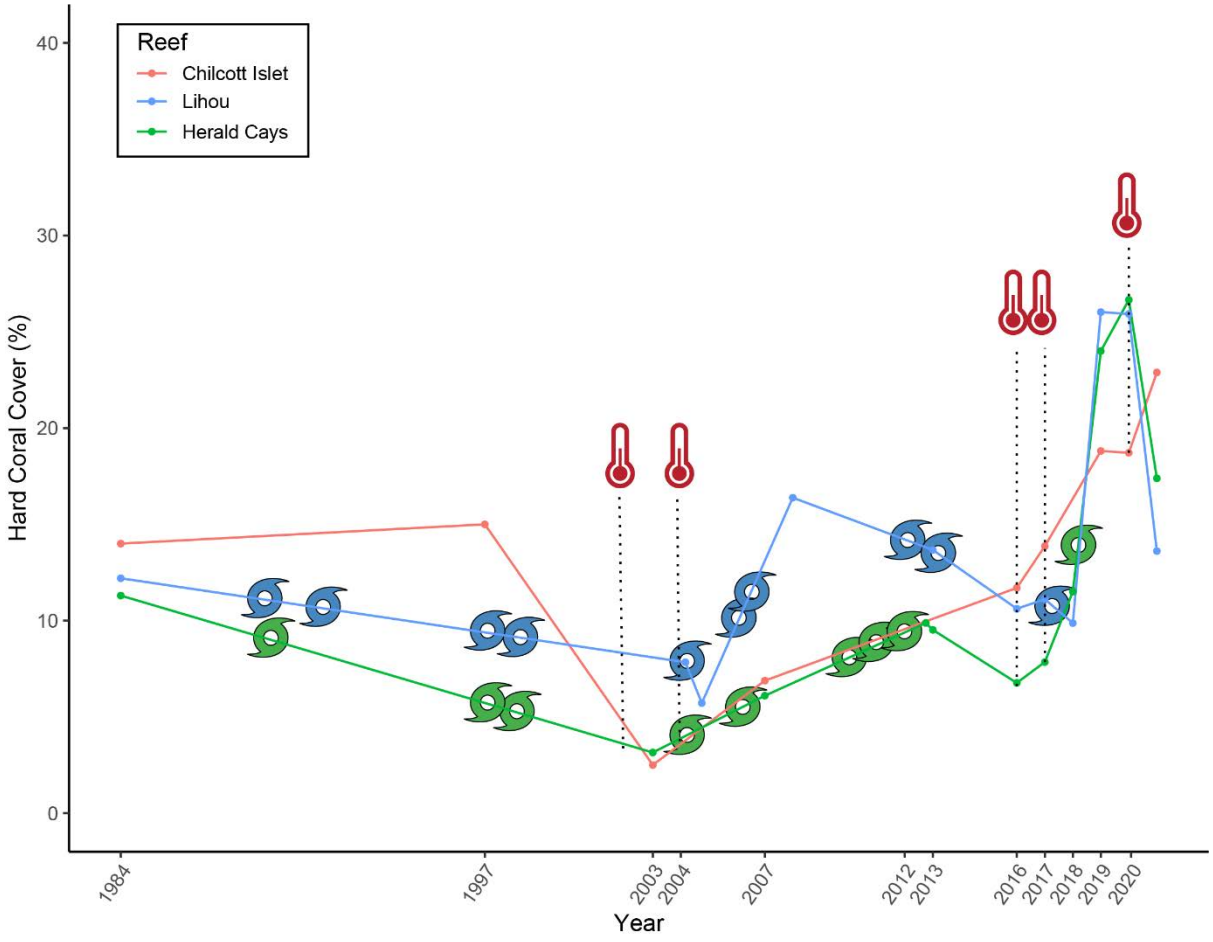


Figure 1.2: Coral cover through time at three reefs in Australia's Coral Sea Marine Park. Points represent surveys, vertical lines represent disturbances: Thermometer icons represent major marine heatwaves, cyclone icons represent cyclones (Category 1-5) affecting reefs of corresponding colours. Marked dates along the x axis represent surveys, therefore the connecting lines represent the general trend between surveys, not actual coral cover. Data taken from Ayling and Ayling 1985; Byron et al. 2001; Oxley et al. 2003, 2004, 2005; Ceccarelli et al. 2008, 2009; Stuart-Smith et al. 2013; Edgar et al. 2015; Harrison et al. 2019; Hoey et al. 2020, 2021.

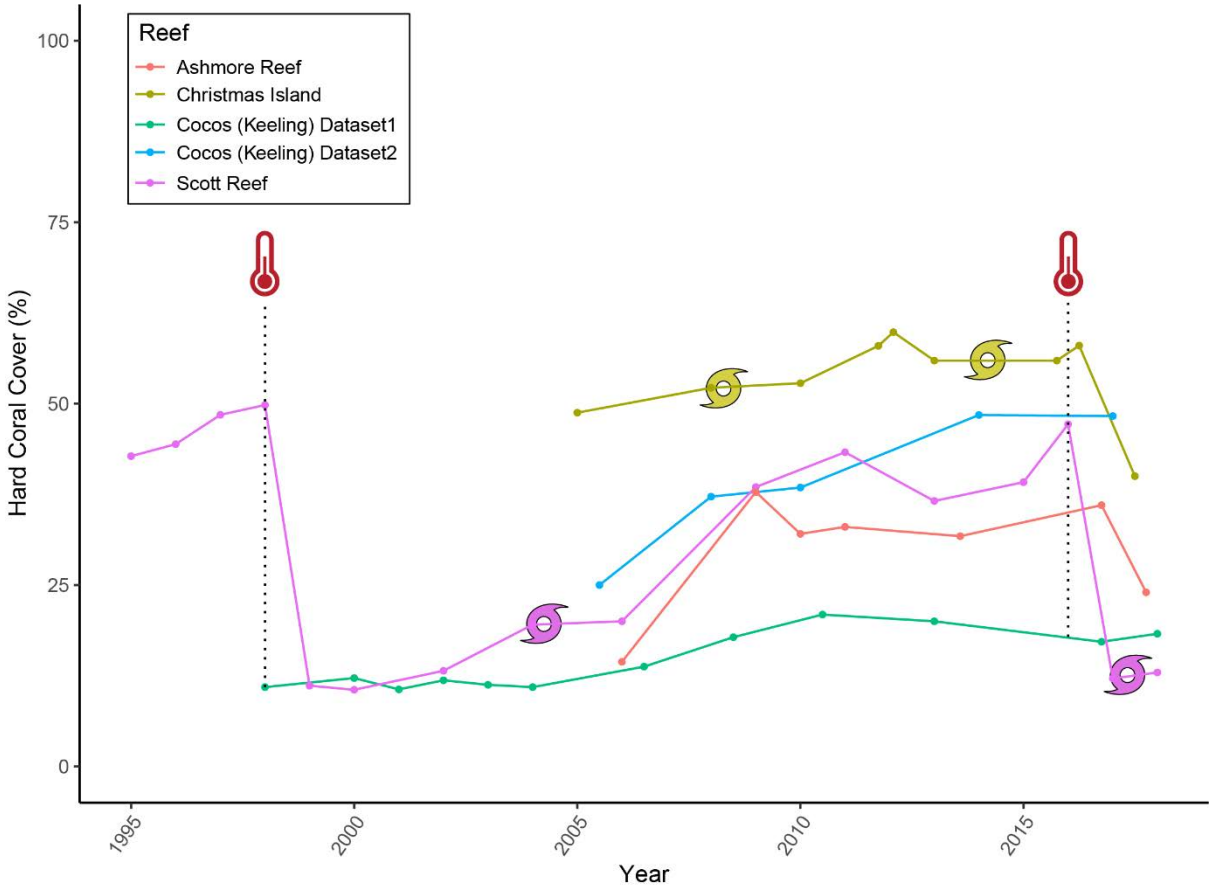


Figure 1.3: Hard coral cover over time for remote reefs in the Eastern Indian Ocean. Points represent surveys, thermometer icons represent major marine heatwaves, and cyclone icons represent cyclones (category 1-5) for the corresponding coloured reef. Data from Gilmour et al. 2019a and BOM.

*note two separate monitoring programs for Cocos (Keeling) have been plotted separately

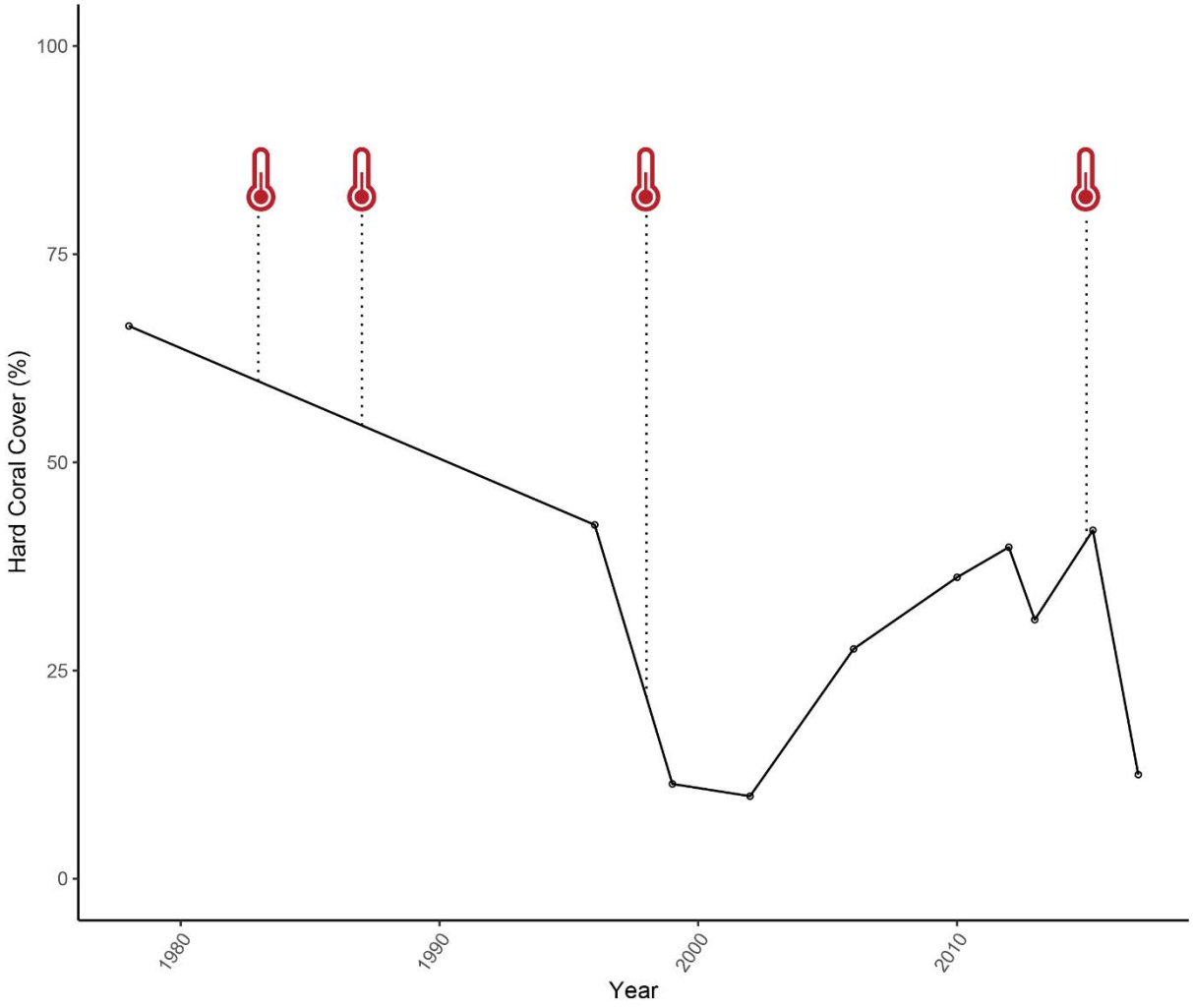


Figure 1.4: Chagos-wide (all reefs/depths averaged) coral cover through time. Points represent surveys, solid lines connecting points represent a general trend, not actual coral cover. Thermometer icons represent major marine heatwaves. Data from Sheppard et al. 2017

1.2.2 Population irruptions of crown-of-thorns starfish

Crown-of-thorns starfish (*Acanthaster* spp; CoTS) are one of the largest and most effective coral predators (Birkeland and Lucas 1990), native to coral reefs throughout the Indo-Pacific. Periodic population irruptions of CoTS have caused significant declines in coral cover on reefs throughout their range, and especially in the western Pacific (Pratchett et al. 2009; De'ath et al. 2012; Kayal et al. 2012; Baird et al. 2013; Pisapia et al. 2019). The cause(s) of population irruptions remains contentious, however anthropogenic pressures, such as declines

in water quality (i.e., elevated nutrients; Birkeland 1982; Brodie et al. 2005; Fabricius et al. 2010), and overfishing (Endean 1969; Sweatman 2008) are thought to exacerbate, if not cause, population irruptions. Even so, population irruptions have been reported on some isolated, oceanic reefs including Cocos (Keeling), the Line Islands, and the Chagos Archipelago (Hobbs et al. 2005; Timmers et al. 2012; Roche et al. 2015), which have very limited exposure to poor water quality or fisheries.

In 2013, high densities (1,624 per km^2) of CoTS coincided with extensive recent coral mortality at Danger Island in the Chagos Archipelago (Roche et al. 2015; Table 1.2). However, it is unknown when or where this population irruption started, nor how long the elevated densities persisted or how much coral was lost. Not being able to ascertain when CoTS irruptions begin, makes it more difficult to pinpoint potential cause(s) (Roche et al. 2015). Large areas of dead coral at the Cocos (Keeling) Islands in 1970 were also attributed to high densities (2500-5000 per km^2) of CoTS (Colin 1977; Table 1.2). However, as in the Chagos, the extent and impacts of these population irruptions is very unclear, due to limited recurrent sampling. Annual and biennial surveys of some locations have delivered a clearer understanding of the effect of CoTS outbreaks on remote reefs, although declines in coral cover are not always apparent. For example, despite reports of 60,000 CoTS km^{-2} at one site at Cocos (Keeling) in 1997, coral cover remained high during the following 9 years of annual surveys, revealing no clear impact on coral cover (Hobbs et al. 2005; Table 1.2). At Kingman Reef in the Line Islands, high densities of CoTS have been apparent throughout biennial surveys from 2000 to 2015 (Brainard et al. 2019) and transects have yielded densities of 660,000 CoTS km^{-2} in 2006 (Timmers et al. 2012; Table 1.2). Whilst the high densities at Kingman Reef were extremely localised, high levels of associated coral loss were recorded at those locations, which may have contributed to the decline in reef-wide coral cover between 2002 and 2008 (Fig. 1.5; Brainard et al. 2019).

It is clear that CoTS irruptions do occur on some isolated reefs, although there is limited knowledge of their effects (Hobbs et al. 2005; Roche et al. 2015; Brainard et al. 2019). This is because most reports of population irruptions of CoTS at isolated reefs are opportunistic (e.g., Roche et al. 2015), and there is limited opportunity for follow-up surveys. The lack of repeat surveys at most locations makes it difficult to fully understand the effect of such disturbances and may also mean that the incidence of population irruptions of CoTS at isolated reefs often go unreported. For example, whilst no recent irruptions have been reported for Christmas Island, there is some anecdotal evidence that CoTS may have been abundant in the past (Edmondson 1946). CoTS have also been recorded in other remote locations, such as Australia's CSMP (Hoey et al. 2020), though high densities have not been recorded. However, this may simply be due to lack of survey effort in some locations.

Table 1.2: Densities of Crown-of-Thorns Starfish reported at remote reefs (820 per km^2 deemed an outbreak)

Location	**Year**	**CoTS Densities (km^{-2})**	**Reference**
Danger Island, Chagos	2013	1,624	Roche et al. 2015
Kingman Reef, Line Islands	2006	660,000	Timmers et al. 2012
Cocos Keeling, Eastern Indian Ocean	1970	2,500-5,000	Colin 1977
Cocos Keeling, Eastern Indian Ocean	1997	60,000	Hobbs et al. 2005

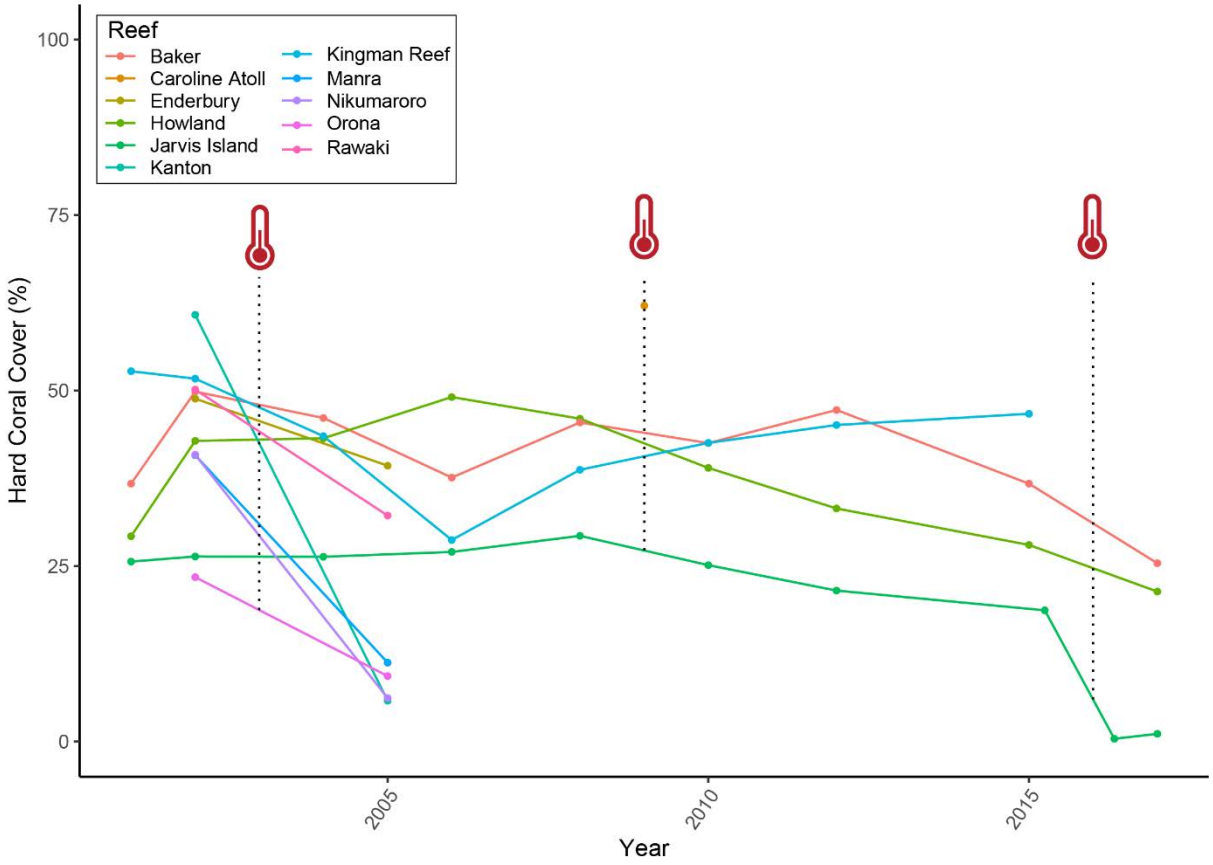


Figure 1.5: Coral cover over time for select reefs in Kiribati (Line and Phoenix Islands). Points represent surveys, and thermometer icons represent major marine heatwaves. Note the thermal anomaly that peaked in 2003 lasted from 2002-2005. Data taken from Barott et al. 2010; Obura and Mangubhai 2011; Brainard et al. 2018, 2019; Vargas-Ángel et al. 2019.

1.2.3 Severe marine heatwaves

Severe marine heatwaves are widely recognised as the foremost threat to coral reefs, often causing extensive coral bleaching and mortality (Glynn 1984; Hughes et al. 2018b). Unlike some chronic pressures, the effects of marine heatwaves are highly pervasive and do not diminish with remoteness (Hughes et al. 2018a; Baumann et al. 2022), rendering isolated coral reefs vulnerable (Graham et al. 2006). Indeed, marine heatwaves have caused significant coral bleaching and mortality at many isolated coral reefs (Sheppard 1999; Alling et al. 2007; Obura and Mangubhai 2011; Gilmour et al. 2013; Hoey et al. 2021). Worryingly, the frequency

and severity of coral bleaching is rapidly increasing on reefs around the world, such that return times between events have declined from 30 years in the early 1980's to 5.9 years in 2017 (Hughes et al. 2018a). Back-to-back bleaching events have already been recorded for two isolated locations (2016 & 2017 in Australia's CSMP, Harrison et al. 2019; and 2015 & 2016 in the Chagos Archipelago, Head et al. 2019), reinforcing the prediction that annual bleaching events could occur within the next two decades (van Hooidonk et al. 2013).

The effects of coral bleaching on coral communities in remote locations are very well studied. Studies assessing changes in coral cover following major bleaching events at isolated coral reefs have reported substantial declines in coral cover (Sheppard 1999; Alling et al. 2007; Smith et al. 2008a; Halford and Caley 2009; Obura and Mangubhai 2011; Sheppard et al. 2017; Brainard et al. 2018; Harrison et al. 2019; Head et al. 2019; Vargas-Ángel et al. 2019). At Scott Reef (Eastern Indian Ocean) in 1998, an 80% decline in hard and soft coral cover was reported, with hard coral cover decreasing from 48.5% in 1997 to <10% in 1999 (Fig. 1.3; Smith et al. 2008; Halford and Caley 2009). Similarly, in the Chagos Archipelago, coral cover declined from 50-70% in 1996 to <12% in 1999 (Fig. 1.4; Sheppard 1999; Sheppard et al. 2017). After a slow recovery (Figs 1.3, 1.4; Sheppard et al. 2008; Smith et al. 2008; Halford and Caley 2009; Gilmour et al. 2013) coral cover at the Chagos Archipelago and Scott Reef in 2015 had reached 41% and 47% respectively, both declining to 12% following another bleaching event in 2015/16 (Sheppard et al. 2017; Gilmour et al. 2019b; Head et al. 2019; Figs 1.3, 1.4). Reefs in the Central Pacific may be particularly vulnerable to strong El Niño events, as the Equatorial Undercurrent bringing cool water to the atolls and islands of Kiribati has been shown to weaken and even shut down during this phase of the ENSO cycle (Maragos et al. 2008). This occurred in 1982, but no biological observations took place at this time, and again during 2002 and 2015/16, where significant bleaching and mortality was observed (Alling et al. 2007; Obura and Mangubhai 2011; Brainard et al. 2018; Vargas-Ángel et al. 2019). Reefs of Kiribati were

particularly affected by the 2002 El Niño, which caused an ongoing heatwave in this location lasting 4 years (2002-2005), peaking at 21 Degree Heating Weeks (DHW): the most significant thermal stress this review found at remote reef locations (Obura and Mangubhai 2011).

Aside from causing localised coral loss, coral bleaching has far reaching effects, with loss of diversity, loss of ecological function, changes in community structure, localised extinctions and loss of 3D complexity reported following major beaching at several remote locations (Halford and Caley 2009; Sheppard et al. 2017, 2020; Gilmour et al. 2019b; Magel et al. 2019). Of particular concern on isolated coral reefs is the loss of bleaching-susceptible taxa as these will be potentially difficult to replace due to the reliance on self-seeding for replenishment. Following the 1998 and 2016 bleaching events in the Chagos Archipelago, the formally common *Diploastrea heliopora* and branching *Seriatopora* spp appear to have been locally extirpated, along with near extinction of the massive coral *Ctenella chagius*, a species only found in the Chagos (Sheppard et al. 2017, 2020). Given recent advances in coral taxonomy showing that coral species are not as pandemic as first thought (Keshavmurthy et al. 2013), and the high likelihood of increasing endemism with isolation (e.g., Adler and Dudley 1994), severe coral bleaching on remote reefs poses a serious extinction risk for corals (Glynn and de Weerdt 1991).

Given the lack of historical and ongoing monitoring in most remote locations, it is highly likely that some coral bleaching events have gone unnoticed (e.g., DeCarlo 2024). Historical sea surface temperature (SST) and degree heating weeks (DHW) data shows multiple cases of anomalous heatwaves at each reef complex assessed in this chapter likely to have caused coral bleaching, with no corroborative surveys of the ecosystem during that time period (Figs 1.3, 1.4, 1.5, 1.6; Table 1.3). For example, prior to 2004, no bleaching had been recorded in the Gilbert Islands (Kiribati) despite evidence of several marine heatwaves above the lower bleaching threshold (Donner et al. 2010). Anomalously high SSTs have been

recorded in most locations as far back as 1982, yet no information on the cover and composition of coral assemblages was available at any location until 1998. Even at locations with consistent monitoring programs, such as the Chagos Archipelago, the effects of two significant heatwaves in the 1980's were never quantified (Fig. 1.4; Table 1.3; Sheppard et al. 2017). For some locations, there is anecdotal evidence of coral bleaching, but no quantitative data (Table 1.3). With more frequent and severe heatwaves predicted for the future, continued recurrent sampling of coral assemblages will be imperative to determine how these isolated reefs may be affected in the future.

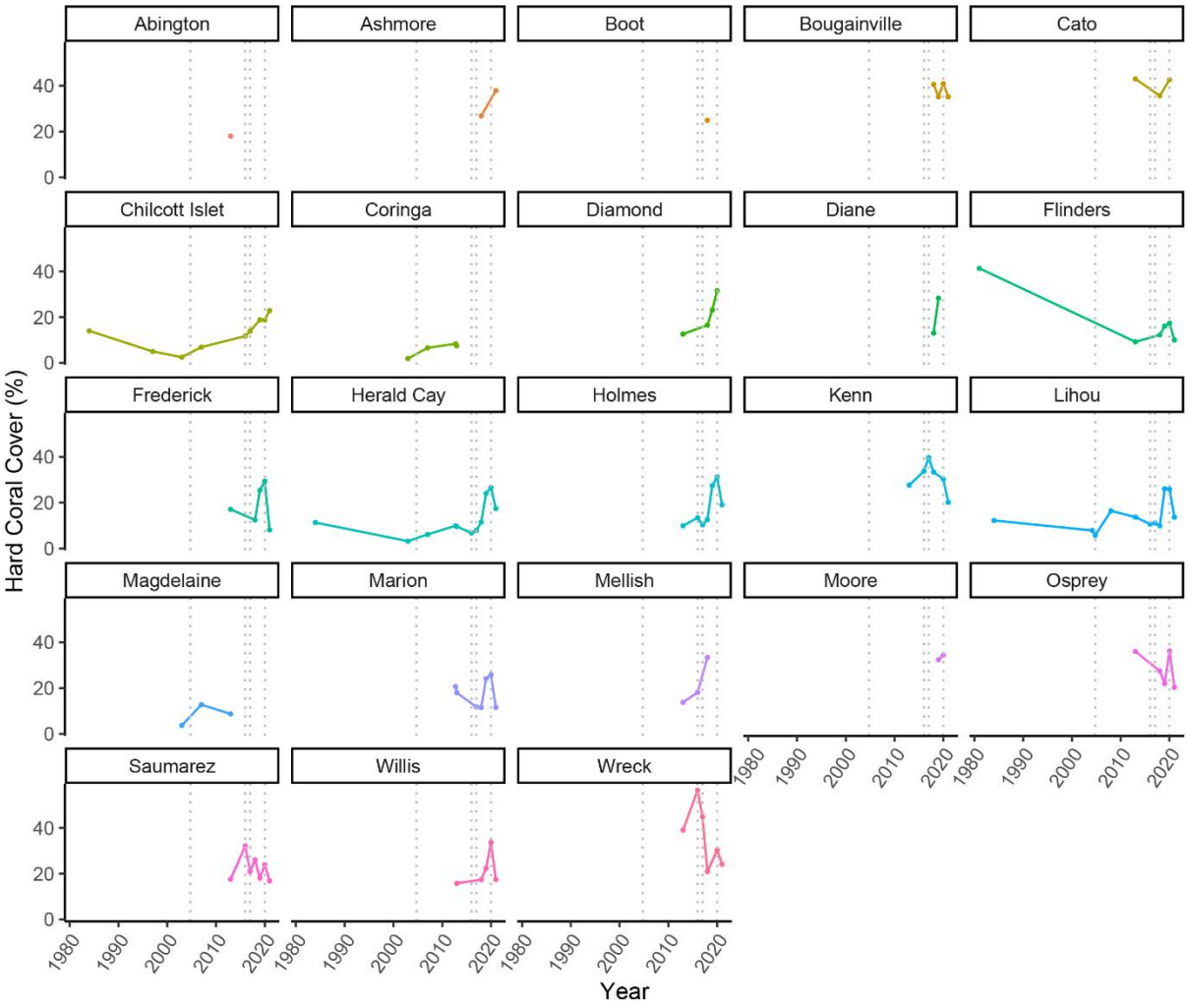


Figure 1.6: Percent hard coral cover through time on the reefs of Australia's Coral Sea Marine Park. Dotted lines represent bleaching events. Data taken from: Done 1982; Ayling and Ayling 1985; Byron et al. 2001; Oxley et al. 2003, 2004, 2005; Ceccarelli et al. 2008, 2009; Stuart-Smith et al. 2013; Edgar et al. 2015; Harrison et al. 2019; Hoey et al. 2020, 2021.

Table 1.3: Bleaching records at remote, isolated coral reefs.

Location	Bleaching Reported	Year	Citation	Notes
Christmas Island	Probable Bleaching	1983	Berry 2000	Mass mortality noted in 1986, attributed to El Niño of 1983.
Christmas Island	Probable Bleaching	1998	Goreau et al. 2000; Gilmour et al. 2019a	No data available but likely to have bleached
Christmas Island	Bleaching	2010	Gilmour et al. 2019a	Moderate bleaching, minor mortality
Christmas Island	Bleaching	2016	Gilmour et al. 2019a	Widespread bleaching and mortality
Cocos (Keeling)	Bleaching	1983	Blake and Blake 1983	Mortality noted in the lagoon by Blake and Blake 1983.
Cocos (Keeling)	Bleaching	2014	Gilmour et al. 2019a	Minor bleaching, no mortality
Cocos (Keeling)	Bleaching	2016	Gilmour et al. 2019a	Minor bleaching (0-10% bleaching)
Scott Reef	Probable Bleaching	1991	Gilmour et al. 2019a	No surveys undertaken
Scott Reef	Bleaching	1998	Wilkinson 2004; Gilmour et al. 2013	High (70-90%) mortality in shallow water communities.
Scott Reef	Bleaching	2010	Gilmour et al. 2013	Moderate bleaching
Scott Reef	Bleaching	2011	Gilmour et al. 2019a	Moderate bleaching
Scott Reef	Bleaching	2013	Gilmour et al. 2019a	Bleaching observed but not quantified
Scott Reef	Bleaching	2016	Gilmour et al. 2019a	Severe (60-90%) bleaching to 20m
Ashmore	Bleaching	2003	Rees et al. 2003	Unquantified bleaching
Ashmore	Bleaching	2010	Heyward et al. 2010	Moderate bleaching
Ashmore	Probable Bleaching	2013	Gilmour et al. 2019a	No surveys undertaken
Ashmore	Probable Bleaching	2016	Gilmour et al. 2019a	Assumed widespread bleaching due to recent mortality following heatwave

Ashmore	Probable Bleaching	2017	Gilmour et al. 2019a	Assumed bleaching due to recent mortality following heatwave
Coral Sea Marine Park	Bleaching	2002	Oxley et al. 2003	Assumed bleaching due to moderate mortality following heatwave, only 4 small reefs in the central CSMP surveyed
Coral Sea Marine Park	Bleaching	2004	Oxley et al. 2004, 2005	Bleaching noted in 2004 and effects quantified in 2005 at one reef in the central CSMP, minor coral mortality.
Coral Sea Marine Park	Bleaching	2016	Harrison et al. 2019	Bleaching and mortality in Central-South CSMP, no surveys for many reefs
Coral Sea Marine Park	Bleaching	2017	Harrison et al. 2019	Less mortality following second event, no surveys for many reefs
Coral Sea Marine Park	Bleaching	2020	Hoey et al. 2020, 2021	Widespread and severe bleaching and mortality
Chagos Archipelago	Probable Bleaching	1983	Sheppard et al. 2017	No surveys undertaken
Chagos Archipelago	Probable Bleaching	1987	Sheppard et al. 2017	No surveys undertaken
Chagos Archipelago	Bleaching	1998	Sheppard et al. 2017	Significant coral mortality
Chagos Archipelago	Bleaching	2016	Sheppard et al. 2017	Significant coral mortality from 40-50% to <10%
Line Islands	Probable Bleaching	1982/3	Brainard et al. 2018	No observations available, but SSTs were high, and other Pacific locations bleached significantly
Line Islands	Probable Bleaching	1998	Brainard et al. 2018	No observations available, but SSTs were high, and other Pacific locations bleached significantly
Line Islands – Jarvis	Bleaching	2015/16	Vargas-Ángel et al. 2019	Significant mortality – 93% decline
Phoenix Islands	Probable Bleaching	1982/3	Brainard et al. 2018	No observations available, but SSTs were high, and other Pacific locations bleached significantly

Phoenix Islands	Probable Bleaching	1998	Brainard et al. 2018	No observations available, but SSTs were high, and other Pacific locations bleached significantly
Phoenix Islands – Kanton	Bleaching	2002/ 3	Obura and Mangubhai 2011; Brainard et al. 2018	Significant bleaching and mortality
Phoenix Islands	Bleaching	2002/ 4	Alling et al. 2007	Significant bleaching and mortality
Phoenix Islands – Howland and Baker	Bleaching	2009/ 2010	Vargas-Ángel et al. 2011	Bleaching with limited mortality
Phoenix Islands – Howland and Baker	Probable Bleaching	2015/ 16	Brainard et al. 2018	Moderate declines in coral cover, but no observations to confirm bleaching
Phoenix Islands – Kanton	Bleaching	2015/ 16	Obura and Manghubai 2011; Brainard et al. 2018	Moderate bleaching, negligible mortality
Gilbert Islands	Bleaching	2004	Donner et al. 2010	Significant bleaching and mortality

1.3 Recovery on remote reefs

Coral recovery following catastrophic disturbances (e.g., Linares et al. 2011; Gilmour et al. 2013), which is generally measured as the time taken for hard coral cover to reach pre-disturbance levels (Graham et al. 2011; Johns et al. 2014) is dependent upon the growth of surviving colonies and successful recruitment of coral larvae (Pearson 1981). The time required for coral cover to increase to pre-disturbance levels is generally >10 years and contingent upon the right conditions (e.g., Gilmour et al. 2013; Pisapia et al. 2016; Figs 1.2, 1.3, 1.4, 1.5). For example, recovery requires larval supply, and good post-settlement conditions including substrate availability and low levels of disturbance (Wakeford et al. 2008; Chong-Seng et al. 2014; Pisapia et al. 2016; Speare et al. 2025). Replenishment of coral assemblages through larval supply is facilitated by strong connectivity to surrounding reefs. Not only are there more

brood-stock for larval production within a viable area, but larval retention in closely connected reef mosaics is also higher (Andutta et al. 2012). For remote reef systems, isolation can reduce connectivity to viable sources of larval supply, thus offsetting any benefits isolation provides against many anthropogenic disturbances (Graham et al. 2006). This constrains capacity for recovery (Smith et al. 2008a; Gilmour et al. 2013), with some systems requiring >10 years to reach pre-disturbance levels of coral cover (e.g., Chagos, and Scott Reef in Western Australia). Further, some reefs experience protracted declines in cover (e.g., Howland and Jarvis in Kiribati), which increases vulnerability to disturbances that are independent of proximity to human populations (Bruno and Valdivia 2016). However, some reefs in the CSMP appear to have experienced relatively rapid increases in coral cover prior to 2020, suggesting fast recovery may be possible in some isolated reefs (Fig. 1.6), although these differences in cover may be in part due to spatial variation among sites surveyed between years. Understanding the ability of coral communities to recover following disturbances is paramount to predicting the maintenance of ecosystem function and resilience, particularly as decadal declines in hard coral cover are recorded (De'ath et al. 2012; Jonker et al. 2019). Recovery at isolated coral reefs is likely conditional upon (i) connectivity and larval dispersal, which influences the local availability of coral larvae and (ii) effective larval settlement and post-settlement growth and survival of corals (Gilmour et al. 2013).

1.3.1 Connectivity and larval dispersal

Connectivity is the process by which individuals of a metapopulation are dispersed among subpopulations (Hanski 1999). In highly fragmented, or isolated, habitats, there is limited dispersal of individuals among subpopulations, which limits opportunities for population replenishment and persistence (Fahrig and Merriam 1994). Following major disturbances and extensive population declines, species persistence is conditional upon the delivery and successful recolonisation of individuals from other distant populations (Fahrig

and Merriam 1985; Adler and Nuernberger 1994). For corals, population connectivity depends mostly upon the dispersal of planktonic larvae (Harrison et al. 1984). Larval connectivity among populations is influenced by a host of biophysical processes (Harrison and Booth 2007), including oceanographic processes that influence movement of larvae (Thompson et al. 2018), the length of time gametes and larvae remain in the plankton before settling (Shanks et al. 2003) and other biological or behavioural processes including larval response to biophysical cues, gregarious behaviour, and predation (Pineda et al. 2010). Connectivity and larval dispersal fundamentally affect the persistence of coral reef populations on isolated reefs (Cowen et al. 2006; Storlazzi et al. 2017).

While potential dispersal of coral larvae is extensive, based on their extended larval competency period (Graham et al. 2008), the settlement success of corals is likely to attenuate very quickly with increasing distance from their natal reefs. Maximum larval longevity, measured in controlled conditions, varies among taxa from 15 days in *Platygyra sinensis* (Tay et al. 2011) to 244 days in *Favites magnistella* (previously *Montastrea magnistella*; Graham et al. 2008), providing some corals with the potential to travel long distances and mix extensively in the right conditions (Wilson and Harrison 1998). Different reproductive modes among species also affect their large-scale dispersal. For example, subpopulations of corals that brood and release mature larvae tend to be more genetically distinct (Ayre and Hughes 2004; Miller and Gunasekera 2017; but see van Oppen et al. 2008), whereas species broadcasting gametes which mix and have long larval durations, are more panmictic (Underwood et al. 2009; Thomas et al. 2020). Despite the potential for externally fertilized larvae to remain competent for long periods of time, larval mortality significantly increases with time spent in the plankton (Graham et al. 2008) and many coral larvae become competent to settle within just 2-3 days of fertilization, where settlement is easily induced given the right cues (Miller and Mundy 2003; Harrington et al. 2004). This suggests long-distance dispersal is limited, since settlement is

likely induced by favourable conditions before the larval duration potential is realized (Ayre and Hughes 2000; Figueiredo et al. 2013). Indeed, very strong stock-recruitment relationships at the scale of individual reefs (Hughes et al. 2000) infer that (even for broadcasting coral species) most larvae are of local origin, leading to suppression of recruitment following extensive coral depletion (Sheppard and Loughland 2002; Sheppard et al. 2002; Gilmour et al. 2013; Hughes et al. 2019a).

Coupling knowledge of larval behaviour and biology with information on hydrodynamic processes provides biophysical models of larval dispersal (Swearer et al. 2019). In the past, these models often contained highly simplified biological and hydrological assumptions, leading to the hypothesis that coral populations were relatively 'open' (Oliver et al. 1992; Szmant and Meadows 2006; Connolly and Baird 2010). But mathematical models have become increasingly sophisticated with considerable improvements in biological and oceanographic inputs (Kough and Paris 2015; Storlazzi et al. 2017; Bode et al. 2019; Gouezo et al. 2021b), and with increased resolution (Saint-Amand et al. 2023) whereby the general consensus now is that coral populations are more 'closed' than previously thought, but that connectivity should be considered on a sliding scale rather than simply 'open' or 'closed' (Levin 2006; Atchison et al. 2008; Brazeau et al. 2011; Kough and Paris 2015; Edmunds et al. 2018). However, few modelling attempts exist for remote and isolated coral reefs due to inherent gaps in our knowledge about the fine-scale hydrodynamics, bathymetry and ecology (e.g., spawning times) of these locations, which differ among coastal and connected coral reefs (e.g., biannual spawning at Scott Reef, Wolanski and Hamner 1988; Gilmour et al. 2009; Vaz et al. 2013). What little evidence there is from hydrodynamics coupled with larval biology is from the Eastern Indian Ocean, and points toward a high likelihood of self-seeding for corals at isolated reefs (Gilmour et al. 2009).

A more accurate way to assess the connectivity among locations, and one which is often used to validate biophysical models, is to determine the relatedness of individuals through genetics (van Oppen et al. 2008; Underwood 2009; Underwood et al. 2009). Since the 1990's, next generation sequencing techniques, such as restriction site associated DNA sequencing (RAD-seq) or the use of microsatellite markers (short, repetitive regions of non-coding DNA), have been used to determine genetic variation among populations (Estoup and Angers 1998). These recent advances in sequencing ability have enabled the integration of population genetics with biophysical models to investigate connectivity among locations (Bode et al. 2019). Analyses of microsatellite data from the broadcast spawner *Acropora tenuis* at remote reefs in the Eastern Indian Ocean have revealed genetically dissimilar populations at each of Scott Reef, the Rowley Shoals, Ningaloo and the Dampier Archipelago (Underwood 2009). The study showed that even rare dispersal events were unlikely, a finding supported by hydrological data in the region showing weak connections between offshore reefs due to current strength, direction and other oceanographic processes (Holloway 1995; Domingues et al. 2007; Gilmour et al. 2009). Whilst the majority of corals at Scott Reef appear self-recruited, genetic evidence does suggest recovery of some taxa is supplemented somewhat by larvae originating from elsewhere (Underwood et al. 2006). Similarly, on Australia's eastern coast, populations of the predominantly brooding coral, *Seriatopora hystrix*, were also shown to be highly genetically isolated at sites along the Great Barrier Reef and especially at Osprey Reef in the CSMP (van Oppen et al. 2008). However, the study did show that *S. hystrix* did produce some sexual larvae that travelled 100's of kilometres, whereby corals at Osprey Reef had some genetic affinity with those on the offshore GBR Ribbon Reef 5 (van Oppen et al. 2008). More extensive genetic sampling at isolated coral reefs is essential to understand patterns of genetic relatedness among coral populations in remote regions, to establish the extent to which isolated reefs are reliant on self-recruitment. If remote, isolated reefs are genetically connected, this could make them

important genetic stepping-stones among subpopulations. A worrying implication of accelerating climate change is the potential loss of genetic stepping-stones (Halford and Caley 2009; Kendall et al. 2013) through (i) the loss of coral on the remote reef due to back-to-back bleaching events, (ii) the change in direction or strength of currents due to changes in temperature and salinity (Vecchi and Soden 2007), and (iii) the effects of temperature on coral larvae (Kendall et al. 2013).

An integrated approach to better understand connectivity on isolated coral reefs would be useful (Edmunds et al. 2018) including the use of demographic studies to better understand the reproductive traits of corals in these locations, combined with both genetic techniques to pinpoint actual geneflow among populations within regions, and improvements in our understanding of surrounding oceanographic processes by deploying a variety of instruments. To improve the predictive abilities of mathematical models in these locations, a better understanding of the physical oceanographic traits of these regions must be achieved through placement of oceanographic instruments (e.g., Acoustic Doppler Current Profilers, or cheaper alternatives such as tilt meters), and more thorough validation through ecological monitoring and genetics (e.g., Bode et al. 2019). Combined, results from such studies would dramatically help us understand the connectivity on remote and isolated coral reefs, improving our understanding of the vulnerability of, and facilitating management of, such populations in the face of global change.

1.3.2 Recruitment and juveniles

Regardless of the origin of coral larvae, population replenishment is also conditional on settlement success and early post-settlement survival (Penin and Adjeroud 2013). Therefore, to monitor recovery or to capture a proxy of recovery potential, it is common to count coral recruits and/or juveniles (Mundy 2000; Jonker et al. 2019; Nozawa et al. 2021; Couch et al. 2023). Not only can future abundance of corals be inferred from these counts, but an idea of

future assemblage composition may also be garnered (Pratchett et al. 2017). It might be expected that the habitat on remote, isolated coral reefs is relatively suited to high recruitment rates owing to the high cover of settlement inducing crustose coralline algae (CCA), and relatively low macro algal cover in the aftermath of disturbances (Sheppard et al. 2008; Gilmour et al. 2013; but see Cannon et al. 2023). Coral replenishment may be constrained or facilitated by differences in habitat-structure that impede or promote larval settlement and/ or post-settlement growth and survival of juvenile corals (Hughes et al. 2007; Graham et al. 2015).

Collecting data on recruitment requires repeat visits to the location ~5 months apart; one to place the recruitment tiles, and one to collect them (Mundy 2000). It also requires accurate knowledge of spawning times, so as to place the tiles at the correct time of year. As remote, isolated reefs are logistically and economically difficult to reach, and data on spawning behaviour is limited, settlement tiles have only been deployed at Scott Reef in the Eastern Indian Ocean, and not at other locations assessed in this chapter (Gilmour et al. 2013). Recruit densities reported on Scott reef, pre disturbance, were relatively high when compared with well-connected reefs in the Great Barrier Reef (Dunstan and Johnson 1998; Hughes et al. 1999), the Dampier Archipelago (Thomson et al. 2021), French Polynesia (Adjeroud et al. 2007), and other Indo-Pacific reefs (Price et al. 2019). However, recruitment collapsed following major bleaching in 1998 in response to the loss of brood-stock, suggesting strong dependence on self-seeding (Gilmour et al. 2013); Table 1.4). Following regrowth of remaining colonies, and a potential recruitment pulse, numbers of recruits had rebounded to their original numbers within 10 years (Gilmour et al. 2013). It should be noted however, that in this case, only recruitment of a single genus (*Acropora*) was reported.

Table 1.4: Mean number of *Acropora* recruits per tile (n=108 year^{-1}) at remote, isolated coral reefs

Reef	Recruits tile^{-1} (± SE)	Year	Citation
Scott Reef	56.00 (10.2)	1996	Gilmour et al. 2013
Scott Reef	25.00 (3.4)	1997	Gilmour et al. 2013
Scott Reef	01.16 (0.2)	1998	Gilmour et al. 2013
Scott Reef	00.00 (0)	1999	Gilmour et al. 2013
Scott Reef	00.15 (0.06)	2002	Gilmour et al. 2013
Scott Reef	01.42 (0.2)	2003	Gilmour et al. 2013
Scott Reef	02.83 (0.5)	2006	Gilmour et al. 2013
Scott Reef	65.50 (14.3)	2008	Gilmour et al. 2013
Scott Reef	55.50 (5.8)	2009	Gilmour et al. 2013
Scott Reef	29.00 (3.05)	2010	Gilmour et al. 2013
Scott Reef	47.00 (6.1)	2011	Gilmour et al. 2013

Another indicator of recovery of coral assemblages is the presence and density of small, juvenile corals (Edmunds 2000). High densities indicate high recovery potential, as small corals have the potential to grow into larger corals and replenish the population. There are slightly more data available for juvenile corals than for recruits at remote coral reefs, possibly because this method requires only a single visit. At Palmyra Atoll in the Line Islands, high densities of juvenile corals (1-40mm diameter) were counted in 2006, although no temporal counts are available (Roth and Knowlton 2009). In the Chagos Archipelago, abundance of juvenile corals (<16cm) was high three years after the 1998 bleaching event (Sheppard et al. 2002, Table 1.5), but the large size of these juveniles suggested a lack of initial recruitment after the mass mortality in 1998. Similarly, following the 2015-16 bleaching event in the Chagos, the number of smaller juvenile corals (~1 year old, <15mm) declined significantly (Sheppard et al. 2017, Table 1.5). Generally, with the exception of reefs within the CSMP and the Phoenix Islands (Table 1.5), pre-disturbance juvenile coral abundance appears relatively high on isolated reefs, even in comparison with well-connected Caribbean reefs (Bak and Engel

1979; Chiappone and Sullivan 1996; Miller et al. 2000), and many reefs in the Indo-Pacific (Bianchi et al. 2006; Adjeroud et al. 2010; Dajka et al. 2019; Couch et al. 2023; but see Glassom and Chadwick 2006). This may reflect corresponding high coral cover (Figs 1.3, 1.4, 1.5) and strong stock-recruitment relationships, which may result in poor recovery capacity following major disturbances and corresponding coral loss (Sheppard et al. 2017; Hughes et al. 2019a; Watt-Pringle et al. 2022).

Whilst juvenile corals may be a good proxy of post-settlement survival, it appears that the majority recruit to eroding substrates following a disturbance (Sheppard et al. 2002). Therefore, perhaps the best proxy of replenishment is to also count the densities of corals recruiting to the gravid population, from which we can infer fecundity and predict potential recruitment pulses (Gilmour et al. 2013). More information on coral size structure, including juvenile densities, recruits and other size classes, should be collected for remote, isolated locations, to try and better understand stock-recruitment relationships.

Table 1.5: Average juvenile coral densities (m^{-2}) for isolated coral reefs. Note different size classes will affect interpretation.

Reef	Juvenile Count (m^{-2})	Year	juvenile size	Reference
Chagos Archipelago	65.8	2001	2-160mm	(Sheppard et al. 2008)
Chagos Archipelago	23.3	2006	0-100mm	Sheppard et al. 2008
Chagos Archipelago (Diego Garcia)	43.02	2012	0-15mm	Sheppard et al. 2017
Chagos Archipelago	39.86	2013	0-15mm	Sheppard et al. 2017
Chagos Archipelago (Northern Atolls)	6.47	2017	0-15mm	Sheppard et al. 2017
Coral Sea Marine Park (Coringa Herald National Nature Reserve)	"Almost none"	2003	0-50mm	Oxley et al. 2003
Line Islands (Kingman and Palmyra)	4.2	2015	1-50mm	Couch et al. 2023
Line Islands (Kingman and Palmyra)	8.6	2018	1-50mm	Couch et al. 2023
Palmyra Atoll (Fore Reef, 10m)	41.5	2006	<40mm	Roth and Knowlton 2009
Palmyra Atoll (Back Reef, 1.5-4.9m)	13.3	2006	<40mm	Roth and Knowlton 2009
Palmyra Atoll (Fore Reef, 14m)	67	2006	<40mm	Roth and Knowlton 2009
Palmyra Atoll (Fore reef, 18m)	43.6	2006	<40mm	Roth and Knowlton 2009
Phoenix Islands (Howland and Baker)	3.2	2015	1-50mm	Couch et al. 2023
Phoenix Islands (Howland and Baker)	1.5	2018	1-50mm	Couch et al. 2023

1.3.3 Other proxies of recovery

The most common metric of recovery available for remote reefs are changes (increases) in coral cover. Following major coral loss (usually due to bleaching), many of the remote locations assessed in this review show recovery of coral cover (Figs 1.2, 1.3, 1.4). One of the best examples is Scott Reef in the Eastern Indian Ocean, which showed recovery of coral cover from 9% following the 1998 bleaching, to 44% within 12 years (Gilmour et al. 2013; Fig. 1.3). Another example is the Chagos Archipelago which, archipelago-wide, also took roughly 12 years to return to pre-1998 levels of coral cover following the 1998 bleaching event (Sheppard et al. 2012; Fig. 1.4). In the historically coral deficient Lihou and Coringa-Herald National Nature Reserves of Australia's CSMP, coral cover following the back-to-back bleaching of 2016/17 (Harrison et al. 2019) increased to levels never before reported for these regions within just a few years (~25% coral cover, Hoey et al. 2020; Fig. 1.2). After significant bleaching in 2002 in the Phoenix Islands, coral cover recovered by 50% in the 6 years following, with researchers estimating a full functional recovery in 8-15 years, provided no other major disturbances occur (Alling et al. 2007; Obura and Mangubhai 2011; Rotjan et al. 2014; Obura et al. 2016). It appears, therefore, that despite poor connectivity, isolated coral reefs do recover over decadal time scales, at least in terms of coral cover. It is important to note that coral cover is a relatively crude metric, which ignores many important functional traits of the coral assemblage such as species composition, 3D complexity and size structure (Viehman et al. 2009; Alvarez-Filip et al. 2011). Indeed, many studies assessing the recovery of coral assemblages in remote, isolated locations note that whilst coral cover may have increased, other traits did not recover. For example, the increases in coral cover in the Phoenix Islands were mostly due to regrowth of surviving colonies, rather than recruitment (Obura et al. 2016; Couch et al. 2023), and the increased coral cover in the Chagos came from small, encrusting corals which provided negligible rugosity (Sheppard et al. 2008). Considering both colony size and

taxonomic identity of a coral directly affect demographics such as growth (Hughes and Connell 1987; Pratchett et al. 2015), mortality (Álvarez-Noriega et al. 2018; Madin et al. 2020; Speare et al. 2022) and reproduction (Richmond and Hunter 1990), measuring coral cover alone can lead to poor predictions of both susceptibility to, and recovery following, a disturbance (Morais et al. 2021). Thus, more information on the changes in coral assemblage structure (community and size) would help better inform our understanding of functional recovery, rather than simply increases in coral cover. The global coral bleaching of 2015-17, and recent 2020 coral bleaching in Australia's CSMP (Hoey et al. 2021) presents another opportunity to record recovery which, for many locations assessed in this chapter, may be the first record of recovery. During a time of unprecedented change, this opportunity should not be missed.

1.4 Conclusions

Although isolated coral reef systems are much less exposed to escalating anthropogenic pressures, these systems are still highly vulnerable to pervasive disturbances that are impacting coral reefs globally. Most notably, isolated coral reefs are increasingly exposed to marine heatwaves that cause severe coral bleaching and mortality (Smith et al. 2008a; Obura and Mangubhai 2011; Sheppard et al. 2017; Head et al. 2019). Other disturbances present on remote, isolated reefs include cyclones which cause localised damage to exposed reef sites, with evidence suggesting they inhibit reef-wide recovery following major bleaching (Oxley et al. 2003; Gilmour et al. 2019a). Furthermore, population irruptions of coralivorous *Acanthaster* spp have been reported at several isolated reefs, even though such disturbances are commonly ascribed to local declines in water quality or overfishing (Endean 1969; Birkeland 1982). Although there are exceptionally high densities of CoTS reported for some sites (e.g., within Kingman Reef, Timmers et al. 2012), declines in coral cover are generally localised, or not quantified at all, and do not appear to affect reef-wide coral cover (Hobbs et al. 2005; Roche et al. 2015; Brainard et al. 2019).

The vulnerability of isolated reefs to major, large-scale disturbances is particularly pronounced due to inherent constraints on recovery capacity, due to limited connectivity. Importantly, existing data shows that coral replenishment at many isolated reefs is heavily reliant on self-recruitment (van Oppen et al. 2008; Underwood et al. 2009). As such, recovery in these systems is largely conditional upon the recovery, growth and ultimate reproduction of existing corals (Gilmour et al. 2013). That said, recovery is likely facilitated by the lack of local stressors on many remote reefs (Gilmour et al. 2013), though there are significant potential regional extinctions of species (Sheppard et al. 2020) with likely consequences for the structure and function of coral assemblages (Gilmour et al. 2013; Sheppard et al. 2017).

With increasing frequency and severity of major bleaching events, and increased severity of cyclones expected into the future, isolated reefs may not have the return time required to recover and are therefore, extremely vulnerable to the effects of climate change (van Hooidonk et al. 2013; Cheal et al. 2017; Hughes et al. 2017; Heron et al. 2018). Indeed, this already appears to be happening, whereby protracted declines in coral cover are evident at many locations despite recovery following the 1998 global bleaching event (although this is accentuated in the current data due to recent bleaching events in 2015/16/17 and 2020). Several locations have already experienced back-to-back coral bleaching events (Chagos, Head et al. 2019; CSMP, Harrison et al. 2019) with bleaching events expected at least twice per decade by 2040 (Heron et al. 2018), and annually in the coming decades (van Hooidonk et al. 2013) at many locations.

Despite several intensive research and monitoring programs in distinct locations (e.g., Scott Reef; Gilmour et al. 2013), there are many gaps in our understanding of coral population dynamics on remote and isolated reefs, largely due to inherent constraints on research and monitoring in such locations. Regular repeat surveys of selected sites are undertaken in the Chagos Archipelago, at Scott Reef and at some locations in the Pacific Remote Islands Marine

National Monument, but otherwise research at remote reef locations is largely fragmented and opportunistic. Focus should be given to sites affected by localised disturbances such as high densities of CoTS, to quantify the actual impact of such disturbances. The collection of more rigorous environmental and coral condition metrics is also important to help better understand and predict coral condition in the coming years (Ryan et al. 2014; Zinke et al. 2018). It should also be noted that the majority of our knowledge on coral assemblages on isolated reefs comes from the sheltered sections of remote reefs/ atolls due to the inaccessibility of exposed sites during rough weather and narrow windows of time within which to survey (e.g., Obura et al. 2011, 75% of sites were at leeward locations; Barott et al. 2010, all sites were within the lagoon). Lastly, further study into genetic connectivity of coral populations at remote reefs would be useful to better understand the sources and sinks of coral larvae at these locations, something which is currently only available for Scott Reef and Osprey Reef in the Eastern Indian Ocean and CSMP, respectively.

In terms of management, from the limited genetic connectivity data available, it is likely that many remote reefs are heavily reliant on self-recruitment following disturbance. Therefore, it is important that management focuses on preventing any further fragmentation of habitat, and reduce disturbances were possible to allow continued replenishment of coral species (Underwood 2009). Maintaining genetic diversity is imperative for adaptation to a rapidly changing environment (Underwood 2009). In particular, lagoonal environments should be protected, since these seem to house some of the highest coral cover (Obura et al. 2011, 85.8% coral cover in the lagoon of Kanton Atoll, Phoenix Islands; Carlton et al. 2015, 86% coral cover within the lagoon of Speakers Bank in the Chagos Archipelago) which may be vital for re-seeding following disturbance, but simultaneously appears to be the most vulnerable habitat, probably due to high residence times of hot water during marine heatwaves (Alling et al. 2007). Lastly, it is imperative that carbon emissions are reduced so as to limit global warming to <2°C.

If this is not achieved, it is unlikely that many of these once pristine, isolated coral reefs will persist as healthy, functioning coral reefs, and will result in significant biodiversity loss and considerable negative human impacts (Hoegh-Guldberg 2011; Frieler et al. 2013).

1.5 Australia's Coral Sea Marine Park

Australia's Coral Sea Marine Park (CSMP) is a very large (978,836 km^2) multi-use marine park located immediately adjacent to the Great Barrier Reef Marine Park (GBRMP). Much of the CSMP comprises deep (up to 6,000m) oceanic habitat, though there are several discrete shallow coral reef systems, with a combined area of approximately 15,000km^2 (Director of National Parks 2018). While there have been recurrent surveys of these reefs (Ayling and Ayling 1985; Oxley et al. 2003, 2004, 2005; Ceccarelli et al. 2008, 2009; Edgar et al. 2015; Harrison et al. 2019), research and knowledge of CSMP reefs is very limited, especially compared to the GBRMP. These surveys suggest there is considerable variation in the cover and composition of corals among regions of the CSMP and among individual reefs. For example, reported estimates of live coral cover in the CSMP range from <5% at Coringa-Herald in the central CSMP (Oxley et al. 2003) to >60% at Osprey Reef in the northern CSMP (Andrews et al. 2008). Reefs in the northern and southern CSMP have been recorded to have relatively high (>40%) coral cover with a preponderance of *Acropora* (Stuart-Smith et al. 2013; Harrison et al. 2019). However, coral cover at reefs in the central CSMP (e.g., Holmes Reef, Chilcott Reef, Herald Cay and Flinders Reef) appears to be suppressed (Ayling and Ayling 1985; Oxley et al. 2003; Ceccarelli et al. 2008; Harrison et al. 2019), possibly due to recurrent coral bleaching events (Oxley et al. 2005; Harrison et al. 2019) and frequent cyclones (Brewer et al. 2007).

Coral bleaching is reported to have affected shallow-water coral assemblages in the CSMP in 2002 and 2004 (Oxley et al. 2004), as well as in 2016 and 2017 (Harrison et al. 2019). Elevated sea surface temperatures (>31°C) in 2002 was assumed to have caused bleaching in

the central region of the CSMP, following reports of recent coral mortality in 2003 (Oxley et al. 2003). Whilst Oxley et al. (2003) reported moderate coral mortality in the Coringa-Herald National Park, there is evidence from unpublished work (Wakeford, unpublished report; Oxley et al. 2003) of significant coral loss on the Flinders Reefs (~100km south-west of the Herald Cays) in the central CSMP. In 2004, 65% of colonies surveyed at Lihou reef in the central CSMP were bleached (Oxley et al. 2004), although this resulted in only ~18% mortality and no significant change in reef-wide coral cover (Oxley et al. 2005). No data exists for other reefs within the CSMP for the 2002 and 2004 events. In 2016, coral bleaching was restricted to central CSMP reefs, where there was a corresponding decline in the abundance *Acropora* and *Pocillopora* corals (Harrison et al. 2019). However, these corals were already low in abundance and contributed relatively little to overall coral cover at these locations, such that there was limited change in coral composition following the bleaching event (Harrison et al. 2019). This lack of fast-growing coral species, will however, likely constrain the capacity for coral recovery across large parts of the central CSMP (Oxley et al. 2005; Ceccarelli et al. 2009). Even on well-connected reef systems, the time required for coral cover to increase to pre-disturbance levels in the aftermath of mass-bleaching and other major disturbances is >10 years, and conditional upon low levels of chronic or acute disturbances (Pisapia et al. 2016). For remote reef systems, isolation from major urban centres moderates exposure to most anthropogenic disturbances, though isolation can also reduce connectivity to viable sources of larval supply, which greatly constrains capacity for recovery (Smith et al. 2008a; Gilmour et al. 2013) and increases vulnerability to disturbances that are independent of close proximity to human populations (Bruno and Valdivia 2016).

Despite recurrent mass-bleaching and exposure to other major disturbances, the recovery and resilience of coral assemblages in the Coral Sea is largely unknown as only 4 of a possible 18 reef systems (Coringa-Herald, Lihou, Flinders and Osprey) have been surveyed

extensively, one of which has not been surveyed since the 1980's (Ceccarelli 2011). This lack of spatial and temporal scope leaves huge gaps in our knowledge and understanding of these reefs. Specifically, (i) the current coral communities on most of these reefs are unknown, (ii) the susceptibility of these coral assemblages to past disturbances (which we expect to have occurred due to satellite data of high sea surface temperatures or through cyclone tracking, but have limited ground-truthed evidence), and (iii) how these reefs are likely to cope with future disturbance are unknown. To better inform the sustainable management in the CSMP, these unknowns must be addressed. The first step is to determine current communities and their susceptibility to contemporary disturbances occurring in the CSMP.

1.6 Thesis objectives

The purpose of the research presented within this thesis was to gain a greater understanding of the vulnerability and resilience of isolated reefs, by investigating spatiotemporal variation in coral assemblages across the CSMP and neighbouring GBRMP. Specifically, this thesis focusses on (i) differences in contemporary coral assemblage structure among regions, habitats and reef systems differing in purported connectivity and disturbance regimes (CSMP vs. GBRMP) and (ii) the differential susceptibility of corals to recent mass bleaching across the CSMP and GBRMP. This research is presented in four independent, but strongly inter-related, chapters:

Chapter 2 compares coral cover and composition among regions and habitats of the CSMP based on extensive sampling conducted between 2018 and 2020 (before coral loss caused by coral bleaching). Comparable sampling was also conducted along outer reefs on the Great Barrier Reef, to understand differences in coral assemblage structure between two marine parks which differ in connectivity and disturbance regimes. This chapter tests the hypotheses that coral cover will be higher in the CSMP owing to relative isolation from many chronic disturbances; that coral cover will be lower on reef crests compared with slopes, due to the

disproportionate impacts of coral bleaching and cyclones in shallow reef environments; and that benthic community composition will vary among regions and zones, with a lack of fragile branching corals in regions impacted by bleaching, cyclones and CoTS. Importantly, this chapter provides a contemporary baseline to assess the effects of future disturbances and determine the key taxa contributing to regional differences in coral community composition.

Chapter 3 compares the abundance of common juvenile scleractinian coral taxa between geographically isolated reefs in the CSMP and more proximal reefs of the GBRMP, aiming to understand differences in resilience and recovery capacity within and between these two distinct reef systems. Here I test the hypothesis that the relative isolation of CSMP reefs from many human- and land-based pressures, combined with oceanic conditions favourable for settlement (such as improved water quality), may result in higher densities of juvenile corals than reefs in the GBRMP. This chapter also assesses the relationship between reef-wide juvenile density and percent cover of *Acropora*, *Pocillopora*, and *Porites,* where isolated reefs in the CSMP expected to rely on self-recruitment are hypothesised to have stronger juvenile-adult relationships compared with more connected GBRMP reefs.

Chapter 4 tests for differences in bleaching susceptibility among coral colonies during mass bleaching in 2020 across 33 reefs of the CSMP and GBRMP. Specifically, this chapter quantifies the likelihood of bleaching among major coral taxa and colony size classes relative to reef-wide bleaching severity, to determine which colonies were most and least susceptible to mass bleaching in 2020. This chapter tests the hypotheses that small corals are less likely to bleach than larger colonies, and that low-moderate bleaching severity will reveal high variation in bleaching susceptibility, whilst increasing bleaching severity will result in an increasing pool of taxa showing signs of bleaching.

Chapter 5 explores interannual variation in coral cover and community composition at 43 sites throughout the CSMP that were sampled in 2020 (during the bleaching) and 2021 (12-

months later). Coral loss is assessed and compared across regions and habitats, where declines in the abundance of individual coral taxa are used to infer differential mortality among taxa, and detect shifts in community composition in the aftermath of the 2020 bleaching. This chapter tests the hypotheses that coral mortality will be higher on reef crests than reef slopes, and that regional differences in coral loss will reflect taxonomic composition, with southern and central CSMP reefs previously dominated by highly susceptible taxa (*Acropora* and *Isopora*) and northern reefs by more robust taxa (*Porites*). Ultimately, this chapter aims to understand if coral taxa identified as highly susceptible to bleaching in Chapter 4 also experienced the greatest mortality.

Chapter 2. Regional differences in coral cover and communities across Australia's Great Barrier Reef and Coral Sea Marine Parks reflect persistent effects of major disturbances.

2.1 Introduction

Spatial heterogeneity in the abundance (which is typically measured based on proportional cover) of hard corals (order Scleractinia), as well as variation in taxonomic composition, occurs in response to biological and environmental processes operating at different scales (Glynn 1976; Done 1982; Edmunds and Bruno 1996). Regional differences in coral cover and composition are apparent due to marked changes in environmental conditions naturally occurring with latitude (i.e., light, temperature, pH) and distance from shore (i.e., water quality, wave action) (Harriott and Banks 2002; Wismer et al. 2009; Moustaka et al. 2019). Coral cover tends to increase with distance from shore, owing to corresponding differences in environmental conditions (Wismer et al. 2009; Segal and Castro 2011; but see Lirman and Fong 2007; Moustaka et al. 2019), and diversity of assemblages increases toward the coral triangle (Stehli and Wells 1971). However, processes operating at smaller scales can mediate regional scale patterns. For example, coral assemblages vary greatly with aspect, wave exposure, habitat complexity and depth (Graus and Macintyre 1989; Graham and Nash 2013; Williams et al. 2013; Aston et al. 2019; Roelfsema et al. 2021). As a result, different zones (e.g., reef crests and reef slopes) within regions can harbour significantly different coral cover and communities (Wismer et al. 2009; Lange et al. 2021), resulting in fine-scale spatial heterogeneity in reef structure and function.

Aside from the effects of natural environmental gradients, regional and local variation in the distribution and abundance of corals is increasingly shaped by the type, frequency and severity of disturbances (Connell 1978; Osborne et al. 2011). Major, acute disturbances, such

as coral bleaching events, cyclones and population irruptions of coral predators, cause widespread coral mortality at regional scales, but effects may differ among reef zones within regions (Fabricius et al. 2008; Furby et al. 2013). For example, the effects of coral bleaching may be spatially extensive (e.g., encompassing multiple regions; Hughes et al. 2018a), but mortality is most conspicuous in shallow zones (e.g., the reef crest), where heat and photic stress are most concentrated (Furby et al. 2013). Similarly, population irruptions of crown-of-thorns starfish (*Acanthaster* sp; CoTS) and corresponding effects on coral cover and composition are not evenly apportioned among different reefs. On Australia's Great Barrier Reef Marine Park (GBRMP), CoTS are most abundant on mid-shelf reefs, with coral loss distributed across zones with the highest cover of preferred coral prey (Kayal et al. 2012; Matthews et al. 2024). Major acute disturbances, which are increasing in frequency and severity (Oliver et al. 2018), are important drivers of spatial variation in coral assemblages (Emslie et al. 2024a). It may be that the benefits afforded by natural gradients (e.g., cross-shelf gradients) are outweighed by the increasing impacts of acute disturbances, which are impacting even the most remote coral reef systems (Baumann et al. 2022).

Whilst disturbances generally result in declines in coral cover, different disturbances have disproportionate impacts on certain coral taxa (e.g., Keesing et al. 2019; Burn et al. 2022), leading to shifts in community composition (Pratchett et al. 2011; Edmunds et al. 2014; Hughes et al. 2018b). Generally, fast-growing branching taxa are most susceptible to a range of disturbances (Keesing et al. 2019; Mudge and Bruno 2023). Severe tropical cyclones and storms are most likely to dislodge or break corals with 'top heavy' morphologies such as branching or tabular taxa, as opposed to 'bottom heavy' massive taxa (Madin et al. 2014). Similarly, the preferred prey of CoTS are tabular and branching *Acropora* (Pratchett 2007; Saponari et al. 2015), though CoTS may exhibit a range of dietary preferences depending on prey availability (Celliers and Schleyer 2007; Burn et al. 2020; Foo et al. 2024). There is also

a well-established hierarchy of susceptibility to coral bleaching, where fast-growing branching taxa (e.g., *Acropora* and *Stylophora*) appear most vulnerable to bleaching and subsequent mortality (Marshall and Baird 2000; Loya et al. 2001), although this is dependent on colony size and the severity of the bleaching event (Burn et al. 2023 [**Chapter 4**]). In the aftermath of such disturbances, coral assemblages often shift away from a dominance of bleaching-susceptible branching and tabular taxa such as *Acropora*, with important ramifications for reef structure and function (Hughes et al. 2018b; Pisapia et al. 2019; Morais et al. 2021; Mudge and Bruno 2023).

Major, acute disturbances occur against a backdrop of chronic anthropogenic pressures, such as poor water quality, fisheries exploitation, and impacts of tourism, which can contribute to coral loss, undermine resilience and inhibit recovery of coral assemblages (Wakeford et al. 2008; Wooldridge and Done 2009; Gil et al. 2015; Pacey et al. 2023). Such pressures are generally most severe closest to urban centres or modified catchments and decline with increasing remoteness (Jupiter et al. 2008; Williams et al. 2015; Fabricius et al. 2016; Roberts et al. 2017). As such, remote oceanic coral reefs are purported to harbour relatively pristine, healthy coral reef communities (Sandin et al. 2008; Barott et al. 2010; Vroom and Braun 2010; Heery et al. 2018; McClanahan et al. 2019b). Although coral assemblages on remote coral reefs are impacted by highly pervasive anthropogenic pressures (e.g., fishing) and effects of anthropogenic climate change (Alling et al. 2007; Gilmour et al. 2013; Bruno and Valdivia 2016; Stuart-Smith et al. 2018; Sheppard et al. 2020), they may have increased resilience due to the lack of chronic pressures (Gilmour et al. 2013; Smith et al. 2016; Harrison et al. 2019; Donovan et al. 2021; but see Baumann et al. 2022).

Australia's Coral Sea Marine Park (CSMP) and adjacent Great Barrier Reef Marine Park (GBRMP) provide an opportunity to compare coral assemblages between isolated, remote reefs and coastal, proximal reefs (e.g., Burn et al. 2024 [**Chapter 3**]). Chronic anthropogenic

pressures that impact coastal reefs in the GBRMP (e.g., sedimentation and eutrophication from land runoff) are likely diminished in the CSMP (Jupiter et al. 2008), while coral assemblages in both marine parks are broadly exposed to major acute disturbances (Brewer et al. 2007; Hughes et al. 2018b; Stuart-Smith et al. 2018; Harrison et al. 2019). Due to the inherent patchiness of acute disturbances, and the large latitudinal extent of the GBRMP and CSMP, coral assemblages are likely to vary regionally within parks (Stuart-Smith et al. 2013; Edgar et al. 2015; Hughes et al. 2018b; Harrison et al. 2019). Reefs in the southern region of the CSMP have been shown to comprise high coral cover and an abundance of fragile branching corals (e.g., *Acropora*; Edgar et al. 2015) even in the aftermath of back-to-back coral bleaching that occurred in 2016 and 2017 (Harrison et al. 2019). In contrast, coral cover has been persistently low (<20%) across many reefs and zones in the central CSMP (Ayling and Ayling 1985; Oxley et al. 2003, 2004, 2005; Ceccarelli et al. 2008, 2009), attributable to recurrent disturbances and/or low recovery capacity (Oxley et al. 2004, 2005; Ceccarelli et al. 2008; Burn et al. 2024 [**Chapter 3**]). Research and knowledge are still very limited for CSMP reefs, especially for some of the most remote reefs, which have been surveyed very rarely (i.e., Ashmore and Boot; Hoey et al. 2020).

The purpose of this chapter was to compare coral cover and composition among zones and latitudinal regions (north, central and south) within each of the CSMP and GBRMP based on extensive surveys conducted in 2018-2020. Specifically, three hypotheses are tested: (1) that coral cover will be higher in the CSMP compared with the GBRMP, reflecting the CSMP's relative isolation from many chronic disturbances; (2) that coral cover will be lower on reef crests compared with slopes, due to the disproportionate impacts of coral bleaching and cyclones in shallow reef environments (Furby et al. 2013; Beeden et al. 2015); and (3) that benthic community composition will vary among regions and zones, with a lack of fragile branching corals in regions impacted by bleaching, cyclones and CoTS. These hypotheses are

grounded in observed spatial variation in disturbance regimes (discussed in Methods), and the resulting data provide a contemporary baseline against which to assess the effects of future disturbances.

2.2 Methods

2.2.1 Study sites

Coral cover and community composition were assessed at 19 reefs throughout the CSMP and at 17 reefs along the outer continental shelf of the GBRMP between April 2018 and March 2020 (Fig. 2.1), during an intermittent period between major marine heatwaves. Reefs were placed into six regions (north, central and south for each marine park) following Burn et al. (2024 [**Chapter 3**]). At each reef, 3-12 sites were surveyed, resulting in 155 unique sites mostly located on the outer edge of reefs, where there was continuous solid reef matrix with a clearly defined reef crest and reef slope, following Pratchett (2005). Sites were surveyed between 1 and 3 times over the survey period, with 50 sites surveyed multiple times. At each site, surveys were conducted within each of two different depth zones: the reef crest (approximately 1-3m depth) and the reef slope (8-10m depth, where possible). In shallow reef environments (e.g., in back reef environments), where maximum depths were less than 9m, the reef slope transects were run along the deepest margin of continuous reef habitats, avoiding extensive areas of sand or rubble. Similarly, it was not always possible to survey the reef crest, due to low tides, limited water depth, and/ or large swells, and in those cases the reef crest transects were run just below the outermost edge of the reef crest (2-4m).

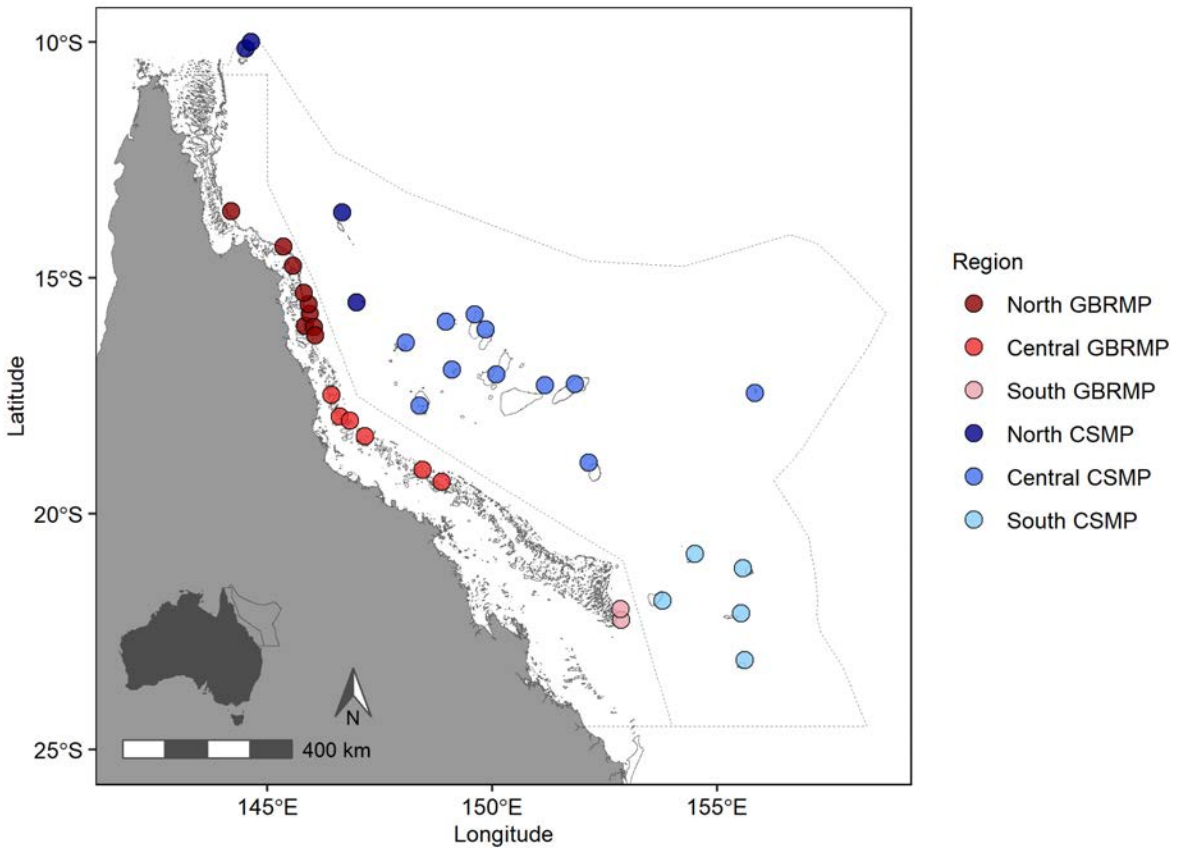


Figure 2.1: Reefs in the Great Barrier Reef Marine Park (GBRMP; n = 17) and Coral Sea Marine Park (CSMP; n = 19) surveyed in 2018-2020. Shades of colour represent latitudinal regions. Dashed lines represent marine park boundaries, with the GBRMP adjacent to the Queensland coast and the CSMP directly to the East

2.2.2 Recent disturbance history

The GBRMP and CSMP were subject to several major disturbances directly prior to and during this study that likely contributed to observed regional and local patterns in coral cover and composition, including marine heatwaves, severe tropical cyclones and population irruptions of CoTS. Coral bleaching is widely considered to be the foremost cause of coral mortality since 2016 (Hughes et al. 2018b; Burt et al. 2019; Eakin et al. 2019), and whilst bleaching can be spatially extensive, impacts vary regionally and with depth (Furby et al. 2013;

Frade et al. 2018). Immediately prior to this study, back-to-back bleaching events in 2016 and 2017 impacted both the GBRMP and CSMP, although the impact was spatially variable (Hughes et al. 2018b, 2019b; Stuart-Smith et al. 2018; Harrison et al. 2019). In the CSMP, bleaching was largely restricted to the central and northern regions, whilst the southern region was relatively unaffected in 2016 with negligible impacts in 2017 (Stuart-Smith et al. 2018; Harrison et al. 2019). The northern CSMP experienced considerable coral mortality, with Osprey Reef experiencing >12 degree heating weeks (DHW; NOAA coral reef watch) resulting in >20% loss of coral cover (Stuart-Smith et al. 2018). Reefs in the central CSMP experienced lower levels of coral loss, but this was attributed to the already low cover of corals in this region (Stuart-Smith et al. 2018). Similarly, in the GBRMP, the northern and central regions experienced the worst bleaching and subsequent mortality in 2016 and 2017, respectively, whilst the south remained relatively unaffected (Hughes et al. 2018b, 2019b; but see Stuart-Smith et al. 2018). An extensive marine heatwave occurred causing mass coral bleaching throughout the CSMP and GBRMP in March 2020, but surveys conducted in 2020 were completed before bleaching-induced coral mortality exceeded background levels of mortality (Burn et al. 2022). Both bleached and healthy corals were included in surveys in 2020. Thus, data from 2020 is not confounded by any impacts of bleaching.

During our study period, the GBRMP was coming towards the end of the fourth population irruption of CoTS, by which time CoTS outbreaks were largely concentrated in the southern region of the GBRMP (Babcock et al. 2020). At the time of our study, the southern (Swains) region of the GBRMP had experienced relative declines of ~50% since the onset of this population irruption in 2012 and were still experiencing active outbreaks (Matthews et al. 2024). There were also two severe tropical cyclones (and several category 1-2 cyclones) that impacted the CSMP and GBRMP immediately prior to, and during our study period. Cyclone Debbie impacted parts of the central CSMP (as a category 2) and central GBRMP (as a category

4) in March 2017, resulting in 55% declines in coral cover in the Whitsunday Island group (Williamson et al. 2019). Cyclone Trevor impacted parts of the far northern GBRMP as a category 3 cyclone in March 2019, tracking ~60 km north of the northernmost surveyed GBRMP reef (Creech). Whilst direct effects on coral communities are not available for Cyclone Trevor, it is expected that some reefs in the northern region of the GBRMP would have experienced significant coral loss (e.g., Fabricius et al. 2008).

2.2.3 Coral cover and community composition

In each zone at each site, three replicate 50m transects were run parallel to the depth contour, with up to 10m between successive transects. Point-intercept transects (PIT) were used to quantify benthic cover and composition, recording the specific organisms or substratum types underlying each of 100 uniformly spaced points (50cm apart) along each transect (following Hoey et al. 2020). Corals were mostly identified to genus (using contemporary, molecular-based classifications for the order Scleractinia). Major growth forms were also distinguished for *Acropora* (tabular, staghorn, and other) and *Porites* (massive *versus* columnar or branching).

2.2.4 Statistical analyses

To test for spatial variation in cover of scleractinian corals, a Generalized Linear Mixed Effects Model (GLMM) was constructed. The model was fit with the fixed effects of region (six regions) and zone (crest and slope), as well as their interaction, with a nested random effects structure of site nested inside reef, nested inside year to capture the hierarchical dependencies within the data and account for temporal and local spatial variability. Combinations of fixed and random effects were fit and tested using maximum likelihood, and were retained only if they improved the fit of the model according to the corrected Akaike Information Criterion (AICc). Coral cover was modelled using a Tweedie distribution with a

log link function to account for the overdispersion and presence of zeros in the data. The model was validated, and residuals visually checked, including tests for overdispersion using the 'DHARMa' package (Hartig 2021). Post-hoc Tukey's pairwise comparisons were calculated using estimated marginal means in the 'emmeans' package (Lenth 2021) to test for significant differences in coral cover among fixed effects. Averages presented in the results are estimated marginal means based on the GLMM.

To test for multivariate differences in the taxonomic composition of hard coral assemblages among regions, two multivariate generalised linear models (mGLM) were constructed, independently testing for variation in each zone. Models fit with a Poisson distribution were tested against those fit with a negative binomial distribution, using model diagnostics generated with the 'plot.manyglm' function and the AICc. The negative binomial models were selected for pairwise multivariate comparisons, conducted using the anova.manyglm function. Likelihood ratio test (LRT) statistics and corresponding p values were produced, both for multivariate pairwise comparisons (i.e., differences in community between each pair of regions) and for univariate scoring of the taxonomic contributions to those overall differences. Taxonomic contributions are calculated based on adjusted p values which controls the family-wise error rate across taxa (Westfall et al. 1993). The dis/similarities in coral composition within and among regions for each zone were visualised using non-metric multi-dimensional scaling (nMDS) plots based on Bray Curtis dissimilarity matrices. Three dimensions were used ($k = 3$), and the rarest taxa ($n = 43$) were pooled into a category of 'Other Scleractinia' to improve the fit of the ordination due to the large size of the dataset. The composition of these 'other' taxa can be found in the Supplementary Material (Fig. S2.2). Species scores were overlaid on the nMDS with taxa identified as significantly driving differences in the mGLMs presented in bold. mGLMs were constructed using the package 'mvabund' (Wang et al. 2021) and community differences were visualised using the package

'vegan' (Oksanen et al. 2020). Plots were created in 'ggplot2' (Wickham et al. 2019). All analyses were conducted in R version 4.1.1 (R Core Team, 2021).

2.3 Results

2.3.1 Hard coral cover

The mean cover of hard (scleractinian) corals across the six regions of the CSMP and GBRMP was 24.4% (± 0.4 SE), and overall coral cover did not differ between marine parks (CSMP = 24.5% ± 0.5 SE; GBRMP = 24.2% ± 1.1 SE). However, there was considerable variation in coral cover within marine parks (Fig. 2.2, Table 2.1).

Coral cover was notably suppressed in the southern GBRMP, with significantly lower cover in both zones (crest = 5.2% ± 1.5 SE; slope = 4.0% ± 1.2 SE) than any other region (Fig. 2.2; Table 2.1). Conversely, coral cover was very high on southern CSMP reef crests (31.3% ± 4.4 SE), central GBRMP reef crests (32.7% ± 6.1 SE) and northern CSMP reef slopes (41.5% ± 6.5 SE). Indeed, coral cover recorded on the reef slope in the northern CSMP was significantly higher than recorded in each of the other 5 regions (Fig. 2.2; Table 2.1). Low to moderate coral cover (18 - 21%) was evident in both zones of the northern GBRMP and central CSMP, northern CSMP reef crests, and southern CSMP and central GBRMP reef slopes (Fig. 2.2, Table 2.1)

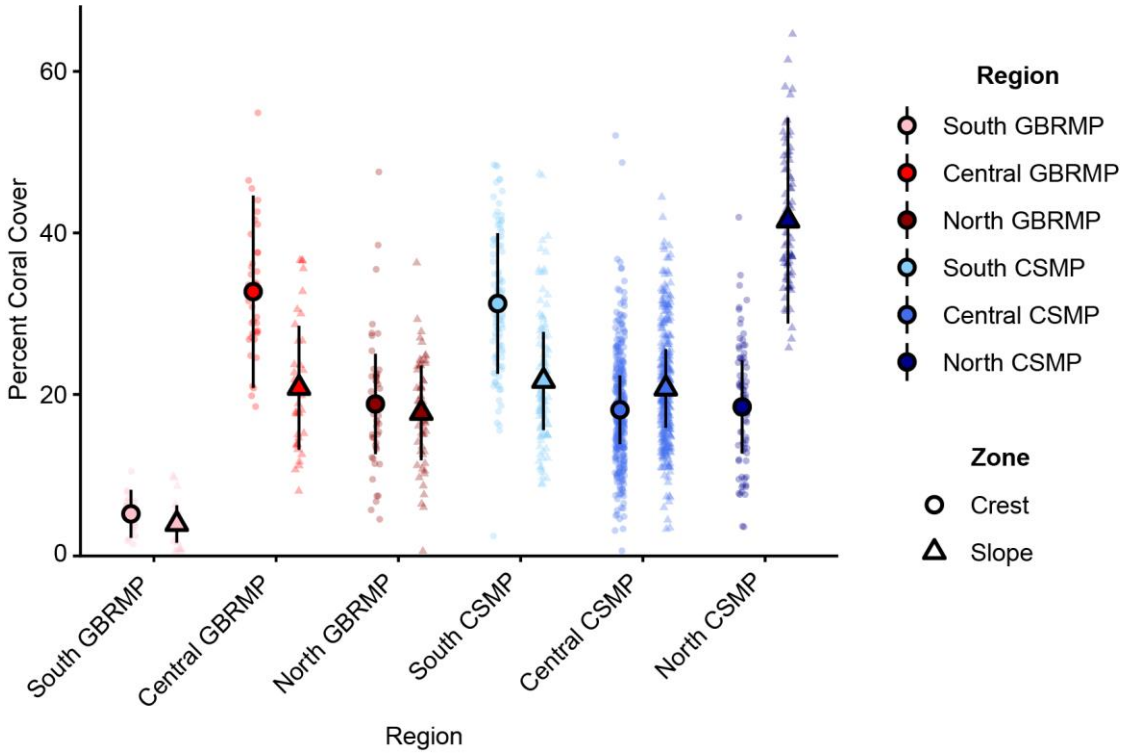


Figure 2.2: Estimated marginal mean percent hard coral cover (± 95% CI) for the reef crest (circles) and slope (triangles) within each region of the CSMP (shades of blue) and GBRMP (shades of red). Faded points represent model fitted predictions with overlaid residuals. Estimated marginal means and predicted residuals account for the fixed and random effects included in the GLMM

Table 2.1: Pairwise comparisons of scleractinian coral cover between combinations of regions for each zone generated using estimated marginal means from the GLMM. Asterisks (*) denote statistically significant differences. Model *df* = 1225

Contrast	Estimate	SE	t-ratio	p-value	
Crest					
South GBRMP – Central GBRMP	-27.5	5.9	-4.64	0.0001	*
South GBRMP – North GBRMP	-13.6	3.2	-4.30	0.0003	*
South GBRMP – South CSMP	-26.0	4.3	-6.02	<0.0001	*
South GBRMP – Central CSMP	-12.9	2.2	-5.76	<0.0001	*
South GBRMP – North CSMP	-13.3	3.0	-4.39	0.0002	*
Central GBRMP – North GBRMP	13.9	5.7	2.44	0.1438	
Central GBRMP – South CSMP	1.5	6.0	0.24	0.9999	
Central GBRMP – Central CSMP	14.6	5.4	2.71	0.0730	
Central GBRMP – North CSMP	14.3	5.8	2.45	0.1399	
North GBRMP – South CSMP	-12.4	4.2	-2.95	0.0379	*
North GBRMP – Central CSMP	0.7	2.8	0.26	0.9998	
North GBRMP – North CSMP	0.4	3.5	0.10	1.0000	
South CSMP – Central CSMP	13.2	3.6	3.69	0.0033	*
South CSMP – North CSMP	12.8	4.1	3.16	0.0203	*
Central CSMP – North CSMP	-0.4	2.6	-0.14	1.0000	
Slope					
South GBRMP – Central GBRMP	-16.9	3.8	-4.39	0.0002	*
South GBRMP – North GBRMP	-13.8	3.0	-4.66	0.0001	*
South GBRMP – South CSMP	-17.7	3.0	-5.82	<0.0001	*
South GBRMP – Central CSMP	-16.8	2.4	-6.95	<0.0001	*
South GBRMP – North CSMP	-37.6	6.4	-5.91	<0.0001	*
Central GBRMP – North GBRMP	3.1	4.0	0.79	0.9699	
Central GBRMP – South CSMP	-0.9	4.0	-0.22	0.9999	
Central GBRMP – Central CSMP	0.1	3.5	0.02	1.0000	
Central GBRMP – North CSMP	-20.7	6.4	-3.24	0.0155	*
North GBRMP – South CSMP	-4.0	3.3	-1.21	0.8309	
North GBRMP – Central CSMP	-3.0	2.7	-1.12	0.8750	
North GBRMP – North CSMP	-23.8	6.1	-3.92	0.0013	*
South CSMP – Central CSMP	0.9	2.6	0.37	0.9991	
South CSMP – North CSMP	-19.9	5.8	-3.45	0.0075	*
Central CSMP – North CSMP	-20.8	5.5	-3.75	0.0025	*

2.3.2 Coral community composition

The most common taxa throughout the six regions, based on their absolute percentage contributions to coral cover, were other *Acropora* (crest = 5.6% ± 0.23 SE; slope = 2.9% ± 0.1

SE), *Pocillopora* (crest = 4.5% ± 0.2 SE; slope = 3.1% ± 0.2 SE), and massive *Porites* (crest = 2.9% ± 0.2 SE; slope = 3.9% ± 0.2 SE). However, there were significant regional differences in the composition of coral assemblages for both the reef crest (mGLM: Res.df = 200, Deviance = 430.7, p = 0.001) and reef slope (mGLM Res. Df = 202, Deviance = 514.2, p = 0.001) zones. Differences in communities were evident among all pairs of regions, except for the central and northern GBRMP communities on the reef slope, which were statistically similar (Table 2.2; Fig. 2.3). The magnitude of difference among communities varied among regions however, with the largest differences in community composition for both the reef crest and reef slope zones occurring between regions in the CSMP (Table 2.2, Fig. 2.3).

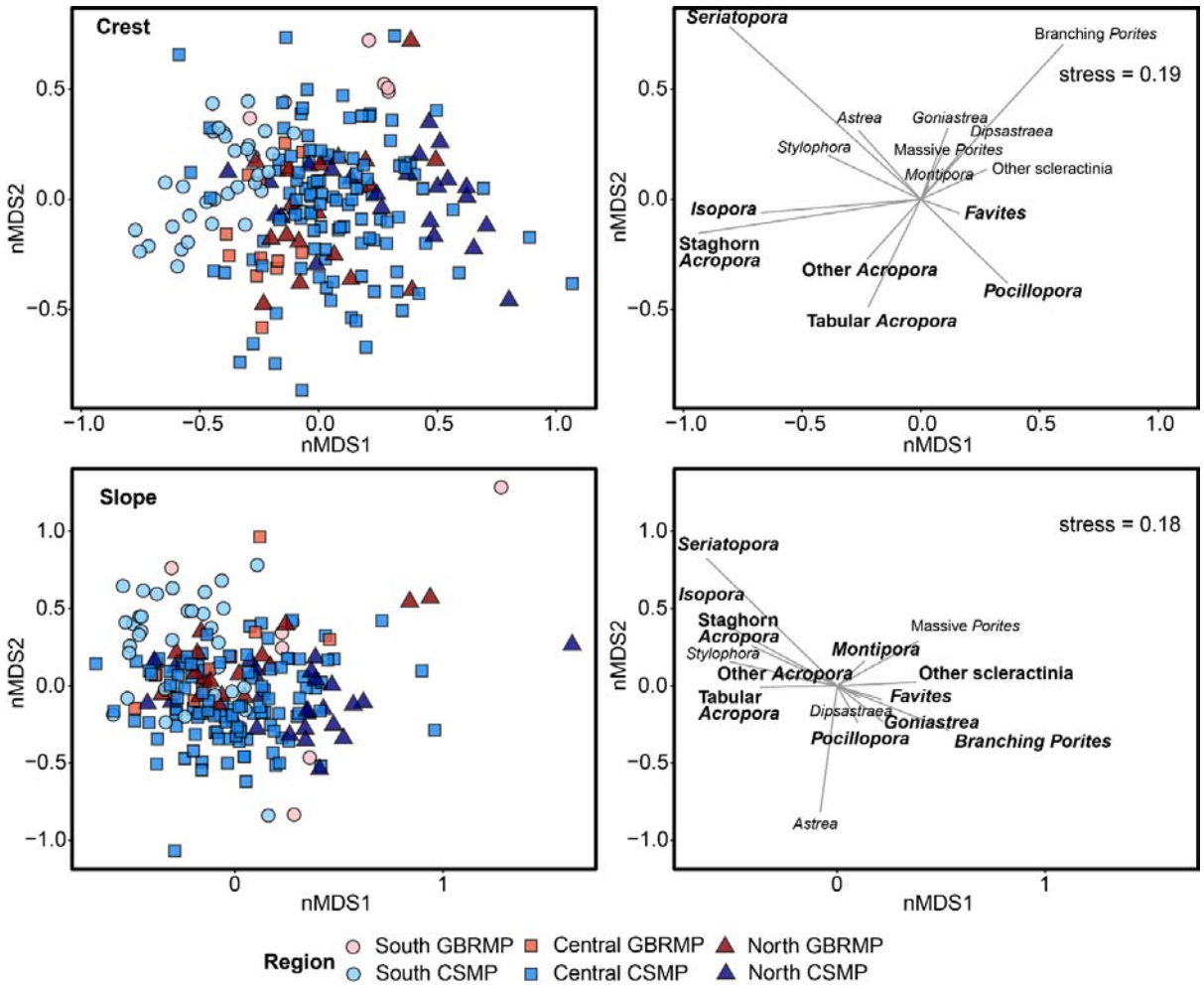


Figure 2.3: Non-metric multidimensional scaling plots showing regional differences in assemblage structure of coral taxa for (top) the reef crest, and (bottom) the reef slope. Each point represents the coral assemblages at each site at each time point. Shades of red represent the GBRMP and shades of blue the CSMP, whilst shapes represent the latitudinal location of the regions (triangles = north, squares = central, circles = south). The relative contributions of taxa to the observed variation in composition are shown as vectors on the right-hand panels, with taxa in bold identified as significantly driving differences in the multivariate GLMs

Table 2.2: Multivariate pairwise contrasts of coral community composition among all regions for each of the reef crest, and reef slope. Significant p values indicate differences in communities and are denoted with an asterisk*. LRT = Likelihood Ratio Test statistic.

Contrast	LRT	Adjusted p value
Crest		
South CSMP – Central CSMP	153.26	0.001 *
South CSMP – North CSMP	141.67	0.001 *
South GBRMP – Central GBRMP	131.06	0.001 *
Central GBRMP – Central CSMP	112.91	0.001 *
South GBRMP – South CSMP	112.01	0.001 *
Central GBRMP – North CSMP	95.01	0.001 *
South GBRMP – North GBRMP	81.15	0.001 *
Central GBRMP – South CSMP	80.17	0.001 *
North GBRMP – South CSMP	78.55	0.001 *
South GBRMP – Central CSMP	73.91	0.001 *
South GBRMP – North CSMP	69.83	0.001*
North GBRMP – North CSMP	45.22	0.021 *
Central GBRMP – North GBRMP	44.86	0.022 *
Central CSMP – North CSMP	36.05	0.028 *
North GBRMP – Central CSMP	31.47	0.037 *
Slope		
South CSMP – North CSMP	182.40	0.001 *
South CSMP – Central CSMP	170.76	0.001 *
South GBRMP – North CSMP	122.01	0.001 *
South GBRMP – Central GBRMP	117.97	0.001 *
Central CSMP – North CSMP	115.12	0.001 *
South GBRMP – Central CSMP	107.34	0.001 *
South GBRMP – South CSMP	105.62	0.001 *
South GBRMP – North GBRMP	99.67	0.001 *
North GBRMP – North CSMP	95.22	0.001 *
North GBRMP – South CSMP	79.00	0.001 *
Central GBRMP – North CSMP	73.78	0.001*
Central GBRMP – South CSMP	72.15	0.001*
North GBRMP – Central CSMP	45.10	0.019 *
Central GBRMP – Central CSMP	41.28	0.030 *
Central GBRMP – North GBRMP	20.96	0.224

On the reef crest, seven taxa were identified in the mGLM as significantly driving the differences among the six regions: Tabular *Acropora* (LRT = 71.67, p = 0.001), other *Acropora* (LRT = 59.05, p = 0.001), staghorn *Acropora* (LRT = 55.71, p = 0.001), *Pocillopora* (LRT = 50.56, p = 0.001), *Isopora* (LRT = 47.69, p = 0.001), *Seriatopora* (LRT = 34.97, p = 0.001), and *Favites* (LRT = 33.27, p = 0.001) (Fig. 2.3; Table S2.1). Crest communities in the southern CSMP were dominated by morphotypes of *Acropora*, and *Isopora*, which were not common throughout the central and northern CSMP (Fig. 2.3; Table S2.1). Similarly, *Seriatopora* was most common in the southern CSMP, and almost entirely absent from the central and northern CSMP (Fig. 2.3; Table S2.1). In contrast, *Pocillopora* was notably rare in the southern regions of both the CSMP and GBRMP in comparison with other regions (Fig. 2.3; Table S2.1). *Acropora* also dominated communities in the central and northern GBRMP, but was almost entirely absent in the southern GBRMP (Fig. 2.3; Table S2.1).

On the reef slope, 11 of the 15 taxa modelled were identified to be significantly driving regional differences in communities: *Pocillopora* (LRT = 73.50, p = 0.001), branching *Porites* (LRT = 64.44, p = 0.001), *Seriatopora* (LRT = 58.63), p = 0.001), *Montipora* (LRT = 42.30, p = 0.001), other Scleractinia (LRT = 36.9, p = 0.001), staghorn *Acropora* (LRT = 35.23, p = 0.001), *Goniastrea* (LRT = 34.37, p = 0.001), *Favites* (LRT = 34.23, p = 0.001), *Isopora* (LRT = 33.42, p = 0.001), tabular *Acropora* (LRT = 30.36, p =0.002), and other *Acropora* (LRT = 26.16, p = 0.002). Similar to reef crest communities, *Pocillopora* was rare in the southern regions of the CSMP and GBRMP in comparison to central and northern regions (Fig. 2.3; Table S2.1). Other similarities between zones included the preponderance of *Isopora* in the southern CSMP and of ‘tabular’ and ‘other’ morphotypes of *Acropora* in the central and northern GBRMP. *Acropora*, again, was almost entirely absent from the southern GBRMP, and *Seriatopora* was largely absent from northern and central CSMP communities (Fig. 2.3; Table S2.1). In contrast to the crest communities, branching *Porites* was a significant

component of the northern CSMP slope community, but was not common elsewhere (Fig. 2.3; Table S2.1). Other Scleractinian taxa also made up a significant component of the northern CSMP (Fig. 2.3; Table S2.1), consisting of a variety of taxa, dominated by *Pavona* (Fig. S2.1).

2.4 Discussion

Given their isolation from major anthropogenic pressure and coastal processes, oceanic reefs in the CSMP were expected to harbour relatively pristine coral assemblages, characterised by high coral cover (Barott et al. 2010), with more diverse population and community structure (Connell 1997). While high coral cover (> 30%) was recorded on some remote, oceanic reefs in the northern and southern regions of the CSMP, coral cover was not consistently high across the marine park. Coral cover in the central CSMP was low and has been recorded to be < 20% since the 1980's (Ayling and Ayling 1985; Oxley et al. 2003, 2004, 2005; Ceccarelli et al. 2008, 2009; Edgar et al. 2015; Stuart-Smith et al. 2018; Harrison et al. 2019). Low coral cover, and the notable absence of *Acropora* spp in the central CSMP have generally been attributed to the high frequency of cyclones that affect this region (Oxley et al. 2004; Brewer et al. 2007). Cyclones can cause direct coral loss (Puotinen et al. 2020), but also prolong recovery through the destabilisation of substrates, and breakage (fission) of large, gravid colonies (Harmelin-Vivien 1994). CSMP reefs have also been subject to severe marine heatwaves in 2002, 2004, 2016 and 2017, which may have caused extensive coral bleaching and coral mortality, especially in the northern and central regions of the CSMP (Oxley et al. 2003, 2004, 2005; Stuart-Smith et al. 2018; Harrison et al. 2019).

Coral cover in the CSMP was not consistently higher than on the outer shelf reefs of the GBRMP, challenging the assumption that remoteness inherently promotes higher coral cover. Coral cover was higher on the reef crest in the central GBRMP than the reef crest in the central CSMP, whereas coral cover was similar of reef slopes between the two regions. Similarly, coral cover did not differ between marine parks on northern reef crests. Coral cover

was only consistently higher in the CSMP for both zones in the south, where coral cover in the GBRMP was exceptionally low (~5%). Like many other major coral reef systems throughout the world, there have been sustained declines in coral cover recorded on the GBRMP (e.g., Mellin et al. 2019a), which are generally ascribed to increasing rates of coral mortality caused by population irruptions of CoTS, severe tropical cyclones, and climate induced coral bleaching (De'ath et al. 2012; Mellin et al. 2019a). Indeed, severe population irruptions of CoTS in the GBRMP (Matthews et al. 2024) were responsible for the very low levels of coral cover (<5%) recorded in the southern GBRMP in 2018-2020. However, the broadly comparable coral cover in the northern and central regions between marine parks potentially reflects similar exposure to other large-scale disturbances such as cyclones and coral bleaching (Hughes et al. 2018b; Stuart-Smith et al. 2018). Like the CSMP, major bleaching events in 2016 and 2017 resulted in significant coral loss throughout much of the central and northern regions of the GBRMP (Hughes et al. 2018b). Despite this, the highest coral cover was recorded on central GBRMP reef crests, suggesting mortality was variable and/or recovery was fast (Emslie et al. 2024a). Similar coral cover between oceanic CSMP reefs and outer-shelf GBRMP reefs also likely reflects similar isolation from coastal processes that affect corals. These processes (e.g.., fluctuations in water quality) drive cross-shelf trends in coral cover, which are most pronounced between inshore and mid-outer shelf reefs (Wismer et al. 2009; Ellis et al. 2017; but see Howley et al. 2018). Therefore, variation in coral cover among regions and zones appear more reflective of recent acute disturbances than environmental gradients operating over regional and local scales.

Major disturbances not only reduce overall coral cover, but can restructure coral assemblages through differential effects among taxa (Hughes et al. 2018b; Zinke et al. 2018; Keesing et al. 2019). Fast-growing branching taxa (e.g., Acroporidae) are highly susceptible to a range of disturbances including coral bleaching (Marshall and Baird 2000), CoTS predation

(Foo et al. 2024), and mechanical damage generated by cyclones and storms (Madin et al. 2014). Thus, recently disturbed communities generally comprise very few of these susceptible taxa (Hughes et al. 2019b; Pisapia et al. 2019; Morais et al. 2021). A conspicuous absence of fragile branching corals was observed in the southern GBRMP, many sites in the central CSMP, and the northern CSMP. In these regions, coral assemblages were dominated by *Porites* and *Pocillopora*. This, combined with lower coral cover (particularly on the reef crest) suggests that recent disturbances have had a major influence on coral assemblages in these regions. In contrast, the southern CSMP had high cover of fast-growing branching taxa (i.e., *Acropora*, *Isopora*, *Seriatopora;* especially on the reef crest), suggesting there have been limited recent effects of major disturbances in this region, and/ or resilience of coral assemblages is high in these areas. While predominance of fast-growing corals is likely to facilitate higher coral cover (Emslie et al. 2024a), these coral assemblages are highly vulnerable to increasing major disturbances and future environmental change (Oliver et al. 2018; Smale et al. 2019; McWhorter et al. 2022).

Reefs with low coral cover and a lack of fast growing *Acropora* were present in both marine parks, however the isolation of CSMP reefs may result in lower recovery potential (Gilmour et al. 2013; Burn et al. 2024 [**Chapter 3**]). Reefs in the CSMP are likely reliant on self-recruitment for replenishment, given the vast distances between reefs (Ayre and Hughes 2004; Gilmour et al. 2013). However, larval retention on oceanic reefs may be relatively low owing to strong unidirectional currents (Ceccarelli et al. 2013), leaving these reefs more reliant on re-growth of remnant colonies to replenish coral cover (Warne et al. 2022). Conversely, reefs in the GBRMP likely receive larval supply from spatially proximal healthy reefs and retain a high proportion of larvae owing to the retention of water within the mosaic of GBRMP reefs (Andutta et al. 2012; Figueiredo et al. 2022; King et al. 2023). Adult coral stock has been supressed (< 20% coral cover) in the central CSMP since the 1980's (Ayling and Ayling 1985;

Oxley et al. 2003, 2004, 2005; Ceccarelli et al. 2008, 2009), which is likely a combination of the effects of persistent disturbances (i.e., cyclones and marine heatwaves) reducing coral cover and slowing recovery processes (Warne et al. 2022) and inherent constraints on recovery owing to isolation (McManus et al. 2021). In contrast, the GBRMP has undergone major fluctuations in coral cover since 2010, highlighting the effects of major disturbances, but also the capacity of reefs to recover (Emslie et al. 2024a). However, if disturbances continue to increase in their frequency, and spatial extent, this capacity for recovery may diminish (Emslie et al. 2024b).

This chapter highlights the role of major disturbances in structuring coral assemblages among latitudinal regions and zones within Australia's CSMP and GBRMP, and underscores apparent limited differences between offshore GBRMP and remote CSMP reefs. Whilst remote reefs in the CSMP have not been impacted by population irruptions of CoTS, or other chronic pressures associated with land and urban centres that affect parts of the GBRMP, corals are still impacted by severe bleaching and tropical cyclones, resulting in low coral cover at many sites. Given the inherent constraints on recovery and replenishment in the CSMP due to isolation (Gilmour et al. 2013; Burn et al. 2024 [**Chapter 3**]), it is concerning that coral cover remains low across both zones of the central CSMP. Whilst on the GBRMP, regionally low coral cover may be compensated by high cover in nearby regions (Andutta et al. 2012; McManus et al. 2021). Moreover, community composition in the central CSMP (and northern CSMP) was not dominated by fast-growing taxa (i.e., *Acropora*) important for structural complexity and recovery (e.g., *Acropora*; Ortiz et al. 2018; Morais et al. 2023). It is still unclear whether the benefits of distance from anthropogenic pressures improve resilience of remote reefs in the face of major disturbances (Smith et al. 2016; Donovan et al. 2021; Baumann et al. 2022), and further work should directly assess the impacts of disturbances in isolation, and importantly, the recovery in the aftermath at reefs throughout the CSMP. As disturbances increase in frequency and severity (Cheal et al. 2017; Frölicher et al. 2018), it is critical to

quantify contemporary coral cover and composition across large spatial scales, to identify areas of resilience and/or vulnerability to disturbance, guide effective conservation strategies tailored to specific reef zones and regions, and to act as contemporary baselines, against which to assess inevitable change in the face of escalating disturbances.

Chapter 3. Comparison of juvenile coral assemblages between Australia's Coral Sea and Great Barrier Reef Marine Parks[1]

[1]*This chapter is published as* **Burn D**, Hoey AS, Pisapia C, Chandler JF, Thompson CA, Pratchett MS (2024) Comparison of juvenile coral assemblages between Australia's Coral Sea and Great Barrier Reef Marine Parks. *Coral Reefs*. 43: 1331-1343

3.1 Introduction

The persistence and replenishment of scleractinian coral populations is fundamentally dependent on the supply and settlement of larvae, as well as subsequent growth and survival of juvenile corals (Pearson 1981; Doropoulos et al. 2015; Holbrook et al. 2018). Replenishment of coral populations is particularly important given recent increases in the frequency and diversity of disturbances that are causing elevated rates of coral mortality (Gardner et al. 2003; De'ath et al. 2012; Ortiz et al. 2018; Mellin et al. 2019a; Bozec et al. 2022). Interspecific differences in recovery and replenishment capacity will also have a major influence on the structure of coral assemblages (Gilmour et al. 2013; Pratchett et al. 2020). The ability for coral populations to recover and reassemble following extensive coral loss may be constrained by larval supply, which may be extremely limited following loss of brood-stock (Chong-Seng et al. 2014; Hughes et al. 2019a), and the early post-settlement survival of recruits (Chong-Seng et al. 2014). As such, the density of juvenile corals may be a useful proxy for the recovery potential of coral populations following disturbance (Penin et al. 2010). With disturbances predicted to increase in frequency and severity (Oliver et al. 2018; Walsh et al. 2019), it is becoming increasingly important to understand differential recovery capacity among reefs and species (e.g., Gilmour et al. 2013).

Where coral recovery and replenishment are conditional upon larval supply and recruitment, the spatial arrangement of reefs, as well as the extent and severity of disturbances, are critical determinants of resilience (Gilmour et al. 2013). This will further affect which species are likely to recover and predominate in the aftermath of disturbances (e.g., (Underwood et al. 2009, 2020). Within more proximal reef systems (where there is limited distance between individual reefs, and/ or continental fringing reefs), coral larvae are likely to be readily exchanged among reefs (Wolanski and Spagnol 2000; Cetina-Heredia and Connolly 2011; Andutta et al. 2012; Golbuu et al. 2012; Figueiredo et al. 2022). In contrast, geographically isolated reefs are likely to be more reliant on self-recruitment at the scale of individual reefs (Jones et al. 2009; Gilmour et al. 2013). Following spatially discrete disturbances, such as cyclones, there is limited risk of compromising all source populations on proximal reefs, whereas comprehensive coral mortality may occur on isolated reefs, leading to recruitment limitation and protracted recovery (Gilmour et al. 2013). However, isolated, oceanic reefs, may also benefit from increased distance from land and corresponding anthropogenic pressures (Box and Mumby 2007; Fabricius et al. 2008; Adjeroud et al. 2010; Thompson et al. 2014). These favourable conditions may play a vital role in facilitating the recovery process, potentially compensating for recruitment limitation.

Coral replenishment is increasingly measured based on the abundance of juvenile corals (corals between 1-5cm diameter; Jonker et al. 2019), which are typically distinguished at the genus or family level. Surveying corals of this size takes into account potentially high levels of early post-settlement mortality experienced by newly settled recruits (Penin et al. 2010) and as such, may be a better proxy of recovery capacity (Graham et al. 2015; Evans et al. 2020). Indeed, the relative abundance of adult corals correlates more with the composition of juvenile corals, rather than recently settled recruits (Penin et al. 2007; Adjeroud et al. 2010; Jonker et al. 2019; Pedersen et al. 2019). Relationships between adult and juvenile corals (hereafter

juvenile-adult relationships) have been assessed within or among sites or reefs located hundreds of metres to tens of kilometres apart (Chiappone and Sullivan 1996; Edmunds 2000; Penin et al. 2010; Penin and Adjeroud 2013; Pedersen et al. 2019), where generally positive relationships suggest that recruitment from external sources may be limited. High local retention and self-recruitment is also evident at the reef scale in high resolution hydrodynamic models (i.e., 100-200m) (Figueiredo et al. 2022; King et al. 2023; Saint-Amand et al. 2023). This is likely exacerbated on isolated reefs. Apparent differences in connectivity between isolated and more proximal reef systems may lead to stronger juvenile-adult relationships on isolated reefs, owing to the increased reliance on self-recruitment.

Beyond the influence of stock-recruitment relationships, juvenile coral abundance varies spatially, in response to a variety of biotic and abiotic factors, many of which differ substantially between geographically isolated, oceanic reefs compared with more proximal, coastal reefs (Jonker et al. 2019; Couch et al. 2023). For example, high wave exposure characteristic of oceanic, isolated reefs (particularly on exposed crest habitats) may lead to lower juvenile coral abundance (Cardini et al. 2012; Mumby et al. 2013; Couch et al. 2023) than on coastal, proximal reefs. Conversely, oceanic, isolated reefs are expected to be less exposed to sedimentation and eutrophication which may benefit newly settled corals (Hunte and Wittenberg 1992; Koop et al. 2001). These differences in environmental factors may lead to contrasting recovery capacities between isolated and proximal reefs, although this has never been tested. Variables which influence the abundance and community structure of juvenile corals may also vary with latitude (Jonker et al. 2019; Nozawa et al. 2021), where coral recruitment and juvenile densities may be decreasing at low latitudes owing to climate change related disturbances (Price et al. 2019; Couch et al. 2023).

The purpose of this study was to compare the abundance and composition of juvenile scleractinian corals between geographically isolated reefs in Australia's Coral Sea Marine Park

(CSMP) and more proximal reefs of Australia's Great Barrier Reef Marine Park (GBRMP), with the aim of better understanding differences (or similarities) in resilience, and especially recovery capacity within and between these two distinct reef systems. First, we test the hypothesis that the relative isolation of CSMP reefs from many human- and land-based pressures, combined with oceanic conditions favourable for settlement (such as improved water quality), may result in higher juvenile coral densities than reefs in the GBRMP. However, following several major bleaching events (Oxley et al. 2003, 2005; Harrison et al. 2019; Hoey et al. 2021; Hughes et al. 2021; Burn et al. 2023 [**Chapter 4**]; Huang et al. 2023) and frequent cyclones (Brewer et al. 2007; Ceccarelli et al. 2013), coral cover on some reefs, especially in the CSMP, remains low. This, combined with anticipated constraints on connectivity among the widely separated reefs in the CSMP (Ceccarelli et al. 2013), may outweigh the positive effects of isolation from coastal processes and anthropogenic pressures, increasing vulnerability to major disturbances. In comparison, the high density and close proximity of individual reefs within the GBRMP may underpin strong population recovery following acute disturbances and localised coral depletion (Hughes et al. 2003; Graham et al. 2006), as there is presumed to be very high levels of inter-reef connectivity in the GBRMP (e.g., Hock et al. 2017; Condie et al. 2021), although this is predicted to decrease under future climate change (Figueiredo et al. 2022). Thus, we also test the hypothesis that juvenile densities will be positively associated with adult cover, where isolated CSMP reefs might exhibit a stronger relationship due to the increased reliance on self-recruitment and local retention, such that reefs with low coral cover and/or poor connectivity may have reduced juvenile abundance regardless of environment. With escalating disturbances, largely driven by emerging effects of global climate change that affect even the most isolated reef systems (Baumann et al. 2022; Gilmour et al. 2022), it is imperative to understand whether isolated reefs might have a higher or lower recovery capacity than more proximal, coastal systems.

3.2 Methods

3.2.1 Study sites

The CSMP lies within Australia's exclusive economic zone, east of the Queensland coast and adjacent to the GBRMP (Fig. 3.1). The CSMP is Australia's largest marine park, covering 989,836km^2 and spanning approximately 15° of latitude and 15° of longitude. There are 34 reef systems (containing numerous individual coral reefs) within the CSMP that collectively cover 15,000km^2 (or 1.5% of the total CSMP area) with individual reefs separated from the mainland by >160km and from one another by large expanses of abyssal waters. In comparison, the GBRMP lies between the CSMP and the Queensland coast of Australia, and covers an area of 344,400km^2, consisting of ~3000 individual coral reefs. Prevailing currents run from East to West from the CSMP toward the GBRMP (Choukroun et al. 2010), with some counterflow (e.g., Coral Sea Counter Current at 16°S) moving Eastward, although this is much weaker (Qiu et al. 2009). This, combined with the large distances between CSMP reefs, suggests poor connectivity among reefs in the CSMP.

Sampling was undertaken at 17 reefs throughout the CSMP and 17 reefs on the outer shelf of the GBRMP between February 2019 and March 2020 (Fig. 3.1). Reefs were selected to gain as wide a spatial representation of each marine park as possible, though only 2 reefs were surveyed in the southern section of the GBRMP, which may not be wholly representative of this region. Between two and 10 sites were surveyed at each reef, giving a total of 124 unique sites. Where sites were surveyed in both years (n = 24), results were averaged across years. Sites were generally positioned on the outer edge of reefs, where there was continuous solid reef matrix with a clearly defined reef crest, and a reef slope extending into deeper habitat. An extensive marine heatwave occurred causing mass coral bleaching throughout the CSMP and GBRMP in March 2020, but surveys were conducted before coral mortality exceeded

background levels (Burn et al. 2022). Thus, data from 2020 is not confounded by any impacts of bleaching.

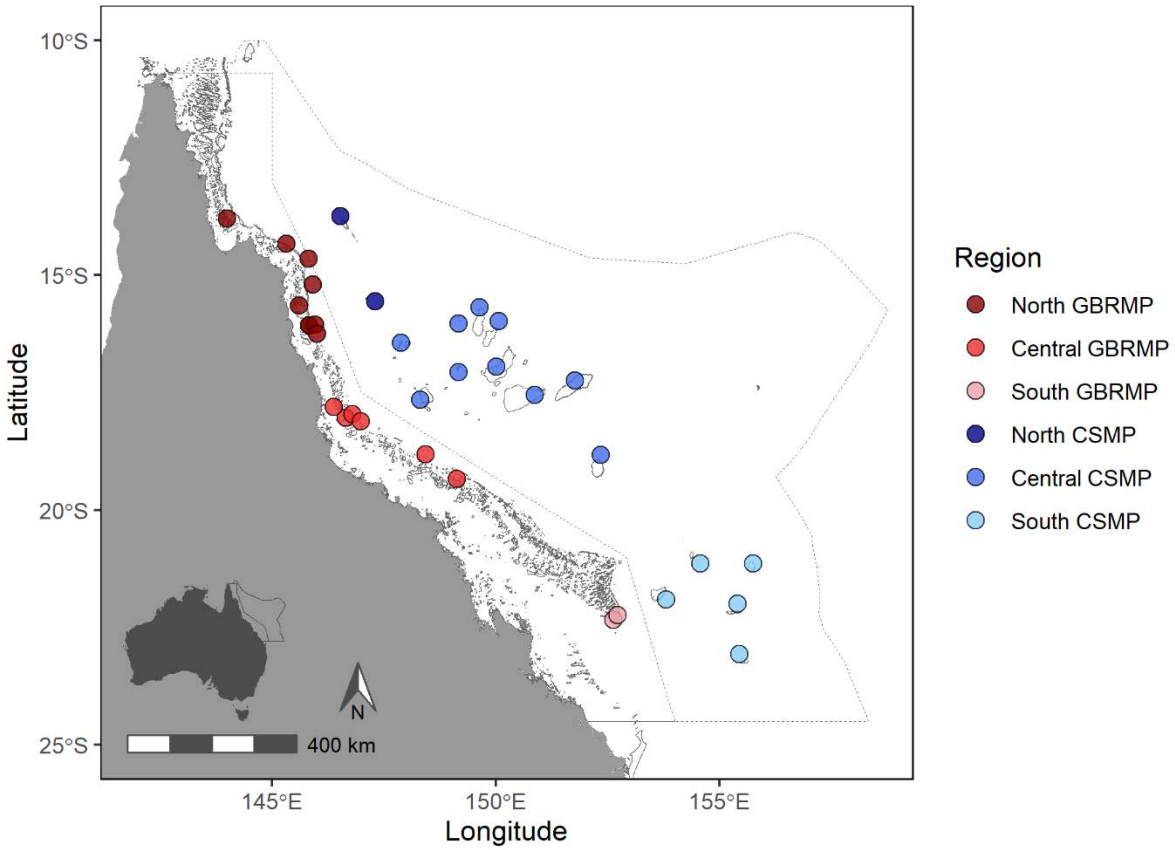


Figure 3.1: Reefs (n = 34) in the CSMP (blue) and GBRMP (red) surveyed in 2019-2020. Shades of colour represent latitudinal regions for each marine park. Dashed lines represent marine park boundaries, with the GBRMP adjacent to the Queensland coast and the CSMP directly to the East

3.2.2 Juvenile coral surveys

Juvenile corals were surveyed using three replicate 10 x 1m belt transects on both the reef slope (8-10m depth) and the reef crest (2-3m depth) (hereafter referred to as habitat), at each of 124 sites (n = 885). Transects were separated by ~45m and coincided with the first 10m of consolidated habitat (i.e., sections of sand or rubble were not surveyed, to ensure consistency

of benthic habitat type among surveys) of 50 m point-intercept transects used to determine benthic cover (see below). All juvenile corals 1-5cm maximum diameter falling wholly or mostly (i.e., >50% of the colony) within the belt were counted and identified to genus. Where possible, surveys were restricted to juvenile corals that directly resulted from larval recruitment, excluding small remnant corals resulting from extensive partial mortality and fragmentation of formally large colonies; however, it is not easy to distinguish between larval recruits versus remnants for some taxa (e.g., massive *Porites*). Therefore, it may be possible that some of the juveniles reported here are artefacts of partial mortality and fragmentation.

3.2.3 Percent cover of common coral taxa

To determine percent cover of different coral taxa, three replicate 50m point intercept transects were undertaken at each habitat within each site (n = 6 per site), following the depth contour and separated by ~5m. Benthic substrate and organisms occurring directly below the tape at 50cm intervals were placed into categories (Sand, Rubble, Pavement, Hard Coral, Soft Coral, Macroalgae, Sponge, and Other). Organisms were identified to the lowest taxonomic unit possible, with corals and macroalgae identified to genus (n = 100 points per transect). Percent coral cover was calculated by dividing the number of points falling on hard coral by the total number of points, minus the number of points falling on sand. This provides a measure of hard coral cover as a function of available hard substrate. This estimate of percent coral cover was calculated for each of the major genera, *Porites*, *Acropora* and *Pocillopora*.

3.2.4 Statistical analyses

<u>Spatial variation in juvenile abundance across the GBRMP and CSMP</u>

Spatial variation in the abundance of juvenile corals was analysed using Generalized Linear Mixed Effects Models (GLMMs), comparing between marine parks (GBRMP and CSMP), among latitudinal regions (three levels) and between habitats (crest and slope).

Separate analyses were undertaken for *Porites*, *Acropora*, *Pocillopora*, and 'other juvenile taxa', which were pooled across the remaining taxa. For *Porites*, *Acropora* and *Pocillopora*, models were fit with a three-way interaction between marine park, region and habitat, with nested random effects of site within reef. For 'other juvenile taxa' the interaction between marine park and region was not included as it did not improve the fit of the model according to the corrected Akaike Information Criterion (AICc) (Table 3.1). Abundance of juvenile corals were modelled against a negative binomial distribution with a log link function to account for the overdispersion in the data.

Table 3.1 Corrected Akaike Information Criterion (AICc) scores and degrees of freedom (df) for combinations of fixed effects tested within each model. Models used for analyses are highlighted in bold.

Model	df	AICc
Acropora ~ 1 + (1|Reef/Site)	4	4004.3
Acropora ~ MarinePark + (1|Reef/Site)	5	3996.6
Acropora ~ MarinePark * Region + (1|Reef/Site)	9	3997.5
***Acropora* ~ MarinePark * Region * Habitat + (1|Reef/Site)**	**15**	**3931.7**
Porites ~ 1 + (1|Reef/Site)	4	4509.1
Porites ~ MarinePark + (1|Reef/Site)	5	4509.2
Porites ~ MarinePark * Region + (1|Reef/Site)	9	4495.7
***Porites* ~ MarinePark * Region * Habitat + (1|Reef/Site)**	**15**	**4482.7**
Pocillopora ~ 1 + (1|Reef/Site)	4	2905.6
Pocillopora ~ MarinePark + (1|Reef/Site)	5	2904.1
Pocillopora ~ MarinePark * Region + (1|Reef/Site)	9	2901.6
***Pocillopora* ~ MarinePark * Region * Habitat + (1|Reef/Site)**	**15**	**2850.7**
OtherTaxa ~ 1 + (1|Reef/Site)	4	4177.9
OtherTaxa ~ MarinePark + (1|Reef/Site)	5	4177.5
OtherTaxa ~ MarinePark + Region + (1|Reef/Site)	7	4162.9
OtherTaxa ~ MarinePark * Region + (1|Reef/Site)	9	4162
OtherTaxa ~ MarinePark + Region * Habitat + (1|Reef/Site)	**10**	**4096.1**

For each model, combinations of fixed and random effects were tested using maximum likelihood (REML = FALSE) and retained only if they improved the fit of the model, based on the AICc (Table 3.1). Each model was validated, and goodness of fit was checked visually and statistically, including checks of simulated residuals and dispersion, using the 'DHARMa' package (Hartig 2021), and tested for zero-inflation using the 'performance' package (Lüdecke et al. 2021). Post-hoc Tukey's pairwise comparisons were calculated using estimated marginal means in the 'emmeans' package (Lenth 2021) to test for significant differences in juvenile coral abundances among fixed effects.

Juvenile-adult relationships between common taxa within marine parks.

The relationship between percent coral cover and juvenile abundance was assessed for each of three most abundant taxa (*Porites*, *Acropora*, and *Pocillopora*), using Spearman's Rank Correlation Coefficients. Separate analyses were undertaken for each marine park; GRBMP (n = 17 reefs) and CSMP (n = 17 reefs), to test whether relationships were stronger or weaker among more isolated reef systems. Percent cover of each taxon from point-intercept transects and juvenile abundance of each taxon from belt transects were averaged across transects, habitats, and sites, to gain a reef-wide percent cover and average juvenile abundance for each taxon.

All statistical analyses were performed in the R statistical and graphical environment version 4.1.1 (R Core Team, 2021), with models built using the "glmmTMB" package (Brooks et al. 2017). Data wrangling was completed in the 'TidyVerse' (Wickham et al. 2019), with plots created using 'ggplot2' (Wickham 2016). GLMMs were not fit for the juvenile-adult relationships due to the models not converging.

3.3 Results

3.3.1 Spatial variation in juvenile coral assemblages

A total of 14,711 juvenile corals from 42 distinct genera were surveyed across 34 reefs (5,265 juvenile corals in the GBRMP and 9,446 in the CSMP) in 2019 and 2020. This equated to an average of 23.72 (± 1.86 SE) and 13.99 (± 0.72 SE) juvenile corals 10m-2 in the GBRMP and CSMP, respectively. Juvenile coral assemblages were dominated by *Porites* (5,376 juveniles; 36.5%), *Acropora* (4,399; 29.9%) and *Pocillopora* (1,555; 10.6%). The remaining 39 taxa were pooled and are hereafter referred to as 'other juvenile taxa', together comprising 23% of the juvenile community.

Whilst densities of juvenile corals were higher in the GBRMP compared with the CSMP for all 4 taxa (*Porites*, *Pocillopora*, *Acropora* and others), this pattern was not consistent across all latitudinal regions or habitats, as evidenced by the interactions in each model (Fig. 3.2; Table 3.1; Table S3.1). Notably, there was a significantly higher density of juvenile *Porites* colonies in the GBRMP, compared to the CSMP, but only in the northern region (Fig. 3.2a; Table 3.2). Significantly more *Acropora* and *Pocillopora* juveniles were also found in the GBRMP, but only in the central regions and only on the reef crest (Fig. 3.2b, c; Table 3.2). For the other juvenile taxa, there were significantly more juveniles in the GBRMP compared to the CSMP across all latitudinal regions and both habitats (Fig. 3.2d; Table 3.2).

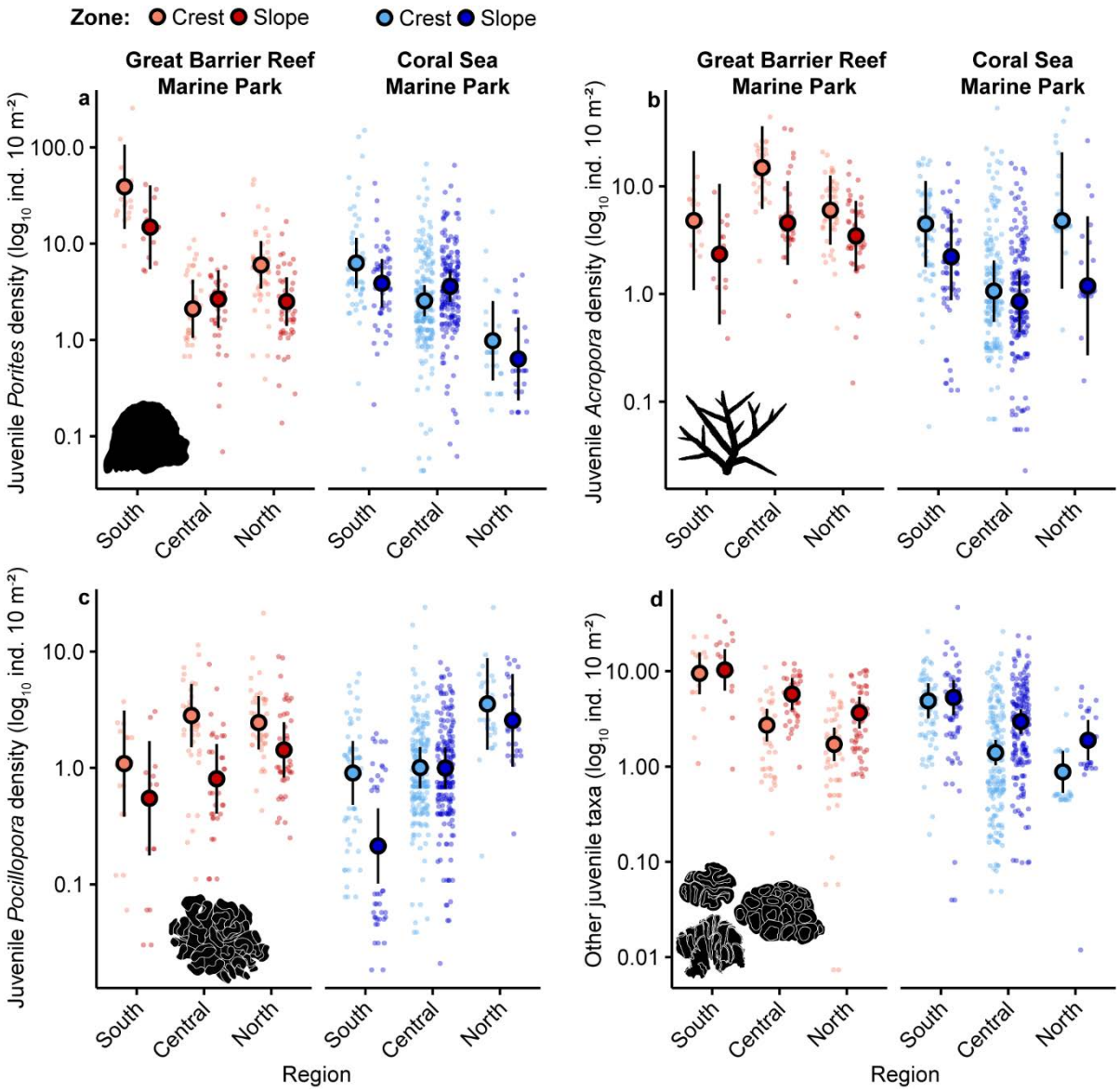


Figure 3.2 Marginal effects plots showing the interactive effects of marine park, habitat and latitudinal region on the density of juvenile (a) *Porites*, (b) *Acropora*, (c) *Pocillopora*, and (d) other juvenile taxa. Bold circles represent estimated marginal means with error bars indicating 95% confidence intervals. Faded points represent model fitted predictions with overlaid residuals. Colours represent marine park (red = GBRMP, blue = CSMP) and shades represent habitat (dark = slope; light = crest). Estimated marginal means and predicted residuals account for the fixed and random effects included in the GLMMs

Table 3.2: Estimated marginal mean density ($10m^{-2}$) of juvenile corals in each marine park. Pairwise contrasts and p values are provided for the comparison between marine parks for each region and habitat for each of four GLMMs. * denotes statistically significant differences

GLMM	Region	Habitat	Estimated marginal means (juveniles $10m^{-2}$) GBRMP	Estimated marginal means (juveniles $10m^{-2}$) CSMP	Contrast estimate	p value
Porites	Northern	Crest	6.035	0.982	5.053	0.0053 *
		Slope	2.502	0.634	1.868	0.0209 *
	Central	Crest	2.106	2.555	-0.448	0.6148
		Slope	2.661	3.599	-0.938	0.4142
	Southern	Crest	39.051	6.309	32.742	0.1034
		Slope	14.848	3.882	10.966	0.1525
Acropora	Northern	Crest	5.996	4.796	1.2	0.7759
		Slope	3.461	1.191	2.271	0.1545
	Central	Crest	14.875	1.065	13.81	0.0398 *
		Slope	4.563	0.851	3.712	0.0779
	Southern	Crest	4.803	4.469	0.33	0.9365
		Slope	2.339	2.216	0.124	0.9524
Pocillopora	Northern	Crest	2.449	3.549	-1.1	0.5342
		Slope	1.428	2.563	-1.135	0.3681
	Central	Crest	2.82	1.008	1.813	0.0494 *
		Slope	0.807	0.997	-0.191	0.5852
	Southern	Crest	1.09	0.905	0.185	0.776
		Slope	0.548	0.214	0.335	0.3044
Other juvenile taxa	Northern	Crest	1.71	0.88	0.832	0.0025 *
		Slope	3.67	1.89	1.785	0.0021 *
	Central	Crest	2.72	1.4	1.323	0.0098 *
		Slope	5.77	2.96	2.801	0.0094 *
	Southern	Crest	9.52	4.89	4.624	0.0176 *
		Slope	10.33	5.31	5.017	0.0172 *

Despite high variability in the density of juvenile corals within regions (at the site and reef level), there were broad latitudinal patterns, especially in the CSMP (Fig. 3.2). In the CSMP, *Porites* was significantly less abundant in the north compared to the south for both habitats (Fig. 3.2a). However, there was no difference among latitudinal regions in the GBRMP. In contrast, *Pocillopora* juveniles appeared to increase in abundance in the north, however this increase was only statistically significant between the south and central regions

on the reef slopes of the CSMP (Fig. 3.2c). On average, there were less juvenile *Acropora* in the central CSMP than other regions, however this was not statistically significant for either habitat (Fig. 3.2b). In contrast, the central region of the GBRMP harboured the highest average density of juvenile *Acropora* for both habitats, although this was also not statistically significant (Fig. 3.2b). Similar to *Porites*, other juvenile taxa were significantly less abundant in the north compared to the south for both habitats, however this was the case in both marine parks (Fig. 3.2d).

On average, total juvenile density was highest on the reef crest (18.84 juveniles ± 1.27 SE) compared to the reef slope (13.98 ± 0.68 SE), however this varied among taxa and latitudinal region (Fig. 3.2). Two regions (central and north) in the GBRMP had a significantly higher density of juvenile *Acropora* on the reef crest compared to the reef slope (Fig. 3.2b), and three regions (central and north GBRMP and south CSMP) had significantly higher densities of juvenile *Pocillopora* on the reef crest compared with the slope (Fig. 3.2c). For other juvenile taxa, the opposite trend was observed, with significantly more juveniles recorded on the reef slope as opposed to the reef crest for each region of both marine parks (Fig. 3.2d). Juvenile *Porites* were significantly more abundant on the reef crest in the northern GBRMP, but significantly more abundant on the slope in the central region of the CSMP (Fig. 3.2a).

3.3.2 Juvenile-adult relationships for common coral taxa

In both marine parks, there was evidence of a positive relationship among reefs between percent coral cover and average density of juveniles for *Acropora* and *Pocillopora*, with the relationship being stronger for *Pocillopora* than *Acropora* (Fig. 3.3b, c). However, juvenile *Porites* showed no significant juvenile-adult relationship in both parks (Fig. 3.3a). Coral cover for each of the three taxa varied between parks, with higher mean cover of *Acropora* in the GBRMP (10.4% ± 0.75 SE) compared with the CSMP (5.7% ± 0.26 SE), but marginally lower

cover of *Porites* and *Pocillopora* in the GBRMP (*Porites*: 3.6% ± 0.22 SE; *Pocillopora*: 3.3 % ± 0.27 SE), compared with the CSMP (*Porites*: 4.8% ± 0.27 SE; *Pocillopora*: 4.7% ± 0.2 SE).

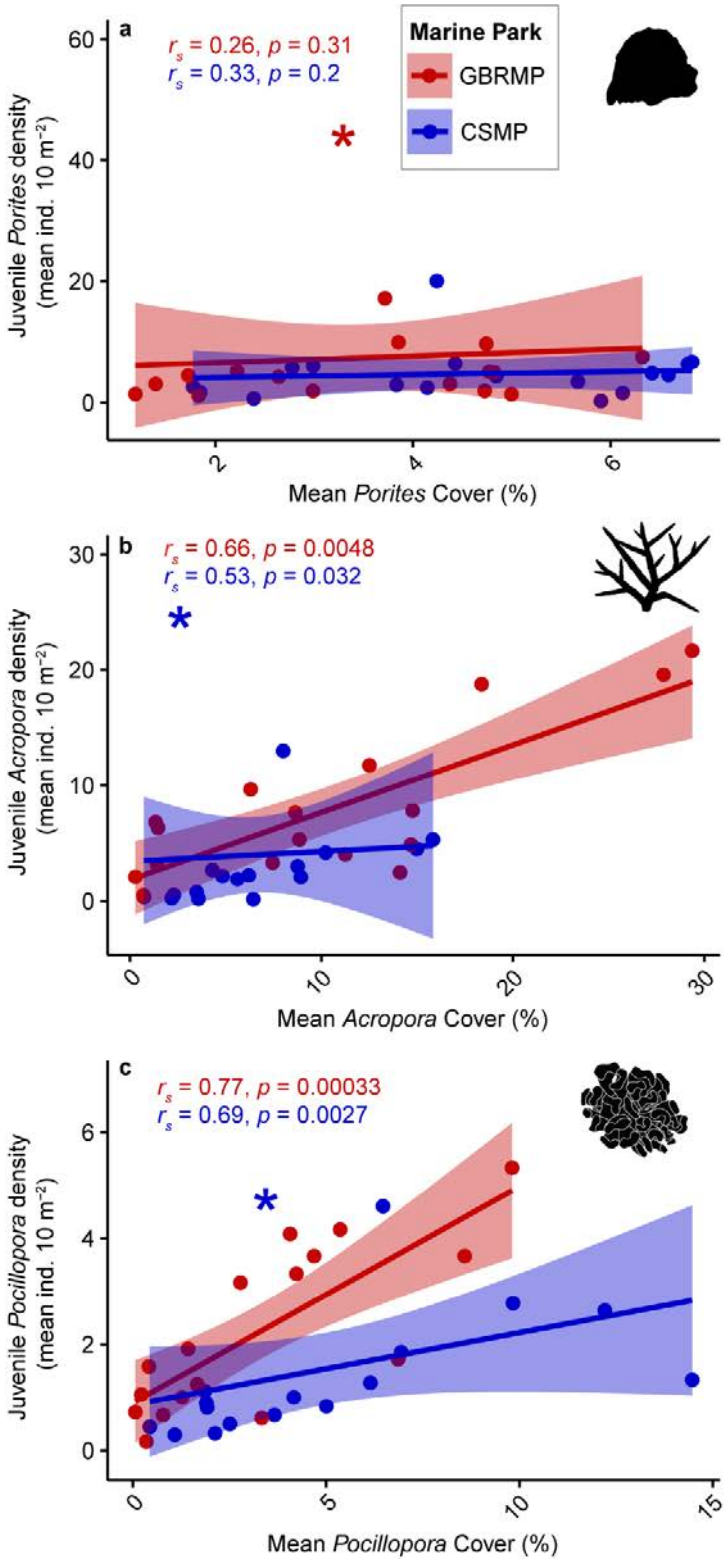


Figure 3.3: The relationship between reef-wide percent cover and mean density of juveniles (10m^{-2}) for (a) *Porites*; (b) *Acropora*; and (c) *Pocillopora*. Colours represent marine parks (red = GBRMP, blue = CSMP). Ribbons represent 95% confidence intervals. Text refers to the r_s (Spearman's Rank Correlation Coefficient), with corresponding p-values.

3.4 Discussion

This study revealed that juvenile corals were much less (42% less) abundant on isolated reefs in Australia's CSMP, compared with more spatially proximal outer shelf reefs of Australia's GBRMP. Comparatively low abundance of juvenile corals in the CSMP is likely a result of a combination of factors, but low adult coral cover found at many reefs is likely limiting local larval production and supply (Gilmour et al. 2013). This may be further compounded by limited connectivity among the widely separated reefs in the CSMP, constraining larval supply from external sources (Ceccarelli et al. 2013; Gilmour et al. 2013; Payet et al. 2024). It is also possible that, despite the relatively high distance from many localised anthropogenic pressures and expected favourable oceanic conditions, there are some factors negatively affecting the settlement and survival of coral recruits in the CSMP (e.g., high abundance of excavating parrotfish *Bolbometapon muricatum*; Penin et al. 2010; Trapon et al. 2013b). Regardless of the cause, low abundances of juvenile corals likely constrain recovery capacity for CSMP reefs, making them particularly vulnerable to sustained and ongoing disturbances.

Reefs in the central CSMP were particularly depauperate of juvenile *Acropora*; a taxon likely to contribute to fast growth and recovery of coral cover in the aftermath of disturbances (Linares et al. 2011; Morais et al. 2021). This likely reflects the suppressed adult stock of *Acropora* in this region, which is attributable to the disproportionate vulnerability of these corals to recurrent cyclones and mass coral bleaching (Loya et al. 2001; Madin and Connolly 2006; Hughes et al. 2018b), which have impacted this area (Oxley et al. 2005; Brewer et al. 2007; Harrison et al. 2019; Burn et al. 2023 [**Chapter 4**]). While many *Acropora* corals produce larvae that are capable of extensive dispersal (Connolly and Baird 2010; Miller et al. 2020; Figueiredo et al. 2022), the large scale of stock depletion in the central CSMP, combined

with inherent constraints to larval exchange among reefs, suggest that there is unlikely to be significant larval recruitment and recovery of *Acropora* corals in this region.

The most common juvenile genus recorded on CSMP reefs was *Porites* (37%), which is among the slowest growing taxa (Pratchett et al. 2015) and will contribute little to increasing coral cover following disturbances (Pratchett et al. 2020). We report relatively high abundances of juvenile *Porites* colonies, combined with low percent cover of *Porites*. This may be partly due to the difficulty in differentiating between true juveniles and fission of larger colonies due to partial mortality. Partial mortality is particularly prevalent in *Porites* (Pisapia and Pratchett 2014), which can result in many small remnant colonies, potentially mistaken here as juveniles. Naturally slow growth rates in this taxon (Pratchett et al. 2015) combined with possible physiological constraints following injury (Henry and Hart 2005; but see Graham and van Woesik 2013) may explain low percent cover reported herein. The community composition of juvenile corals in the central CSMP reinforces the notion that this region has poor recovery capacity, which is supported by the persistently low (< 20%) records of coral cover since the 1980's (Ayling and Ayling 1985; Oxley et al. 2003, 2004, 2005; Ceccarelli et al. 2008, 2009; Hoey et al. 2020, 2021).

Whilst abundance of juvenile corals was higher on the GBRMP compared with the CSMP, recorded densities (~2.4 juvenile corals m^{-2}) are low compared to many published studies. Previously in the GBRMP, 6.9 juvenile corals m^{-2} were recorded on the mid-continental shelf in 2009 (Trapon et al. 2013b, 2013a), with substantially more recorded on the outer- continental shelf in 2008 (11.2 juvenile corals m^{-2}; Jonker et al. 2019) and 2019 (6.3 - 26.9 juvenile corals m^{-2}; Emslie et al. 2019). However, the methods employed in the latter two studies account for available substrate (excluding substrate not covered with crustose coralline algae or turf algae), which may inflate juvenile abundances when compared with those reported here. Nevertheless, our estimates of juvenile abundance are among the lowest reported,

particularly when compared with other Indo-Pacific reefs (Table 3.3). Juvenile abundance was comparatively low at several Caribbean locations (Table 3.3), as well as the Maldives and Seychelles archipelagos in the aftermath of the 2016 bleaching event, and Wake Atoll and the Phoenix Islands; two other remote, isolated Pacific locations (Table 3.3). The low densities of juvenile corals reported herein may reflect the impact of recent cumulative disturbances occurring in the GBRMP and CSMP (De'ath et al. 2012; Mellin et al. 2019a), and may be reflective of subsequent loss of recovery capacity, even on well-connected reefs (Graham et al. 2015; Ortiz et al. 2018; Hughes et al. 2019a).

Table 3.3: Juvenile coral densities reported in the literature. All densities have been standardised to abundance $1m^{-2}$. Means provided are taken from the text or extracted from figures. The sampling unit for each dataset is provided to clarify when means were extrapolated up or down.

Region	Location	Year	Mean Juvenile density (m^{-2})	Unit displayed	Sampling unit	Citation
Caribbean	Curacao, Bonaire	1974 – 1975	15, 18	Curacao mean, Bonaire mean	$1m^2$ quadrats	Bak and Engel 1979
Caribbean	Florida	1994	< 1 – 4	Range of site level means	$1m^2$ quadrats	Miller et al. 2000
Caribbean	Florida	1993 – 1994	1.18 – 3.74	Range of site level means	$1m^2$ quadrats	Chiappone and Sullivan 1996
Caribbean	Florida	1995	7.6 – 8.4	Range of depth level means	$0.25m^2$ quadrats	Edmunds et al. 2004
Caribbean	Jamaica, USVI	1994 – 1995	5.2 – 18.1	Range of site level means	$0.25m^2$ and $1m^2$ quadrats	Edmunds and Bruno 1996
Caribbean	USVI	1994 – 2001	13.84 – 21.6	Range of year level means	$0.25m^2$ quadrats	Edmunds 2004
Caribbean	Various countries (no sea urchins present)	2003 – 2004	2.5 – 12.9	Range of site level means in algal zones	$1m^2$ quadrats	Carpenter and Edmunds 2006
Caribbean	Various countries (sea urchins present)	2003 – 2004	4.5 – 32.3	Range of site level means in urchin zones	$1m^2$ quadrats	Carpenter and Edmunds 2006
Indo-Pacific	American Samoa	2015 2018	4.8 (0.41) 5.7 (0.56)	Mean (± s.e)	$1m^2$ quadrats	Couch et al. 2023
Indo-Pacific	CSMP	2019 – 2020	1.39 (± 0.07)	Mean (± s.e)	10m x 1m belt transect	Present study
Indo-Pacific	French Polynesia	2003	7.9	Mean	10m x 1m belt transect	Penin et al. 2007
Indo-Pacific	French Polynesia	2004	6.4	Mean	10m x 1m belt transect	Penin and Adjeroud 2013

Indo-Pacific	GBRMP	2019 – 2020	2.4 (± 0.18)	Mean (± s.e)	10m x 1m belt transect	Present study
Indo-Pacific	Line Islands	2015 2018	4.2 (0.52) 8.6 (0.81)	Mean (± s.e)	1m^2 quadrats	Couch et al. 2023
Indo-Pacific	Maldives	1999	29	Mean	0.09m^2 quadrats	McClanahan 2000
Indo-Pacific	Maldives	2000 – 2002	~3.32 – 7.96	Range of means	1m^2 quadrats	Bianchi et al. 2006
Indo-Pacific	Maldives	2006 – 2007	17.4 – 38.2	Range of depth and reef type means	0.72 m^2 quadrats	Cardini et al. 2012
Indo-Pacific	Maldives	2017	2.88 (± 0.97)	Mean (± s.e)	10m x 1m belt transect	Pisapia et al. 2019
Indo-Pacific	Main Hawaiian Islands	2013 2016 2019	7.3 (0.75) 5.8 (0.81) 10.9 (1.20)	Mean (± s.e)	1m^2 quadrats	Couch et al. 2023
Indo-Pacific	New Caledonia	2007	5.6	Total mean	10m x 1m belt transect	Adjeroud et al. 2010
Indo-Pacific	North Marianas Islands	2014 2017	8.2 (0.68) 13.2 (1.23)	Mean (± s.e)	1m^2 quadrats	Couch et al. 2023
Indo-Pacific	Phoenix Islands	2015 2018	3 (0.85) 1.4 (0.61)	Mean (± s.e)	1m^2 quadrats	Couch et al. 2023
Indo-Pacific	Seychelles	2008 – 2017	12.3 12.8 4.2	Mean in 2008 Mean in 2011 Mean in 2017	0.25m^2 quadrats	Dajka et al. 2019
Indo-Pacific	South Marianas Island	2014 2017	9.2 (0.96) 10.3 (0.82)	Mean (± s.e)	1m^2 quadrats	Couch et al. 2023
Indo-Pacific	Wake Atoll	2014 2017	1.5 (0.33) 1.4 (0.26)	Mean (± s.e)	1m^2 quadrats	Couch et al. 2023
Red Sea	Eilat, Israel	2000 – 2001	42.09 – 172.92	Range of site level means	3m x 0.2m belt transect	Glassom and Chadwick 2006

Positive relationships between juvenile and adult corals were found for *Acropora* and *Pocillopora*, but not for *Porites* for both the GBRMP and CSMP, with the relationships being stronger in the GBRMP compared to the CSMP. This finding contradicts our initial hypothesis that the isolation of CSMP reefs might lead to a greater reliance on self-recruitment and local retention, thus strengthening the relationship. Stock-recruitment relationships for corals are expected to be strong at the reef scale regardless of isolation as genetic evidence suggests most larvae are of local origin (Hughes et al. 2000; Ayre and Hughes 2004; Underwood et al. 2020). Whilst self-recruitment (the proportion of recruits that originated from larvae produced by the same reef) may be high on isolated reefs of the CSMP, it is likely that local retention (the proportion of larvae produced by a reef that settles on the same reef) is low, weakening stock-recruitment relationships (Burgess et al. 2014). Local retention may be greater for GBRMP reefs due to the ebb and flood of tides that might bring larvae back to natal reefs (Andutta et al. 2012), whereas larval dispersal in the CSMP may be driven by predominant unidirectional oceanic currents (Ceccarelli et al. 2013), which tend to be fast on isolated reefs (Black et al. 1990). The weaker juvenile-adult relationship for *Acropora* in the CSMP compared with the GBRMP may also be related to the limited range and low level of *Acropora* cover. At lower cover, the supply of larvae may be more variable and dependent on local hydrodynamics. If *Acropora* cover increases, larval supply may become more predictable, resulting in a stronger (likely non-linear) relationship (Gilmour et al. 2013). However, *Acropora* take at least 5 days to develop into larvae and become competent to settle, resulting in a relatively long pelagic period (i.e., in comparison with *Pocillopora*), and a higher likelihood of being flushed away from the reef of origin (Figueiredo et al. 2013). Moreover, differences in demographic or physiological traits important for reproduction, not accounted for in coral cover estimates, might account for the weaker relationships in the CSMP, such as colony size (Hughes 1984).

Remote, oceanic coral reefs are expected to be isolated from most local anthropogenic stressors (e.g., poor water quality, coastal development), and limited connectivity among coral assemblages on isolated reefs may also promote localised adaptation to changing environmental conditions (Marzonie et al. 2023). However, isolation can also reduce connectivity to viable sources of larval supply, constraining capacity for recovery from disturbances that are independent of coastal/human proximity (Smith et al. 2008a; Gilmour et al. 2013; Bruno and Valdivia 2016). As disturbances increase in frequency and severity (McWhorter et al. 2022), the benefits afforded by isolation may be outweighed by constraints to connectivity and resilience. Our study has revealed low abundances of juvenile corals on isolated reefs in the CSMP, in combination with low abundance of brood-stock (particularly fast-growing *Acropora*), posing a significant constraint on post-disturbance recovery capacity of isolated coral assemblages. Work on specific constraints to larval recruitment and recovery in isolated reef systems is still warranted, noting that constraints to larval supply may be further compounded (or moderated) by early post settlement growth and survival.

Chapter 4. Differential bleaching susceptibility among coral taxa and colony sizes, relative to bleaching severity across Australia's Great Barrier Reef and Coral Sea Marine Parks[2]

Publication

[2]**Burn, D.**, Hoey, A.S., Matthews, S., Harrison, H.B., Pratchett, M.S (2023) Differential susceptibility among coral taxa and colony sizes, relative to bleaching severity across Australia's Great Barrier Reef and Coral Sea marine parks. *Marine Pollution Bulletin*, 191: 114907

4.1 Introduction

Anthropogenic climate change is leading to increased incidence and severity of marine heatwaves (Hobday et al. 2016; Oliver et al. 2018; Skirving et al. 2019), which on coral reefs, is directly linked to widespread mass coral bleaching and mortality (Hughes et al. 2017, 2018a; Skirving et al. 2019). Prolonged exposure to elevated temperatures and/or extreme short-term increases in temperature can disrupt the symbiotic relationship between corals and zooxanthellae (Symbiodiniaceae), resulting in declines in intracellular densities or performance of zooxanthellae. Such declines in the densities of zooxanthallae cause the coral to appear pale or white (bleached), and greatly constrains the capacity of the coral host to obtain energy (Glynn 1984; Douglas 2003). The frequency and severity of marine heatwaves and corresponding mass-bleaching episodes has increased markedly in the last few decades (Hughes et al. 2018a, 2019b; Oliver et al. 2018) and is predicted to continue to increase under ongoing climate change (van Hooidonk et al. 2013; Skirving et al. 2019; Li and Donner 2022).

Coral taxa are widely reported to vary in their bleaching susceptibility (e.g., Baskin 1998; Loya et al. 2001). Generally, fast growing and finely branched corals (e.g., *Stylophora* and *Acropora*) are most susceptible to bleaching, whereby a very large proportion of colonies (approaching 100%) exhibit bleaching (Marshall and Baird 2000; Baird and Marshall 2002; Pratchett et al. 2013; Hughes et al. 2017; Harrison et al. 2019; McClanahan et al. 2020) and high levels of mortality (Brown and Suharsono 1990; Fujioka 1999; Loya et al. 2001; Baird and Marshall 2002). In contrast, coral taxa with massive and encrusting morphologies (e.g., *Lobophyllia* and *Porites*) appear to be more tolerant, with lower incidence of bleaching and mortality (Fisk and Done 1985; Glynn 1993; Loya et al. 2001; Baird and Marshall 2002; Pratchett et al. 2013; Hughes et al. 2017; Harrison et al. 2019; but see Guest et al. 2016). Differences in bleaching responses among taxa have been linked to a variety of traits related to both the coral host (e.g., densities of fluorescent proteins: Salih et al. 2000; mass transfer rates: van Woesik et al. 2012; respiration rates and colony integration: Baird and Marshall 2002; reviewed in Wooldridge 2014) and their photosynthetic symbionts (e.g., clade type: Rowan et al. 1997; symbiont plasticity: Grottoli et al. 2014; also see Baker 2004). Regardless of the mechanism, differential bleaching susceptibility among coral taxa in the Great Barrier Reef Marine Park (GBRMP) has resulted in dramatically altered coral communities (Johns et al. 2014; Hughes et al. 2018b, 2019a; Pratchett et al. 2020), with potential long-term consequences for ecosystem function (Richardson et al. 2018; McWilliam et al. 2020). Importantly, the cumulative effects of multiple disturbances will likely incur different community responses (Hughes et al. 2019b; Marzonie et al. 2023), though some taxa (e.g., *Acropora*) appear disproportionately susceptible to a range of disturbances (Pratchett et al. 2014; Hughes et al. 2018b; Madin et al. 2018; Keesing et al. 2019).

Coral colony size has also been suggested to influence bleaching susceptibility and subsequent mortality (Hoeksema 1991; Mumby 1999; Loya et al. 2001; Shenkar et al. 2005;

Brandt 2009; van Woesik et al. 2012; Depczynski et al. 2013; Pratchett et al. 2013; Álvarez-Noriega et al. 2018). Small corals have less resources and a smaller surface area and are therefore more likely to suffer whole colony mortality than partial mortality by any given disturbance (Madin et al. 2014). Despite this, some studies suggest small corals may be more resistant to bleaching than larger colonies (Mumby 1999; Shenkar et al. 2005; Depczynski et al. 2013) due to favourable surface area to volume ratios and/or the diversity of symbionts they harbour. Some coral species harbour a greater variety of symbiont types during early ontogeny, possibly allowing for a more flexible bleaching response than their adult conspecifics (e.g., *Acropora tenuis*: Abrego et al. 2008, 2009). Small colonies also have significantly higher mass transfer rates than larger colonies owing to their high surface area to volume ratio, allowing for more efficient diffusion of both CO_2 and oxygen radicals and subsequent maintenance of photosynthesis (van Woesik et al. 2012). But even within taxa, size-based bleaching response appears to vary among locations and bleaching events. For example, small (<5cm diameter) *Pocillopora* colonies at Lizard Island in the GBRMP were reported to be more susceptible to bleaching mortality than larger congeners (>5cm diameter) during the 2016 bleaching event (Álvarez-Noriega et al. 2018). However, small *Pocillopora* corals (<10cm diameter) were found to be less susceptible to bleaching than their larger congeners (>50cm diameter) during an earlier bleaching event in French Polynesia (Pratchett et al. 2013). Variability in size selectivity within taxonomic groups, among regions could be related to differences in species composition within a genus, symbiont type, genotype or the host's ability to switch or shuffle symbionts (Goulet 2006; Sampayo et al. 2008), but the mechanisms behind this inconsistency in size-based bleaching are still unknown. The disproportionate loss of larger corals following concurrent bleaching events would impact stock-recruitment relationships and impair recovery potential of coral assemblages (Hughes et al. 2019a; Pisapia et al. 2020). However, the persistence of juveniles may act as a buffer against shifts in community composition and aid

in recovery following such disturbances (Chong-Seng et al. 2014; Álvarez-Noriega et al. 2018; Doropoulos et al. 2022).

Differential bleaching susceptibility (both within and among taxa) may influence the population and community structure of reef-building corals, though the selectivity of such disturbances is inherently linked to the magnitude of marine heatwaves and corresponding severity of mass-bleaching episodes (Hughes et al. 2017, 2018b). The greatest selective pressures on coral community composition and size structure are likely realised under moderate heatwaves and bleaching episodes as only the most sensitive corals will be affected. In contrast, extreme heatwaves will likely result in high incidence of bleaching and mortality across all corals, regardless of size or species (Hughes et al. 2017). It is often assumed therefore, that increasingly severe mass-bleaching events simply affect an ever-increasing range of different coral taxa, and the most susceptible species are always the first and worst affected (Hughes et al. 2017).

The objective of this study was to explicitly test for differences in bleaching susceptibility among major coral taxa and colony size classes relative to the overall proportion of corals that bleached in 2020 at each of 33 reefs (reef-scale bleaching severity) across Australia's Great Barrier Reef Marine Park (GBRMP) and Coral Sea Marine Park (CSMP). With accelerating climate change, and unprecedented disturbances on coral reefs, we are having to re-assess much of what we know about the vulnerability and resilience of coral assemblages (Hughes et al. 2018b, 2019b; McWilliam et al. 2020). Previous coral bleaching events, combined with a suite of other acute and chronic disturbances, have already altered both size structure and taxonomic composition of coral assemblages (Johns et al. 2014; Hughes et al. 2018b; Mellin et al. 2019b; Dietzel et al. 2020). Many of the bleaching susceptible taxa (e.g., *Acropora*) are already much less common on reefs subject to recurrent disturbances (e.g., Pratchett et al. 2011) and there is evidence to suggest coral colonies are getting smaller (Dietzel

et al. 2020; Pisapia et al. 2020). Contemporary knowledge of colony size and taxon-based susceptibility to coral bleaching is, therefore, critical to inform potential effects of sustained and ongoing ocean warming on the structure and function of coral reef ecosystems.

4.2 Methods

4.2.1 Survey sites

This study is based on field surveys conducted from 16 February to 23 March 2020, during a widespread mass-bleaching event in the Great Barrier Reef Marine Park (GBRMP) and adjacent Coral Sea Marine Park (CSMP). Heat stress was spatially extensive and severe across this region, with many reefs exceeding levels of heat stress expected to elicit coral bleaching (Fig. S4.1). Sampling was conducted at 17 reefs on the GBRMP and 16 reefs in the CSMP (Fig. 4.1). At each reef 1-6 sites (n = 90 sites) were surveyed. Sites were generally positioned on the outer rim (i.e., avoiding lagoon habitat) of reefs where there was continuous reef matrix with well-defined shallow crest (~2m depth) and adjacent slope extending into deeper water, to ensure comparable habitats were sampled across reefs.

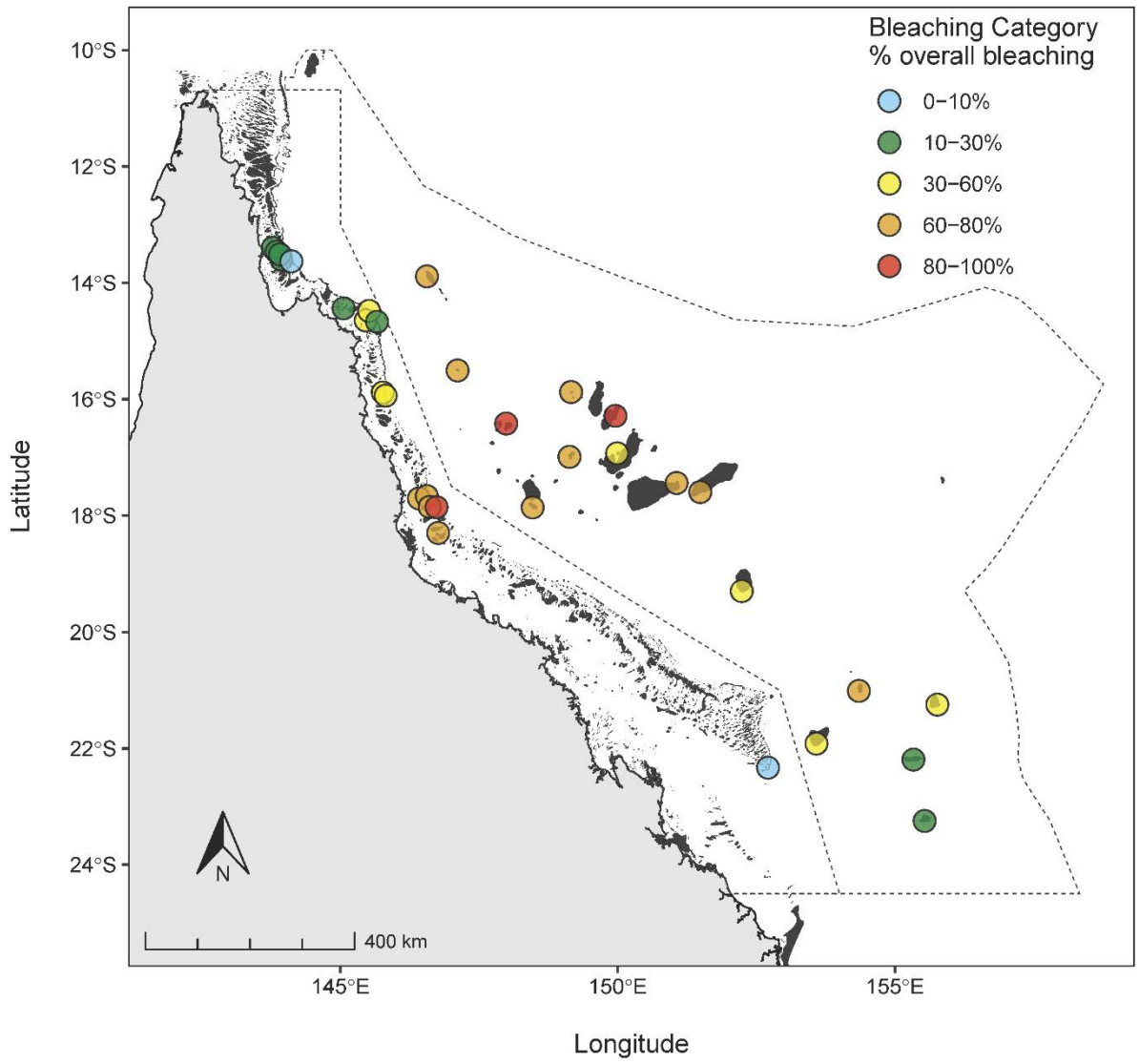


Figure 4.1: Map of 33 reefs surveyed in the Coral Sea Marine Park and Great Barrier Reef Marine Park in February-March 2020. Colours represent the reef-scale bleaching severity category for each reef, determined by the overall percent of corals surveyed on each reef that were bleached. Dotted lines represent marine park boundaries, with the Great Barrier Reef Marine Park adjacent to the coast, and the Coral Sea Marine Park directly to the East.

4.2.2 Bleaching susceptibility

To quantify size- and taxon-based bleaching susceptibility, three replicate 10 x 1 m belt transects were surveyed in each of two habitats, the reef slope (~8-10 m depth) and the reef crest (~2m depth), at each site. Each transect was laid parallel to the reef contour and at a constant depth, with 40-50m between adjacent transects. All scleractinian corals within each belt were identified to genus, and further resolved (where appropriate) into morphological groups (e.g., acroporids were split into 'tabular', 'staghorn' and 'other' and poritids into 'massive', 'branching', and 'encrusting with uprights' (e.g., *Porites rus*)). The 10 most common morpho-taxa (hereafter referred to as 'taxa') were selected for our statistical model, where only taxa with >5 colonies present in each bleaching category and size class were included in the model. The taxa 'other *Acropora*' and 'massive *Porites* were selected in our model and are henceforward referred to throughout as '*Acropora'* and 'massive *Porites*', respectively. Each coral was placed into one of five size classes based on maximum colony diameter (juveniles: ≤5cm, small: 6-20cm, medium: 21-40cm, large: 41-60cm and very large: >60cm diameter) and later collapsed into two classes (juveniles: ≤5cm and adults: >5cm diameter) to increase power in the model. For all colonies ≤5cm maximum diameter, a concerted effort was made to discern sexually derived juveniles from small colonies resulting from fission of larger colonies. It should be noted, however, that some small colonies classified here as 'juveniles' may include ramets derived from the partial mortality of larger colonies. Bleaching status of individual colonies was scored based on eight health categories (Healthy; Pale; <50% partially bleached; >50% partially bleached; 100% bleached; 5-50% bleaching-induced partial mortality; 51-99% bleaching-induced partial mortality; and 100% bleaching-induced recent mortality). These health categories were later pooled binomially as either 'bleached' (inclusive of pale colonies through to bleaching-induced recent mortality) or 'not bleached' to allow for greater statistical power.

4.2.3 Statistical analyses

There is increasing evidence that temperature measurements (e.g., Degree Heating Weeks, DHW) alone are not reliable indicators of bleaching severity, especially following concurrent disturbances (McClanahan et al. 2019a, 2020; DeCarlo 2024). Rather, a suite of interacting factors (e.g., sunlight, water flow, nutrient levels, historic temperature variability, rate of temperature increase) have been shown to affect the susceptibility of corals to bleaching (Maina et al. 2008; Grottoli et al. 2014; Ainsworth et al. 2016; Safaie et al. 2018; Sully et al. 2019; DeCarlo et al. 2020; Winston et al. 2022; Sahin et al. 2023). Therefore, rather than use one or more metrics of heat stress, we used a proxy for reef-scale bleaching severity that is independent of the likely causes of bleaching and simplified the modelling framework. Each of the 33 reefs were assigned to one of five levels of reef-scale bleaching severity based on the overall proportion of colonies that were bleached across all sites and habitats surveyed; i) 'low' (0-10% bleaching), ii) 'moderate' (11-30% bleaching), iii) 'high' (31-60% bleaching), iv) 'very high' (61-80% bleaching) and v) 'extreme' (>80% bleaching), following Hughes et al. (2017). The levels of reef-scale bleaching severity assigned also related to the severity of bleaching recorded at the colony scale. The proportion of colonies experiencing 100% bleaching (i.e., total loss of zooxanthellae) and/or partial mortality resulting from bleaching (as opposed to partial bleaching or paling) increased with each increasing reef-scale bleaching severity category (Fig. S4.2). The taxonomic composition of coral communities did not differ among severity categories (PERMANOVA: $F = 1.11$, $df = 2$, $R^2 = 0.137$, $p = 0.339$). Corals were more likely to bleach on the reef crest compared to the reef slope, which was consistent among genera and reef-scale bleaching severity categories (See supplementary material for statistical model; Fig. S4.3). Therefore, data were pooled across habitats in the final analysis.

A Bayesian hierarchical generalized linear model was constructed to investigate the effects of three variables (reef-scale bleaching severity, taxa, and colony size) on bleaching

susceptibility. Three two-way interactions between taxa, reef-scale bleaching severity, and colony size were modelled to investigate how bleaching susceptibility among taxa varied with respect to both colony size and reef-scale bleaching severity. Additionally, region (GBRMP vs CSMP) was included as a random factor to account for different bleaching susceptibilities between oceanic and continental shelf reefs. The model was fit against a zero-one inflated beta distribution, using weakly informative priors. Posteriors were generated via a No-U-Turn sampler (NUTS), run for 5000 iterations (excluding the first 1000 warmup samples) from each of the three chains, with a thinning rate of 10. All chains were found to be well mixed and converged (Rhat ~1) on a stable posterior. Goodness of fit was assessed statistically using leave-one-out cross-validation, ensuring all Pareto-k estimates were below 0.5, and visually using a posterior probability check.

Marginal effects plots with 66% and 90% highest posterior density credible intervals (CrI) and posterior distributions were produced to show how bleaching susceptibility varied with respect to taxa, reef-scale bleaching severity and colony size individually as well as marginal effects plots to show the interactive effects. CrI reported in the text refer to 90% CrI. Pairwise contrasts are reported as odds ratios, meaning that where the upper and lower bounds of the associated CrI contain 1, very strong evidence of a difference is not found.

All data was analysed using R 4.1.1 (R core team 2018) using the “brms” package to fit the hierarchical models (Bürkner 2017), with the “emmeans” (Lenth 2021) package used for pairwise comparisons of marginal means, and computation of 66% and 90% CrI. Comparisons of coral composition among bleaching severity categories were conducted using the “vegan” (Oksanen et al. 2020) package.

4.3 Results

Of the 38,414 distinct coral colonies within the 10 most common taxa recorded across the 90 sites, 22,129 (57.6%) colonies displayed some signs of bleaching, ranging from apparent paling or localised and partial bleaching to extensive bleaching or recent mortality of the entire colony. The factors affecting the likelihood of a colony to bleach are complex, as evidenced by three positive two-way interactions in our model. Whilst some taxa (e.g., *Stylophora:* 64% [CrI 49 - 85%]; *Pocillopora*: 54% [CrI 37 - 76%]; and *Goniastrea*: 54% [CrI 34 - 73%]) had a higher tendency to bleach than others (Fig. S4.4a), the likelihood of different taxa to bleach was dependent on colony size, and on reef-scale bleaching severity (Figs 4.2a, 4.2b). Furthermore, whilst juvenile corals (≤5cm diameter) were generally less likely to bleach than adult corals (>5cm diameter) (juveniles: 44% [CrI 25 - 65%]; adults: 48% [CrI 29 - 68%]; contrast ratio: 1.16 [CrI 1.01 - 1.32]; Fig. S4.4b, Table S4.1a), this was contingent on the coral taxon, and the severity of the bleaching (Fig. 4.3).

The rank order of bleaching susceptibility among taxa was dependent on the reef-scale bleaching severity, shown clearly by the interaction between taxa and bleaching severity in our model (Fig. 4.2a). When reef-scale bleaching severity was low (0-10%) or extreme (81-100%), posterior distributions for the likelihood of bleaching among taxa converged, and differential susceptibility among taxa was not clear. However, moderate (11-30%) to high (31-60%) severity categories produced the most pronounced differential susceptibilities among the 10 modelled taxa (Fig. 4.2a). Under conditions of moderate (11-30%) reef-scale bleaching severity, there was strong evidence that the likelihood of bleaching in *Stylophora* (45% [CrI 26 - 68%]) and *Pocillopora* (43% [CrI 23 - 63%]) was higher than all but one of the other taxa in the model (Fig. 4.2a; Table S4.2). Under conditions of high (31-60%) reef-scale bleaching severity, *Stylophora* (73% [CrI 56 - 89%]) and *Pocillopora* (66% [CrI 49 - 85%]) remained very likely to bleach more than all other taxa modelled, but the likelihood of bleaching

increased for several other taxa (*Montipora*: 55% [CrI 34-75%], *Astrea*: 55% [CrI 33 - 75%], *Goniastrea*: 54% [CrI 31 - 73%], and *Acropora* 53% [CrI 34 - 74%]; Fig. 4.2a; Table S4.2). Notably, during low to high (0-10% - 31-60%) reef-scale bleaching severities, massive *Porites* was consistently among the least likely taxa to exhibit bleaching (Low: 16% [CrI 4 - 31%]; Moderate: 20% [CrI 7 - 34%]; High: 30% [CrI 12 - 46%]; Fig. 4.2a; Table S4.2), but during very high (61-80%) reef-scale bleaching severities, massive *Porites* appeared among the most susceptible taxa (66% [CrI 47 - 82%]), becoming much more likely to bleach in comparison with *Cyphastrea* (contrast ratio: 0.46 [CrI 0.31 - 0.66]), *Dipsastraea* (contrast ratio: 0.56 [CrI 0.35 - 0.80]) and *Platygyra* (contrast ratio: 0.48 [CrI 0.30 - 0.67]) colonies (Fig. 4.2a; Table S4.2). In fact, the rank order of taxonomic bleaching susceptibility shifted considerably depending on the reef-scale bleaching severity category (Fig. 4.2a).

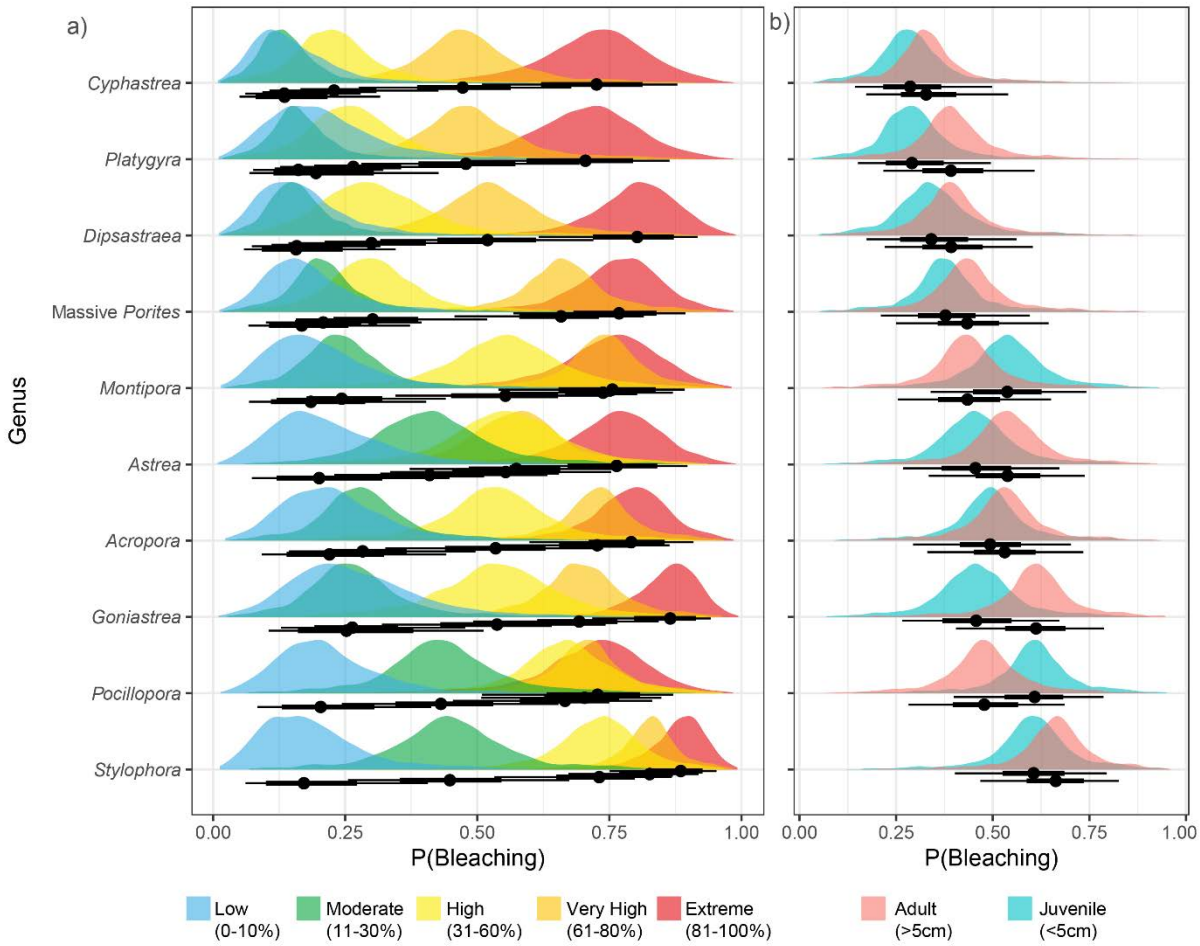


Figure 4.2: Marginal posterior distributions for the interactions between taxa and reef-level bleaching severity (a) and taxa and colony size (b). Points represent estimated marginal means, thick and thin lines represent 66% and 90% credible intervals, respectively.

The rank order of taxonomic susceptibility was also somewhat dependent upon the colony size (Fig. 4.2b). For five of the ten taxa modelled (*Astrea*, *Goniastrea*, *Platygyra*, massive *Porites* and *Stylophora*), there was evidence that adult corals were more likely to bleach than their juvenile congeners, with strong evidence that *Goniastrea* and *Platygyra* adults bleach more readily than the juveniles (*Goniastrea* adults: 61% [CrI 46 - 83%]; *Goniastrea* juveniles: 46% [CrI 26 - 67%]; *Goniastrea* contrast ratio: 1.87 [CrI 1.18 - 2.62]; *Platygyra* adults: 39% [CrI 19 - 57%]; *Platygyra* juveniles: 29% [CrI 11 - 45%]; *Platygyra* contrast ratio:

1.59 [CrI 1.01 - 2.24]; Fig. 4.2b; Table S4.1b). However, the opposite was found for *Pocillopora* and *Montipora*, where the likelihood of bleaching in juveniles was very high when compared to congeneric adults (*Pocillopora* adults: 48% [CrI 28 - 67%]; *Pocillopora* juveniles: 61% [CrI 44 - 81%]; *Pocillopora* contrast ratio: 0.59 [CrI 0.41 - 0.79]; *Montipora* adults: 43% [CrI 27 - 66%]; *Montipora* juveniles: 54% [CrI 33 - 74%]; *Montipora* contrast ratio: 0.66 [CrI 0.44 - 0.92]). For three taxa (*Acropora*, *Cyphastrea* and *Dipsastraea*), there was no evidence of a difference in the bleaching susceptibility between colony sizes (Fig. 4.2b; Table S4.1b). Assessing different colony sizes resulted in a different rank order of taxonomic susceptibility to coral bleaching, but this is likely to also be contingent upon the severity of the bleaching.

The differential susceptibility to bleaching between the two size classes was most pronounced during low (0-10%), moderate (11-30%) and extreme (81-100%) reef-scale bleaching severities. Adult corals were much more likely to bleach at lower severities compared with juvenile corals (adults (low): 25% [CrI 11 - 43%]; juveniles (low): 13% [CrI 4 - 24%]; contrast ratio (low): 2.11 [CrI 1.25 - 3.04), and much less likely to bleach than juveniles at extreme severities (adults (extreme): 74% [CrI 59 - 90%]; juveniles (extreme): 83% [CrI 71 - 94%]; contrast ratio (extreme): 0.59 [CrI 0.42 - 0.78]; Fig. 4.3, Table S4.3).

Estimates were also computed for the interactions between taxa and colony size for each reef-scale bleaching severity category (Fig. 4.3). The differential susceptibility between size classes changed for some taxa depending on the reef-scale bleaching severity (Fig. 4.3). Most taxa followed the results of the two-way interactions, where juveniles were less likely to bleach at lower severities and more likely to bleach at extreme severities. For example, juvenile *Acropora* colonies were much less likely to bleach than their adult counterparts during low (0-10%) reef-scale bleaching severity (*Acropora* adult (low): 29% [CrI 10 - 50%]; *Acropora* juvenile (low): 16% [CrI 4 - 31%]; *Acropora* contrast ratio (low): 2.12 [CrI 1.12 - 3.26]). In contrast, juvenile *Acropora* colonies were equally likely to bleach as the adults during

moderate, high and very high severities, and became much more likely to bleach during extreme (81-100%) severities (*Acropora* adult (extreme): 74% [CrI 59 - 93%]; *Acropora* juvenile (extreme): 83% [CrI 69 - 95%]; *Acropora* contrast ratio (extreme): 0.59 [CrI 0.35 - 0.83]). However, juvenile *Pocillopora* and *Montipora* were unlikely to show increased bleaching likelihood in comparison to their adult congenerics at low reef-scale bleaching severities (*Pocillopora* adults (low): 21% [CrI 6 - 38%]; *Pocillopora* juveniles (low): 20% [CrI 5 - 35%]; *Pocillopora* contrast ratio (low): 1.07 [CrI 0.57 - 1.67]) and became much more likely to bleach than their adult congenerics as severity increased (Fig. 4.3; Table S4.4). For some taxa, such as *Goniastrea* and *Platygyra*, the juveniles remained much less likely to bleach than adult congenerics, until bleaching severity became extreme (81-100%), whereby the likelihood of adults bleaching was equal to that of juveniles (Fig. 4.3; Table S4.4).

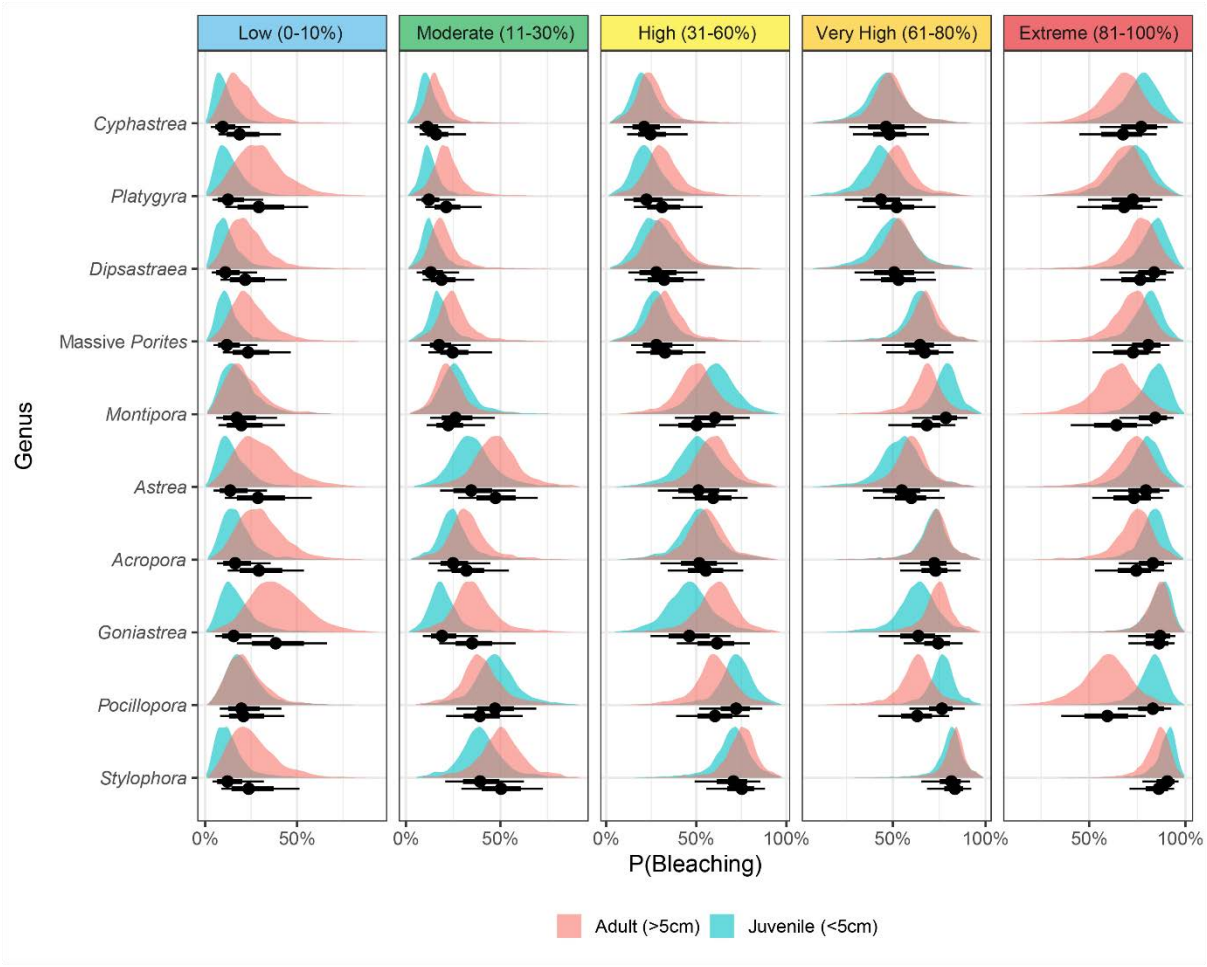


Figure 4.3: Marginal posterior distributions for the interaction between taxa and size class, varying by reef-level bleaching severity. Each panel represents a reef-scale bleaching severity category, with blue distributions representing juvenile colonies and red distributions representing adult colonies per taxon. Points represent estimated marginal means, thick and thin lines represent 66% and 90% credible intervals, respectively.

4.4 Discussion

The incidence of mass bleaching recorded during 2020 in the Great Barrier Reef Marine Park (GBRMP) and the Coral Sea Marine Park (CSMP) varied greatly among coral taxa, reflecting widely reported taxonomic differences in bleaching susceptibility (e.g., Brown and Suharsono 1990; Glynn 1993; Loya et al. 2001; Baird and Marshall 2002; Guest et al. 2012; Bayraktarov et al. 2013; Pratchett et al. 2013; Hughes et al. 2018b; Pisapia et al. 2019).

However, taxonomic differences in bleaching susceptibility did not simply become less apparent with increases in reef-scale bleaching severity. Rather, the rank order of the bleaching susceptibility was dependent on our proxy of bleaching severity (see also Hughes et al. 2017) with different coral taxa being disproportionately affected during low versus high levels of reef-scale bleaching severity. For example, massive *Porites* exhibited very low incidence of bleaching on reefs where reef-scale bleaching severity was low to high (i.e., <60% of colonies bleached), but was among the most susceptible taxa at reefs with very high (61-80% of colonies bleached) and extreme (>80% of colonies bleached) bleaching severity (Fig. 4.2a). Massive *Porites* are generally considered to be among the least susceptible coral taxa to temperature stress (Loya et al. 2001; Hughes et al. 2017), though massive *Porites* do bleach and sometimes die during particularly severe heatwaves, when bleaching impacts even the most thermally tolerant corals, or during recurrent bleaching events (Grottoli et al. 2014; Burn et al. 2022). Our data suggest that massive *Porites* are disproportionately affected during severe bleaching, such that increasingly severe bleaching events may ultimately lead to declines in abundance of these corals. Any declines in the abundance of massive *Porites* will be further compounded by their slow growth and limited capacity for recovery in the aftermath of such disturbances (Pratchett et al. 2020; Morais et al. 2021).

While bleaching susceptibility varied with reef-scale bleaching severity for some coral taxa (most notably, massive *Porites*), there were also some taxa that were more or less impacted than others regardless of overall bleaching severity. Therefore, despite more severe events being likely to affect a wider range of coral taxa than mild events, it appears a subset of sensitive taxa will always be disproportionately more affected than others. The susceptibility of these taxa is consistent with those of other studies where fast growing, branching taxa (e.g., *Stylophora*, *Pocillopora* and *Acropora*) were more likely to bleach than slow growing, massive taxa (Fisk and Done 1985; Brown and Suharsono 1990; Glynn 1993; Fujioka 1999; Marshall

and Baird 2000; Loya et al. 2001; Baird and Marshall 2002; Pratchett et al. 2013; Hughes et al. 2018b; Harrison et al. 2019). However, there were some notable exceptions. *Goniastrea* was among the most susceptible in our study, similar to findings from Thailand and the GBRMP (Brown et al. 2014; Hughes et al. 2017). In contrast, Loya et al. (2001) reported minimal change in the cover and abundance of *Goniastrea* following the 1998 bleaching in Japan, leading to suggestions it was one of the more bleaching tolerant coral taxa. It may be that *Goniastrea* is highly susceptible to bleaching but rarely dies, and it is rates of whole colony mortality that ultimately dictate differential susceptibility to mass-bleaching and corresponding shifts in coral assemblages (Woesik et al. 2011). Alternatively, differences in the species composition of *Goniastrea* among locations (including recent changes in the taxonomy of *Goniastrea*; Huang et al. 2014) may have contributed to the differences among studies. Similarly, differences in the composition of coral species, symbionts, or genotypes within coral genera may have contributed to the observed differences in bleaching susceptibility in our study (Manzello et al. 2019; Marzonie et al. 2023).

With the most sensitive taxa bleaching at lower reef-scale severities, changes in composition are likely to occur following low to mid-level bleaching incidence, especially given the predisposition of those corals to be the primary target of other major disturbances occurring on the reef (i.e., crown-of-thorns starfish: Keesing et al. 2019; severe storms: Madin et al. 2018). Changes in community composition are however, dependent on incidence of bleaching translating to colony mortality, which for lower severity bleaching may take several months to manifest (Baird and Marshall 2002), if at all. However, as the severity of the temperature stress increases, and a wider subset of coral taxa are affected by bleaching, future community composition is likely to be shaped by the differential mortality and/or recovery of coral taxa, rather than differential bleaching susceptibility (Leggat et al. 2019; Pratchett et al. 2020). Moreover, the large distances (typically >100km) and deep waters (1-3km deep)

separating reefs within the CSMP, and CSMP reefs from adjacent reef systems (e.g., GBR and New Caledonia), may limit the larval input from other reefs (Ceccarelli et al. 2013). This could constrain replenishment of coral populations and exacerbate shifts in the composition of coral communities, especially if disturbances are frequent and severe (Gilmour et al. 2013). Further monitoring of these populations may provide important insights into possible shifts in community structure.

Whilst some studies have provided evidence of increasing bleaching tolerance in susceptible taxa (e.g., *Acropora*) following recurrent bleaching events (Guest et al. 2012; Pratchett et al. 2013), we found the differential susceptibilities of those thermally sensitive taxa are much the same as those reported in past studies from the GBRMP and CSMP (Marshall and Baird 2000; Hughes et al. 2017; Harrison et al. 2019). Further work should be conducted to determine if any temporal changes exist in taxonomic bleaching susceptibility in the CSMP and GBRMP following this most recent event. This is particularly important, especially considering the effects of past disturbances are likely to influence effects of those in the future (Hughes et al. 2019b) and as the effects of potential protective mechanisms diminish with climate change (Ainsworth et al. 2016).

Overall, juvenile corals (≤5cm diameter) exhibited lower incidence of bleaching (44%) than adult (>5cm diameter) colonies (48%). Lower bleaching susceptibility in juvenile corals has been documented previously (Hoeksema 1991; Mumby 1999; Loya et al. 2001; Brandt 2009; Phongsuwan and Chansang 2012; Depczynski et al. 2013) and is generally attributed to symbiont type or mass transfer efficiency (reviewed in Wooldridge 2014). However, some existing studies do report contrasting patterns of size-based differences in bleaching susceptibility (Loya et al. 2001; Brandt 2009; Álvarez-Noriega et al. 2018) and we similarly show herein, that the bleaching response is taxon-specific, and dependent on the severity of the bleaching. Transformations in coral size structure and topographic complexity may therefore

be exacerbated by susceptibility of specific colony size classes or influenced by the severity of the bleaching event. There is some suggestion that community size structure is shifting toward dominance of smaller coral colonies, owing to the increased turnover following recurrent disturbances (Done 1999; Pisapia et al. 2020; but see Dietzel et al. 2020). This could benefit taxa whose juveniles were most tolerant to bleaching (e.g., *Stylophora*, massive *Porites*, *Platygyra*, and *Astrea*) and those that mature at smaller colony sizes, but negatively impact taxa whose juveniles were significantly more susceptible (e.g., *Montipora* and *Pocillopora*).

In conclusion, this study shows that taxonomic differences in bleaching susceptibility are contingent upon both overall bleaching severity and colony size. Differing severities among locations and events will therefore, be likely to result in different community compositions, with moderate stress events highlighting taxonomic differences in the susceptibility to bleaching more clearly than extreme events, where almost all zooxanthellate corals are likely to be susceptible to bleaching. Furthermore, our study highlights the need to account for the size structure of a coral assemblage when determining bleaching susceptibility, where differential susceptibility of certain colony sizes may lead to shifts in size structure for some taxa. As bleaching events become more frequent, it is likely that coral genera with high tolerance for heat stress, such as *Cyphastrea, Platygyra* and *Dispastraea* will be selected for (Álvarez-Noriega et al. 2018; Hughes et al. 2019b), but if bleaching events become more severe, it is likely that the abundance of even these heat-tolerant taxa will significantly decrease. To further understand what future assemblages on corals reefs may look like, we need to continuously monitor both community size structure and composition following disturbances of differing severities. Understanding the initial susceptibility combined with the long-term effects of disturbance and other demographic traits influencing the capacity to recover will be paramount in elucidating the long-term effects of bleaching events on coral communities. Future research should aim to understand what proportion of bleached corals

recover so we may better understand the relationship between bleaching susceptibilities and likelihood of bleaching related mortality. Finally, as this 2020 event was the third major bleaching event in five years on reefs in the GBRMP and CSMP, it is important to examine the temporal implications of recurrent bleaching effects on coral assemblages. Combined, this knowledge will give us a much clearer understanding of how coral assemblages will persist into the future.

Chapter 5. Changes in coral cover and composition following the 2020 mass bleaching event in Australia's Coral Sea Marine Park

5.1 Introduction

Coral bleaching is one of the foremost threats to corals, contributing to widespread coral loss and reef degradation (Eakin et al. 2010, 2019; Hughes et al. 2017; Sully et al. 2019; Tebbett et al. 2023). Mass coral bleaching is generally attributed to anomalously high ocean temperatures, which disrupt the critical relationship between corals and their photosynthetic symbionts (Brown 1997; Lesser 1997). The corresponding loss of pigment within the coral results in a pale or 'bleached' appearance, and the loss of energy derived from the symbionts results in decreased fitness (Gold and Palumbi 2018; Leinbach et al. 2021). While some corals may recover, severe or prolonged thermal stress often results in extensive coral mortality (Jones 2008; Hughes et al. 2018b; Leggat et al. 2019).

Coral taxa vary in their susceptibility to bleaching and subsequent mortality (Marshall and Baird 2000; Loya et al. 2001; Smith et al. 2008b; Hughes et al. 2018b; Harrison et al. 2019; Pisapia et al. 2019). Fast-growing, structurally complex branching taxa (e.g., *Acropora* and *Stylophora*) are among the most susceptible to thermal stress, often experiencing significant bleaching and mortality (Loya et al. 2001; Baird and Marshall 2002; Burn et al. 2023 [**Chapter 4**]). In contrast, massive, slow-growing taxa (e.g., *Porites*) are generally more resilient and often dominate reef assemblages in the immediate aftermath of severe bleaching events (Burt et al. 2008; Roff et al. 2014; Pisapia et al. 2019; Pratchett et al. 2020). The selective effects of bleaching can alter the structure and function of coral reef ecosystems, with important ramifications for organisms dependent on branching corals for food and habitat (Graham et al. 2007; Alvarez-Filip et al. 2015; Pratchett et al. 2018; Estrada-Saldívar et al. 2019). However, extreme or cumulative thermal stress may result in a shift in traditional hierarchies of

susceptibility, where even tolerant taxa suffer significant bleaching and mortality (Mumby et al. 2001; Grottoli et al. 2014; Hughes et al. 2018b; Burn et al. 2023 [**Chapter 4**]). The resulting comprehensive loss across coral taxa will exacerbate changes in structure and functions, with further declines in 3D complexity and carbonate budgets (Rogers et al. 2014; Perry and Alvarez-Filip 2019; Ryan et al. 2019).

Quantifying differential loss among coral taxa following bleaching is not only important for understanding the short- to medium-term changes in reef structure and function, but also for projecting the likelihood of recovery and reassembly (Baker et al. 2008; Kayal et al. 2018; Pratchett et al. 2020). The 'boom and bust' population dynamics of highly susceptible taxa (e.g., *Acropora*) can result in recovery if return time between disturbances allows for regrowth and larval replenishment (Gilmour et al. 2013; Gouezo et al. 2019; Pratchett et al. 2020; Morais et al. 2021). However, the comprehensive loss of all taxa following extreme thermal stress might result in protracted recovery or failure of community reassembly (Johns et al. 2014; Pratchett et al. 2020; Speare et al. 2022), which may result in unpredictable temporal shifts in coral cover and composition (Emslie et al. 2024a). Successful recovery also depends on adequate larval supply, settlement, and survivorship, which are heavily influenced by local and regional connectivity (Gilmour et al. 2013; Doropoulos et al. 2015; Burn et al. 2024 [**Chapter 3**]; Speare et al. 2025).

The extent of bleaching-induced mortality within and among coral taxa is strongly linked to regional differences in accumulated heat stress, often measured in degree heating weeks (DHW, °C-weeks; Eakin et al. 2019), with >8 DHWs typically causing severe mortality (Hughes et al. 2018b; but see Hughes et al. 2021 for consecutive events). However, the extent of coral mortality may be conflated by other environmental conditions (Eakin et al. 2010; Yee and Barron 2010; Hughes et al. 2018b; Suggett and Smith 2020; Donovan et al. 2021). Notably, bleaching impacts vary with depth (Furby et al. 2013; Baird et al. 2018b; Winslow et al. 2024),

turbidity (Sully and van Woesik 2020; Donovan et al. 2021), and exposure to waves and tides (Green et al. 2019; Wyatt et al. 2020). Reef slopes, with reduced irradiance and cooler temperatures, may experience lower mortality than reef crests (Furby et al. 2013; Muir et al. 2017; Baird et al. 2018b; Winslow et al. 2024). Clear, oligotrophic waters on oceanic reefs may exacerbate light stress and mortality compared to turbid nearshore environments, where heterotrophic feeding opportunities are greater (Sully and van Woesik 2020; Donovan et al. 2021; Page et al. 2023). However, oceanic reefs may benefit from reduced anthropogenic stressors and proximity to cooler, deeper waters, potentially conferring resilience to climate change (Smith et al. 2008a; Halford and Caley 2009; Harrison et al. 2019; but see Baumann et al. 2022).

The purpose of this study was to quantify coral loss across the remote, oceanic reefs of Australia's Coral Sea Marine Park (CSMP) following the fifth recorded mass bleaching event in 2020 (Hoey et al. 2020). Significant bleaching was observed across the marine park, predominantly affecting fast-growing branching taxa (e.g., *Stylophora*, *Pocillopora*, and *Acropora*; (Burn et al. 2023 [**Chapter 4**]). As bleaching severity increased, traditionally robust (*Goniastrea* and massive *Porites*) became disproportionately affected, highlighting the potential for severe heat stress to override established susceptibility hierarchies (Burn et al. 2023 [**Chapter 4**]). However, phenotypic bleaching responses alone do not necessarily equate to mortality (McClanahan 2004; Harrison et al. 2019; Page et al. 2023), and ultimate susceptibility is determined by the extent to which different corals die. This study examines regional and habitat-based coral loss, focusing on differential loss among taxa to inform understanding of community shifts. We hypothesise that coral mortality will be higher on reef crests than reef slopes, where temperature and irradiance are more extreme and the highest bleaching incidence was recorded (Furby et al. 2013; Burn et al. 2023 [**Chapter 4**]; Winslow et al. 2024). Moreover, we hypothesise that regional differences in coral loss will reflect

taxonomic composition, with southern and central CSMP reefs previously dominated by highly susceptible taxa (*Acropora* and *Isopora*) and northern reefs by more robust taxa (*Porites*) (Edgar et al. 2015; Harrison et al. 2019). However, the 2020 mass bleaching event was one of the most severe on record (Smith 2024), which may result in comprehensive mortality, even for more tolerant taxa (Burn et al. 2023 [**Chapter 4**]).

5.2 Methods

5.2.1 Survey sites

Sampling was undertaken at 13 reefs throughout the CSMP between February 2020 and March 2021 (Fig. 5.1). Reefs were selected to gain as wide a spatial representation of the CSMP as possible. One to six sites were surveyed at each reef (n = 43) in both 2020 and 2021. Sites were generally positioned on the outer edge of reefs, where there was continuous solid reef matrix with a clearly defined reef crest, and a reef slope extending into deeper habitat. An extensive marine heatwave occurred causing mass coral bleaching throughout the CSMP in March 2020 (Fig. 5.1), but surveys were conducted in February 2020 before coral mortality exceeded background levels (Burn et al. 2022). Thus, data from 2020 acts as an appropriate baseline against which to assess effects of bleaching (see **Chapter 2**). Heat stress (measured as degree heating weeks, DHW) was extracted using the NOAA Coral Reef Watch 5km product V3.1 (Liu et al. 2018) for each site, and plotted as a heat map (Fig. 5.1; Table S5.1).

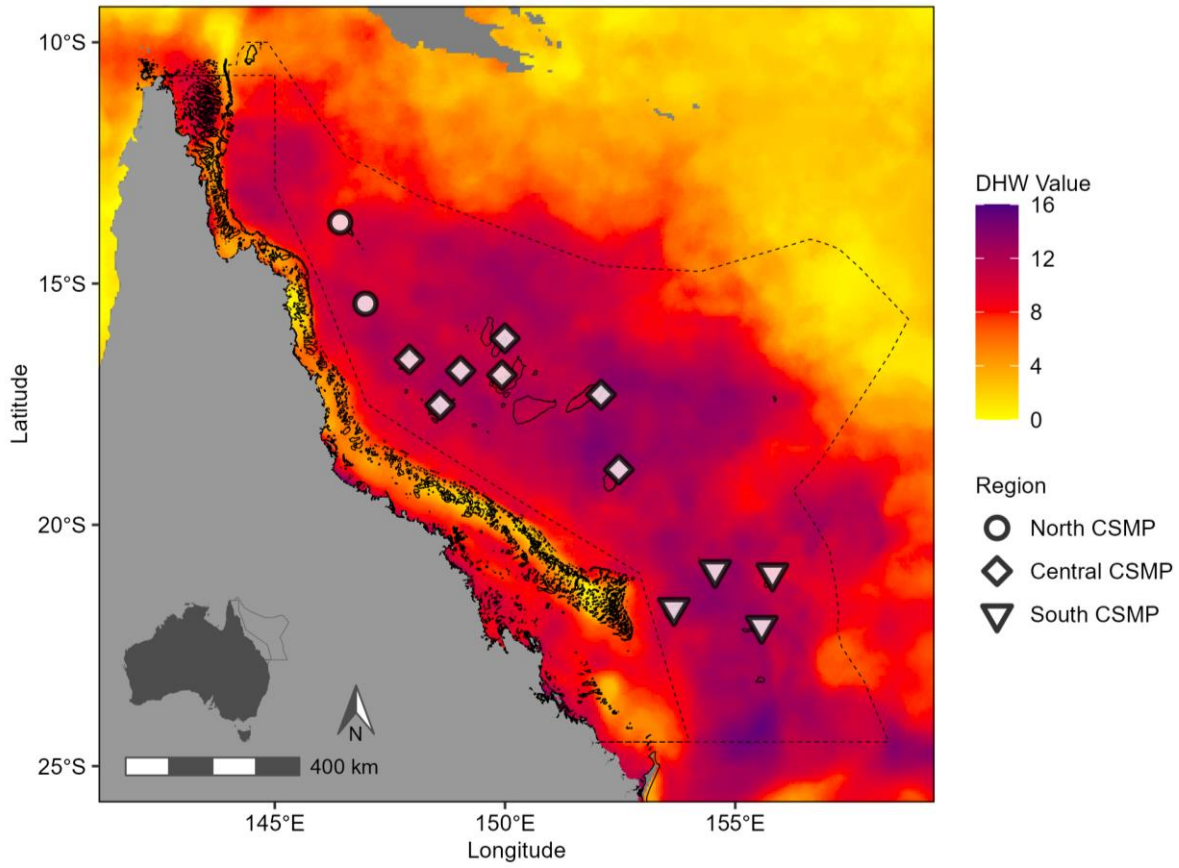


Figure 5.1 Reefs (n = 13) in the Coral Sea Marine Park (CSMP) surveyed in 2020 and 2021. Shapes represent three regions. Heat map underlay represents maximum DHW for March 2020. Dashed lines represent CSMP boundaries to the east of the Queensland coast. DHW data extracted from NOAA CRW 5km product.

5.2.2 Percent cover and composition of coral taxa

To determine percent cover of coral taxa, three replicate 50m point intercept transects were undertaken at each of the reef crest and reef slope (hereafter 'habitat') within each site (n = 6 per site), following the depth contour and separated by ~10m. Benthic substrate and organisms occurring directly below the tape at 50cm intervals were placed into categories, with corals identified to genus (n = 100 points per transect), or further resolved into morpho-genera (i.e., *Acropora* was split into staghorn, tabular, and other, and *Porites* was divided into massive and branching). Percent coral cover was calculated by dividing the number of points falling on

hard coral by the total number of points, minus the number of points falling on sand. This provides a measure of hard coral cover as a function of available hard substrate.

5.2.3 Statistical analyses

Changes in coral cover

Inter-annual change in the cover of scleractinian corals was analysed using a Generalized Linear Mixed Effects Model (GLMM), comparing between years (2020 and 2021), among regions (north, central and south) and between habitats (crest and slope). The model was fit with a three-way interaction between year, region and habitat, with nested random effects of site within reef to account for the hierarchical structure of the data, and temporal autocorrelation. Coral cover was modelled against a Tweedie distribution (Dunn and Smyth 2005) with a log link function to account for the overdispersion in the data.

The best model was selected after testing the fit of combinations of fixed and random effects using maximum likelihood (REML = FALSE) and retained only if they improved the fit of the model, based on the corrected Akaike Information Criterion (AICc; Table 5.1). For each model, goodness of fit was assessed, and validated, including checks of simulated residuals and dispersion, using the 'DHARMa' package (Hartig 2021), and tested for zero-inflation using the 'performance' package (Lüdecke et al. 2021). Post-hoc Tukey's pairwise comparisons were calculated using estimated marginal means in the 'emmeans' package (Lenth 2021) to test for significant differences coral cover among fixed effects.

Table 5.1 Selection of models tested, with degrees of freedom and AICc scores. The best model is highlighted in bold.

Model	df	AICc
CoralCover ~ 1 + (1|Reef/Site)	5	4014.929
CoralCover ~ Year + (1|Reef/Site)	6	3865.281
CoralCover ~ Year * Region + (1|Reef/Site)	10	3857.142
CoralCover ~ Year * Region * Habitat + (1|Reef/Site)	**16**	**3702.724**

Changes in coral communities

Relative change in coral cover for each of the 10 most common taxa was calculated independently for each region and habitat combination. Relative mean changes are presented with associated standard errors for each region–habitat combination, but no statistical tests were conducted on these individual taxon-level changes, as the survey design and sample size were not appropriate for robust taxon-specific inference. Instead, community-level changes were formally tested.

The dis/similarities in coral composition between years were visualised independently for each region and habitat using non-metric multi-dimensional scaling (nMDS) plots based on Bray Curtis dissimilarity matrices. All region-habitat combinations except for north-crest and south-slope were subject to square-root transformation, and all combinations were subject to Wisconsin double-standardisation prior to visualisation. Taxa occurring <40 times in each combination were characterised as 'rare' and pooled into a category of 'Other Scleractinia' to improve the fit of the ordinations due to the large size of the dataset. Three dimensions were used (k = 3) for the central and southern regions (k = 2 for the north) to further improve the fit. Species scores were overlaid on the nMDS plots for the 10 most common taxa per region.

PerMANOVA were calculated independently for each region and habitat to calculate statistical differences in community composition between years.

All statistical analyses were performed in the R statistical and graphical environment version 4.1.1 (R Core Team, 2021), with models built using the "glmmTMB" package (Brooks et al. 2017). Community differences were visualised and analysed using the package 'vegan' (Oksanen et al. 2020). Data wrangling was completed in the 'TidyVerse' (Wickham et al. 2019), with plots created using 'ggplot2' (Wickham 2016).

5.3 Results

5.3.1 Changes in coral cover

Overall, coral cover in the CSMP declined from 29.5% (± 0.9 SE) in 2020 to 18.0% (± 0.8) in 2021, representing a relative loss of 38.9%. However, declines in coral cover varied among the regions and habitats (Table 5.2; Fig. 5.2). In the southern and central regions, significant declines were observed in both habitats, with regional relative declines of 44.3% and 42.7%, respectively. In the northern region, significant reductions in coral cover were recorded in reef slope habitats, declining from 57% to 45.2% (a relative decline of 20.7%; Table 5.2, Fig. 5.2), but no change was recorded on reef crests, where coral cover increased marginally from 14.6% to 15.8%, corresponding to a relative increase of 8.2% (Table 5.2, Fig. 5.2).

Table 5.2 Estimated marginal mean coral cover for each region and habitat in 2020 and 2021. Contrast estimates and corresponding p-values derived from Tukey's pairwise comparisons indicate significant differences in coral cover (%) between years. * denote statistically significant differences.

Region	Habitat	2020 (emmean (SE)	2021 (emmean (SE)	Contrast estimate	p-value
South	Crest	34.1 (3.9)	22.6 (2.7)	11.5	<0.0001 *
	Slope	27.3 (3.2)	12.8 (1.6)	14.54	<0.0001 *
Central	Crest	24.1 (1.9)	13.3 (1.1)	10.81	<0.0001 *
	Slope	27.0 (2.1)	16.0 (1.3)	11.00	<0.0001 *
North	Crest	14.6 (3.1)	15.8 (3.4)	-1.18	0.6506
	Slope	57.0 (10.8)	45.2 (8.7)	11.89	0.0254 *

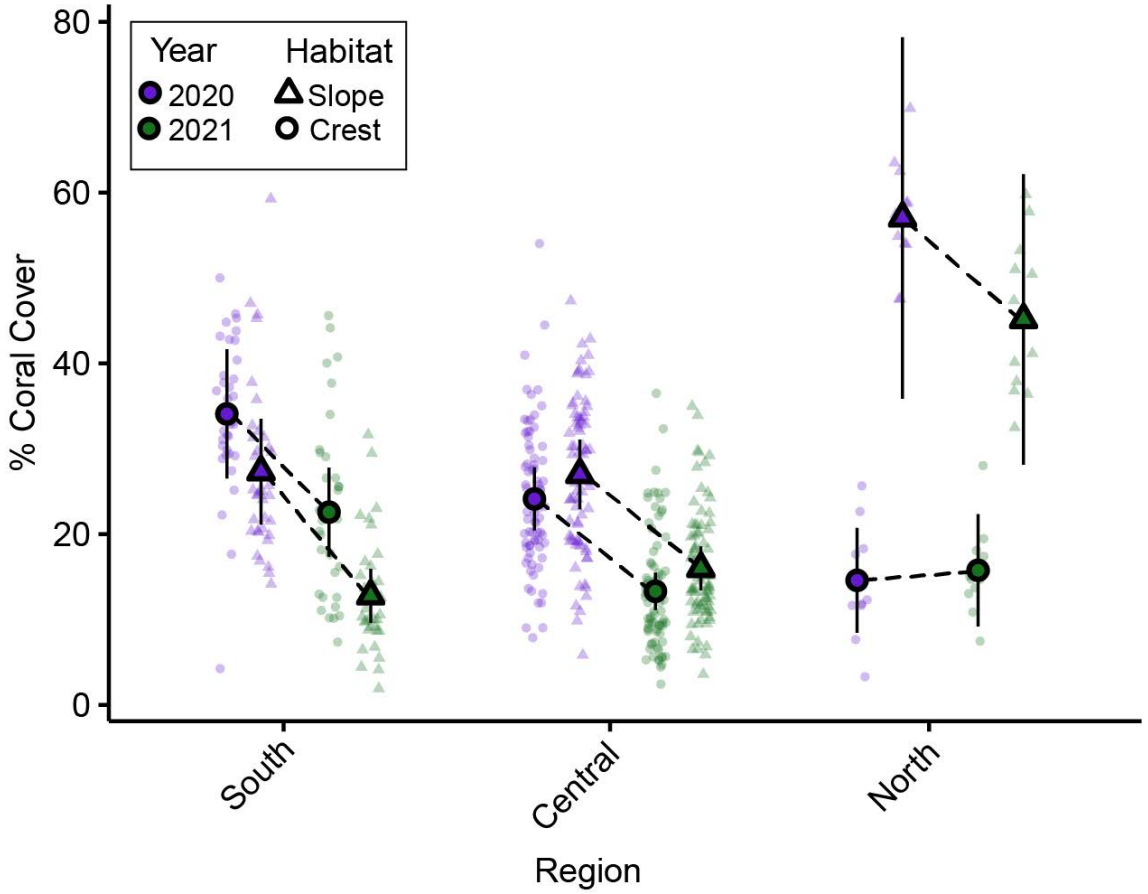


Figure 5.2: Estimated marginal mean (± SE) percent live coral cover in 2020 (purple) and 2021 (green) on the reef crest (circles) and slope (triangles) in the south, central and north Coral Sea Marine Park.

5.3.2 Relative susceptibility among coral taxa

Relative changes in coral cover varied among coral taxa following bleaching in 2020, however, taxa with the highest relative losses differed among regions of the CSMP (Fig. 5.3). In the northern CSMP, *Favites* exhibited the greatest relative loss in both habitats, most notably declining by 95% on the slope (from 5.5% ± 1.0 SE in 2020 to 0.3% ± 1.2 SE in 2021) (Fig. 5.3; Table S5.2). In contrast, relative increases were observed for *Montipora*, *Astreopora*, *Goniastrea*, and *Platygyra* on the crest, and massive *Porites* on the slope (Fig. 5.3; Table S5.2). However, due to low initial cover, these increases translated to only minor absolute changes on the reef crest (Table S5.2). In the central CSMP, *Stylophora* experienced the highest relative decline in cover, declining by 90% on the crest and 79.7% on the slope (Fig. 5.3; Table S5.2), whilst *Astreopora* experienced a relative increase of 56.4% on the crest, and an 11.1% decrease on the slope (each equating to negligible absolute changes; Fig 5.3; Table S5.2). Tabular and other *Acropora* also exhibited substantial relative losses on central crests (-81.8% and -69.8% respectively), while *Isopora* (-61%) and massive *Porites* (-59.9%) experienced substantial relative losses on central CSMP reef slopes (Fig 5.3; Table S5.2). Notably, massive *Porites* was among taxa exhibiting the least relative changes in the north, yet experienced substantial relative declines in both habitats in the central and southern CSMP (>55% across both regions; Fig. 5.3; Table S5.2). In the southern CSMP, relative losses were observed across all taxa, except for staghorn *Acropora* on the crest, which exhibited a small relative increase of 10.6% (equating to an absolute rise of only 0.1%; Fig 5.3; Table S5.2). On the reef crest, *Stylophora* and branching *Porites* exhibited relative declines of 84.4% and 81.3%, respectively (Fig 5.3; Table S5.2). On the slope, *Seriatopora* exhibited the greatest relative decline, with a reduction of 94.4%, followed by *Goniastrea*, which declined relatively by 73% (Fig 5.3; Table S5.2).

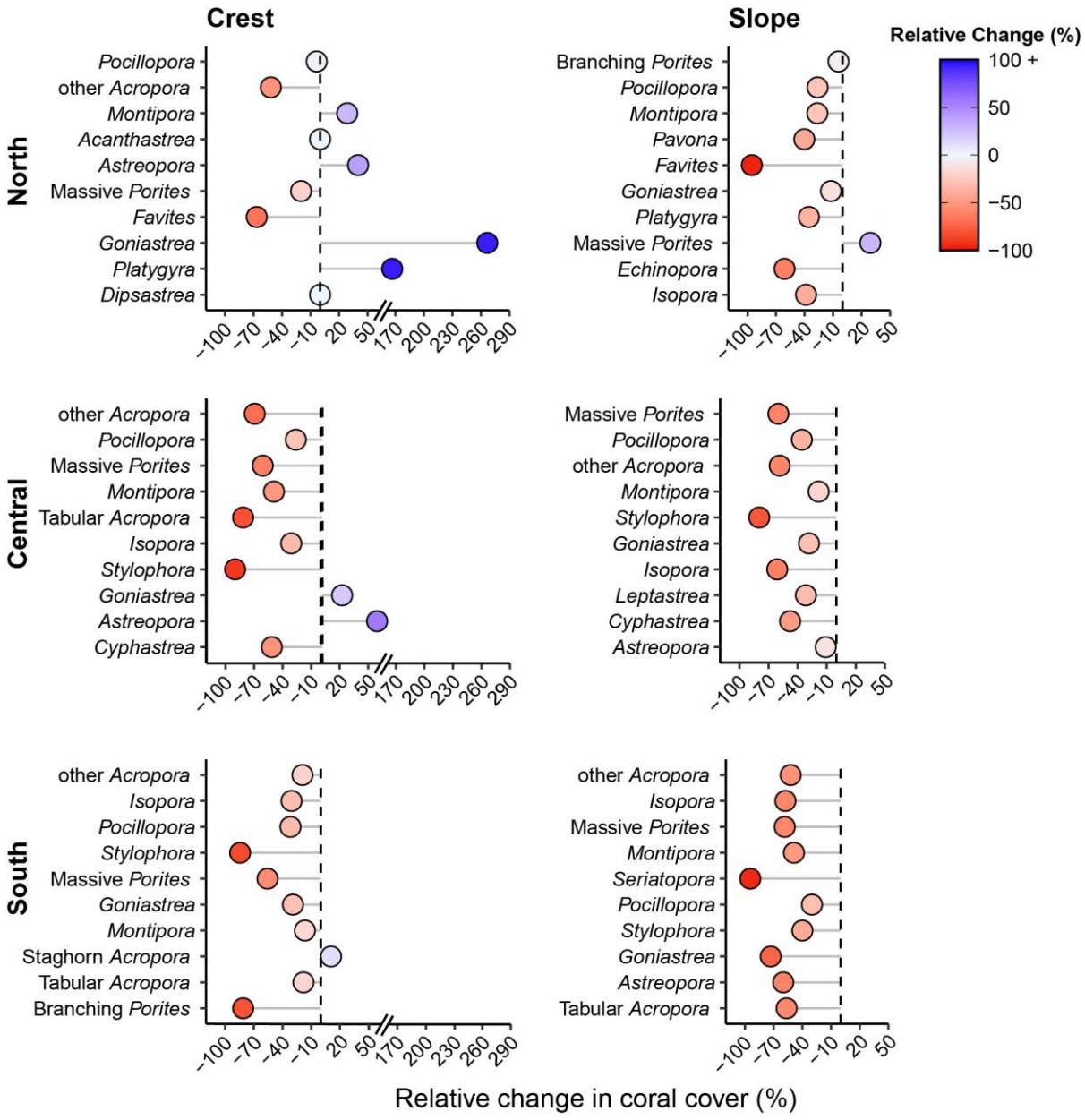


Figure 5.3 Relative change in coral cover for the 10 most common taxa (in 2020) per habitat per region. Taxa are ordered by absolute abundance (most common at the top). Points falling on the vertical dashed line (white) represent no change in percent cover. Points falling to the left of the line (shades of red) indicate declines, and points falling to the right (shades of blue) indicate increases in coral cover.

5.3.3 Shifts in coral communities

While there were substantial and disproportionate relative losses among coral taxa, it was dependent on initial dominance of susceptible taxa as to whether this resulted in significant changes in overall coral community composition (Fig. 5.4). In the northern CSMP, there were no significant shifts in community composition for either the reef crest (df = 1, R^2 = 0.107, F = 0.722; p = 0.557) or slope (df = 1, R^2 = 0.175, F = 1.28, p = 0.35) (Fig. 5.4). Indeed, the most common taxa in the northern CSMP were among those that experienced the lowest declines in cover with *Pocillopora* on the reef crest only experiencing a 3.6% relative decline from 9.3% ± 1.5 SE in 2020 to 8.9% ± 1.4 SE in 2021, and branching *Porites* declining on the reef slope from 9.6% ± 4.8 SE to 9.2% ± 3.4 SE (a relative loss of 4.3%) (Fig. 5.3). Similarly, there were no significant changes in community composition in the southern CSMP (crest: df = 1, R^2 = 0.03, F = 0.685, p = 0.651; slope: df = 1, R^2 = 0.035, F = 0.795, p = 0.629) (Fig. 5.4). The three most common taxa on southern reef crests experienced only moderate relative declines (other *Acropora*: -19.2%; *Isopora*: -30.6%, *Pocillopora*: -31.7%, Table S5.2), whilst all taxa experienced high and similar proportional losses on southern reef slopes, with the least susceptible taxon in this habitat experiencing a 30% relative loss (Fig. 5.3; Table S5.2). In the central CSMP, significant changes in community composition occurred in both habitats. On the crest (df = 1, R^2 = 0.117, F = 6.87, p = 0.001) and the slope (df = 1, R^2 = 0.063, F = 3.492, p = 0.001), communities lost large proportions of the most common taxa, including other *Acropora* and massive *Porites*, both of which experienced relative declines exceeding 58% (Figs 5.3, 5.4; Table S5.2).

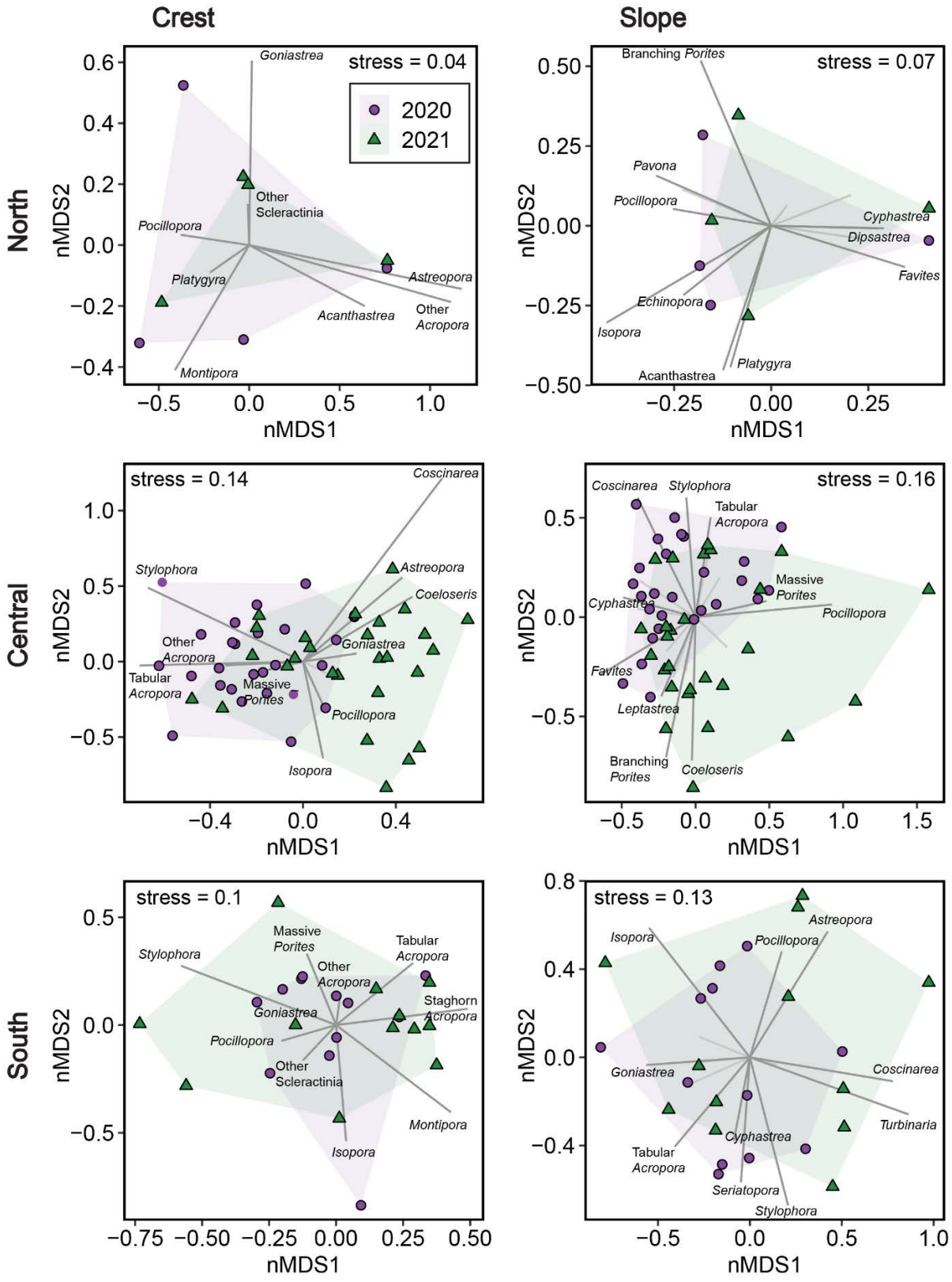


Figure 5.4: Non-metric multidimensional scaling plots visualising coral community composition in 2020 (purple centroid), and 2021 (green centroid) for the north (top) central (middle) and south (bottom), reef crests (left column) and slope (right column). Each point represents the coral assemblage

at each site, with colours and shapes representing year (purple circles = 2020, green triangles = 2021). The relative contributions of taxa to the observed variation in composition are shown as vectors underlaid on each plot.

5.4 Discussion

A relative decline of 38.9% in coral cover was recorded across the CSMP between February 2020 and March 2021, in the aftermath of the 2020 coral bleaching event, during which 57.6% coral colonies exhibited signs of bleaching (Burn et al. 2023 [**Chapter 4**]). This decline included a 37.8% overall relative reduction on reef crest habitats (from 27.5% to 17.1%) and a 40.3% relative reduction on reef slope habitats (from 31.5% to 18.8%). This extent of coral bleaching and mortality reflects the intensity of the heatwave, with all reefs throughout the CSMP affected by heat stress exceeding the threshold of 8 DHW expected to cause severe bleaching and mortality (9.25 – 12.83 DHW, Table S5.1; Hughes et al. 2018b, 2021). However, this result contrasts markedly with the impacts of previous bleaching events in 2016 and 2017 in the central CSMP, where similar heat stress (up to 12 DHW) elicited significant bleaching, yet only a 14.4% proportional coral loss (equating to a 3% absolute decline; Harrison et al. 2019). The seemingly increased impact of bleaching on central CSMP reefs in 2020 may be, in part, a result of recent increases in cover of susceptible taxa (e.g., *Acropora*, which reached >7% cover on central crest habitats, up from 4% in 2016; Harrison et al. 2019). However, it is possible that the extensive spatial footprint of severe heat stress in 2020 (Smith 2024) has diminished conditions previously conferring resilience to coral assemblages in the CSMP (Harrison et al. 2019; Baumann et al. 2022).

Fast-growing branching taxa (*Acropora*, *Pocillopora* and *Stylophora*) are generally among the most susceptible taxa to severe marine heatwaves, not only exhibiting disproportionate levels of bleaching, but also mortality (Marshall and Baird 2000; Loya et al.

2001; Swain et al. 2016). Indeed, *Stylophora*, *Seriatopora*, and *Acropora* exhibited high levels of bleaching in February 2020 (Burn et al. 2023 [**Chapter 4**]), and subsequently suffered some of the highest proportional mortality throughout the central and southern CSMP. However, mortality levels for *Pocillopora* were much lower than expected, given the level of bleaching recorded (Burn et al. 2023 [**Chapter 4**]) with only a 3.6% relative decline on northern CSMP reef crests (from 9.25% in 2020 to 8.91% in 2021). On the other hand, slow-growing massive taxa are generally considered resilient to bleaching and mortality (Marshall and Baird 2000; Loya et al. 2001; Levas et al. 2013), yet *Favites* experienced the highest relative decline in the northern CSMP, and massive *Porites* exhibited similar relative decline to *Acropora*, with losses exceeding 50% in both habitats of the central and southern regions. These findings show that differential bleaching among coral taxa does not necessarily reflect the subsequent levels of mortality, and supports hypotheses from previous work suggesting that massive *Porites* joins the ranks of the most susceptible taxa when bleaching severity becomes extreme (Burn et al. 2023 [**Chapter 4**]).

Despite marked differences in relative mortality among coral taxa, the relative abundance of susceptible taxa ultimately determined the magnitude of coral loss and concomitant shifts in community composition. Low abundance of the most susceptible taxa (e.g., *Favites*, *Stylophora*, *Seriatopora*), and high abundance of the least susceptible (e.g., branching *Porites*, *Pocillopora*) contributed to the absence of significant community changes in the northern and on southern CSMP reef crests. Notably, *Favites* and *Pocillopora* accounted for 1.71% and 63% of the northern crest community, respectively, resulting in minimal changes in overall cover, despite differences in relative mortality. Conversely, similar relative declines across common taxa resulted in no shift in composition on southern CSMP slopes, where communities were still dominated by *Acropora* (Table S5.2). Significant shifts in community composition were only evident in the central CSMP region, and were driven by significant

declines in dominant taxa (*Acropora* and massive *Porites*) resulting in a predominance of *Pocillopora* (Table S5.2). Regardless of community shifts, overall declines in the abundance of complex branching taxa will reduce habitat complexity (Alvarez-Filip et al. 2011; Darling et al. 2017; Magel et al. 2019; Morais et al. 2022) with broader impacts on other reef organisms (Graham and Nash 2013; Rogers et al. 2014; Alvarez-Filip et al. 2015; Darling et al. 2017; Ceccarelli et al. 2024).

The selective and directional effects of climate induced coral bleaching on coral assemblages in isolated locations is further compounded by the inherent constraints to resilience imposed by increased reliance on self-recruitment (Halford and Caley 2009; Holbrook et al. 2018; Burn et al. 2024 [**Chapter 3**]). Isolated reefs suffering significant coral loss often experience a concomitant decline in recruitment or juvenile densities (Alling et al. 2007; Gilmour et al. 2013; Sheppard et al. 2020; see **Chapter 1**), with implications for recovery potential. Isolated reefs may rely on re-growth of remnant colonies to initiate recovery before a critical mass of gravid colonies can sustain recruitment (Gilmour et al. 2013). Importantly, despite significant coral loss in 2021, the northern CSMP still harboured high coral cover (45% on reef slopes), dominated by branching *Porites* and *Pocillopora*, suggesting sufficient brood-stock for recovery, albeit with low abundance of other fast-growing taxa (*Acropora*, *Isopora*, *Stylophora*). In contrast, many reefs in the central and southern CSMP have now dropped to critical levels of coral cover (<15%) with a notable lack of fast-growing *Acropora* in the central region (<2%; Table S5.2). Diminished source populations of *Acropora*, a taxon that drives fast recovery owing to its fast growth rates and high recruitment (Johns et al. 2014; Pratchett et al. 2015; Gouezo et al. 2019; Morais et al. 2023), may result in protracted recovery on many central CSMP reefs (Burn et al. 2024 [**Chapter 3**]). However, the relative resilience of *Pocillopora* to bleaching in the CSMP may provide an alternative pathway to recovery, with fast growth and high recruitment conducive to recovery in other systems (e.g., Moorea;

Pratchett et al. 2013; Tsounis and Edmunds 2016). Furthermore, the brooding reproductive strategy in some *Pocillopora* species, coupled with their relatively short larval duration, may enhance self-seeing on isolated reefs (Harii et al. 2002).

Recovery and/or reassembly of coral assemblages fundamentally depends on disturbance regimes, whereby the frequency and severity of disturbances influences recovery and reassembly (Pratchett et al. 2020). Projected increases in the frequency and intensity of marine heatwaves and cyclones (Cheal et al. 2017; Li and Donner 2022; McWhorter et al. 2022) may reduce the cover of susceptible taxa before recovery is realised (Hughes et al. 2017; Gouezo et al. 2019), and favour taxa more resilient to heat stress (e.g., *Pocillopora*). The time required for recovery to pre-disturbance states on other reef systems can be >10 years, and is contingent on a lack of both acute and background disturbances (Burt et al. 2008; Wakeford et al. 2008; Gilmour et al. 2013; Pisapia et al. 2016; Gouezo et al. 2019). Remote CSMP reefs have reduced exposure to many of the background pressures that impact coastal reefs (e.g., sedimentation, pollution, overfishing), and may therefore, provide conditions conducive for recovery, given enough time between acute disturbances (Gilmour et al. 2013). But, given the high frequency of cyclones in the CSMP (Oxley et al. 2003; Brewer et al. 2007), and five bleaching events since 2002 (Oxley et al. 2003, 2005; Harrison et al. 2019; Burn et al. 2023 [**Chapter 4**]), the likelihood of recovery is uncertain.

The widespread and significant loss of coral in the CSMP, and particularly the substantial loss of typically resilient massive *Porites* corals in the central and southern regions, highlights the severity of the 2020 coral bleaching event, and the vulnerability of these assemblages to increasingly extreme thermal stress (Oliver et al. 2018; Skirving et al. 2019; Burn et al. 2023 [**Chapter 4**]). Continued monitoring and research is essential to determine whether coral assemblages in the CSMP can recover or reassemble into their pre-disturbance communities or if shifts toward a dominance of *Pocillopora* on some reefs will lead to a new

ecological state (e.g., Moorea, Pratchett et al. 2011) with long-term implications for biodiversity, ecosystem function, and recovery potential. Specifically, future research should aim to disentangle the relative demographic contributions of growth, recruitment and early life processes to recovery on isolated reefs (Doropoulos et al. 2015; Gouezo et al. 2019; Speare et al. 2025). More work is also required to understand size-based coral loss in the CSMP, including survival of juvenile corals, which may have differential susceptibility to bleaching (Álvarez-Noriega et al. 2018; Burn et al. 2023 [**Chapter 4**]; Winslow et al. 2024) and serve as critical seed banks for replenishment (Doropoulos et al. 2022). Given the escalating frequency and intensity of disturbances predicted under climate change (Cheal et al. 2017; Oliver et al. 2018; Li and Donner 2022; McWhorter et al. 2022), it is imperative to enhance our understanding of the processes shaping coral recovery and resilience on remote and isolated reefs, which are highly vulnerable in the face of environmental change (Baumann et al. 2022).

Chapter 6. General Discussion

6.1 Vulnerability of coral assemblages in Australia's Coral Sea Marine Park

Remote, isolated coral reefs, including those within Australia's Coral Sea Marine Park (CSMP), are expected to support relatively healthy coral reef communities owing to their separation by distance from many chronic anthropogenic and land based pressures, which represent a perennial threat to many coastal reef systems (Sandin et al. 2008; Barott et al. 2010; Riegl et al. 2010; Williams et al. 2015). Remote reefs are nevertheless impacted by major acute disturbances, such as cyclones and marine heatwaves, which can cause significant coral loss (Gilmour and Smith 2006; Alling et al. 2007; Vargas-Ángel et al. 2019). The frequency, extent and intensity of major acute disturbances is increasing, mostly related to highly pervasive effects of climate change (Cheal et al. 2017; Hughes et al. 2018a; Oliver et al. 2018), which reduces opportunities for recovery in the period between successive disturbances, and has already resulted in protracted declines in the cover of live corals on many remote and isolated reefs (Brainard et al. 2018; Sheppard et al. 2020; Lange et al. 2021). The absence of chronic pressures may nonetheless provide increased resilience for isolated and remote coral assemblages, allowing for relatively rapid recovery in the aftermath of major disturbances (e.g., Gilmour et al. 2013). Conversely, recovery on isolated reefs may be highly dependent on self-recruitment due to limited proximity to other (less perturbed) reef systems and corresponding constraints on connectivity (Gilmour et al. 2013; Grimaldi et al. 2024).

Logistical difficulties of surveying remote coral reefs have resulted in considerable spatial and temporal gaps in our knowledge of coral dynamics on many remote reef systems, limiting our understanding of the effects of major disturbances, and the likelihood of recovery in a changing environment (**Chapter 1**). In Australia's CSMP, shallow coral reef systems are among the most well studied of the diverse array of habitats present within the marine park

(Ceccarelli et al. 2013), yet many knowledge gaps persist, relating to contemporary coral assemblage structure, response to disturbances, and especially capacity to recover from disturbances. Previous work has demonstrated marked variation in coral assemblages throughout regions of the CSMP, with reports of near pristine coral assemblages (>40% coral cover) in the northern and southern regions of the CSMP, and persistently low coral cover (<20%) on many reefs in the central CSMP (Byron et al. 2001; Oxley et al. 2003, 2004, 2005; Ceccarelli et al. 2008, 2009; Stuart-Smith et al. 2013; Edgar et al. 2015; Harrison et al. 2019). Low coral cover in the central CSMP is generally attributed to high frequency of cyclones (Ceccarelli et al. 2008) as well as more recent impacts of marine heatwaves, with coral bleaching documented in 2002, 2004, 2016 and 2017 (Oxley et al. 2003, 2004, 2005; Stuart-Smith et al. 2018; Harrison et al. 2019). However, our understanding of coral assemblage dynamics and the specific effects of different disturbances in the CSMP is limited by the lack of routine monitoring and spatially restricted sampling (Oxley et al. 2003, 2004, 2005; Ceccarelli et al. 2008, 2009; Stuart-Smith et al. 2013, 2018; Edgar et al. 2015; Harrison et al. 2019).

This thesis highlighted marked differences in coral assemblages across the CSMP and GBRMP, that were apparent even before the 2020 mass bleaching, and likely reflect regional differences in vulnerability to different disturbances and recovery potential (**Chapter 2**). Despite the CSMP's isolation from chronic pressures, not all regions harboured high coral cover before the 2020 bleaching (**Chapter 2**). In the central CSMP, coral cover on most reefs was low (<25%) with a notable suppression of fast-growing taxa, contributing to the body of research suggesting this region is persistently affected by cyclones and bleaching events (Ayling and Ayling 1985; Oxley et al. 2003, 2004, 2005; Ceccarelli et al. 2008, 2009; Stuart-Smith et al. 2013; Edgar et al. 2015). Moreover, the abundance of juvenile corals was low, with a conspicuous lack of *Acropora* juveniles, likely due to inherent constraints on connectivity

combined with low adult stock of *Acropora* (**Chapter 3**). Whilst there was some evidence of increasing coral cover and cover of *Acropora* in the central CSMP between 2017 and 2020 (**Chapters 1**, **2**, **5**; (Harrison et al. 2019), this recovery was disrupted by the 2020 bleaching event, with coral cover declining from 24.1% and 27% (reef crest and slope, respectively) in 2020, to 16% and 15.8% in 2021 (**Chapters 4**, **5**). The near complete loss of *Acropora* in the central CSMP after the bleaching resulted in significant shifts in community composition (**Chapter 5**), with potential ramifications for reef structure and function (Graham et al. 2007; Darling et al. 2017; Richardson et al. 2018; Estrada-Saldívar et al. 2019; Perry and Alvarez-Filip 2019; Morais et al. 2022). The predicted increasing frequency and severity of disturbances (van Hooidonk et al. 2013; Cheal et al. 2017; Oliver et al. 2018; Li and Donner 2022), combined with inherent constraints on recovery due to poor connectivity, will likely continue suppressing coral cover on the central CSMP.

In contrast, the southern CSMP supported high coral cover (>30%) on reef crests, dominated by fast-growing, branching taxa, indicating limited impacts from past disturbances but highlighting vulnerability to future environmental change (**Chapter 2**). Abundance of juveniles was low, albeit higher than the central CSMP and with a predominance of *Acropora* juveniles, suggesting an improved capacity to recover (**Chapter 3**). This vulnerability became evident in 2020, when mass bleaching led to a 33.7% and 53.1% relative decline in coral cover on the reef crest and slope, respectively (**Chapters 4, 5**). Coral loss was driven by declines across all taxa, highlighting the severity of this event and resulting in a community composition that remained similar, but with reduced overall coral cover. Declines were evident in fast-growing branching taxa (*Acropora*, *Isopora*, *Stylophora*), which were highly susceptible to bleaching (**Chapter 4**), but also in traditionally robust taxa, (massive *Porites*), which only bleached in extreme conditions (**Chapter 4**). The 2020 bleaching event is the most significant disturbance recorded to date on southern CSMP reefs, yet average coral cover still remained

>10% for both reef crests and slopes, with *Acropora* still dominant on reef crests. If sufficient time passes between successive disturbances, the absence of chronic anthropogenic pressures, coupled with the persistence of fast-growing taxa, may facilitate the recovery of the southern CSMP reefs.

The northern CSMP exhibited high coral cover (>40%) on reef slopes, but low cover on reef crests (14.6%), dominated by a mixture of slow-growing, stress-tolerant branching *Porites*, and faster growing, typically bleaching-susceptible *Pocillopora* before bleaching in 2020 (**Chapter 2**). This suggests that previous disturbances (possibly bleaching in 2016; Stuart-Smith et al. 2018) may have suppressed other susceptible taxa (e.g., *Acropora*). But the dominance of tolerant taxa (e.g., branching *Porites*) may confer resilience to future disturbances (Hughes et al. 2019b). Again, juvenile densities were low, but juvenile communities were dominated by fast-growing *Pocillopora* and *Acropora* (**Chapter 3**). Whilst the 2020 bleaching event caused a 20.7% decline in coral cover on reef slopes, the preponderance of relatively resilient taxa (including *Pocillopora* which bleached but did not die; **Chapters 4**, **5**) resulted in maintenance of relatively high coral cover in 2021 (45% coral cover), and no shift in community composition (**Chapter 5**). Coral assemblages in the northern CSMP will likely continue to persist with a dominance of *Pocillopora* and branching *Porites*, where reef crests may exhibit increases in coral cover, given the propensity of *Pocillopora* to rapidly grow and reproduce (Pratchett et al. 2011).

Although coral cover in the northern and southern CSMP was relatively high, which may be reflective of isolation from many chronic pressures, cover was not consistently higher than on comparable outer-shelf reefs of the GBRMP (**Chapter 2**). Furthermore, geographically isolated reefs in the CSMP had 69% fewer juvenile corals than the more connected GBRMP, reinforcing the challenges of post-disturbance recovery in isolated systems (**Chapter 3**). This suggests that isolation alone does not confer resilience, particularly when disturbances are

severe and recovery potential is constrained (Favoretto et al. 2020; Baumann et al. 2022). A key difference between the two marine parks was the presence of population irruptions of crown-of-thorns starfish (CoTS; *Acanthaster* cf. *solaris*), which had severely impacted the southern GBRMP (Matthews et al. 2024). Whilst *Acanthaster* cf. *solaris* is present in the CSMP, outbreak populations have not been recorded to date, although population irruptions have been reported on other isolated, oceanic coral reefs (Timmers et al. 2012; Roche et al. 2015).

Together, the findings of this thesis suggest that the CSMP was already highly vulnerable to disturbances before the 2020 bleaching event and exhibits limited capacity for recovery. The suppression of coral cover in 2021, combined with the prominent decline of both *Acropora* and *Porites*, signals a concerning trajectory for post-disturbance recovery, particularly in the central CSMP. While the northern CSMP retained relatively high coral cover, and the southern CSMP retained its community structure, the long-term resilience of these regions remains uncertain, as continued exposure to severe bleaching events and cyclones may erode their capacity to withstand future disturbances (Ainsworth et al. 2016).

Although remote and isolated reefs are often perceived as relatively pristine due to their distance from direct anthropogenic pressures, this research underscores that climate-driven disturbances can exert severe and lasting impacts, with limited capacity for natural recovery in isolated systems. The constraints on larval supply and recruitment, combined with the increasing frequency of extreme thermal stress events, may challenge the long-term persistence of coral assemblages in the CSMP, as it has on other isolated reef systems (Smith et al. 2008a; Brainard et al. 2018; Vargas-Ángel et al. 2019; Sheppard et al. 2020; Baumann et al. 2022; Couch et al. 2023). Understanding the interplay between disturbance history, connectivity, and taxon-specific resilience will be critical for predicting reef futures in a rapidly changing climate.

6.2 Future directions

The research presented in this thesis highlights large-scale spatial variation (>1,000s km²), emphasising distinct differences in coral cover and composition between the CSMP and GBRMP, which has significant utility for understanding the differential disturbance regimes and anthropogenic pressures affecting isolated oceanic reefs (CSMP), compared to highly-connected, coastal reef systems (GBRMP), and corresponding effects on reef structure, function and resilience. Future work is required to target finer-scale variation, especially within the northern and central CSMP to identify reefs or sites with exceptionally high (or low) coral cover. Identifying such locations (e.g., bright spots; Cinner et al. 2016; Hoey et al. 2020) could be critical for targeted management and conservation, serving as potential source reefs or areas of resilience (Hock et al. 2017; Gouezo et al. 2021a). Understanding the drivers of resilience in these sites could provide valuable insights for enhancing reef management.

With evidence of significant coral loss and shifts in community composition in **Chapter 5**, more work is required to understand how changes in coral cover, communities and size structure may impact the organisms dependent on them for food and habitat (Richardson et al. 2018; Stuart-Smith et al. 2018; Ceccarelli et al. 2024). Ongoing monitoring of fish assemblages will be important to capture any lag-effect from the impacts of this 2020 bleaching event (Graham et al. 2007; Pratchett et al. 2018). Further research is warranted to explicitly test for relationships between live coral cover, structural complexity and reef fish assemblages in the CSMP (Darling et al. 2017), where other benthic organisms or habitat types may compensate for functions traditionally provided by scleractinian corals in areas with low coral cover. For example, calcifying algae (e.g., *Halimeda* spp and crustose coralline algae; CCA) may maintain structural complexity important for reef fishes, or contribute to reef accretion (Cornwall et al. 2023), while habitats dominated by other benthic types (e.g., rubble) may serve as important habitats for crypto-benthic fishes or invertebrates (Wolfe et al. 2021).

Understanding these dynamics could provide insight into the extent to which benthic community shifts alter reef ecosystem functioning.

This thesis highlights the critical need for ongoing monitoring to track coral recovery, and identify processes driving recovery, following the declines documented in **Chapter 5**. **Chapter 3** infers poor recovery potential for CSMP reefs through low densities of juvenile corals, but further research is needed to (i) quantify annual variation in juvenile coral densities to strengthen the hypotheses presented herein (Wallace 1985; Irizarry-Soto and Weil 2009; Edmunds 2013), and (ii) deploy recruitment tiles to better understand if constraints to recovery indeed lie in limited larval supply, or instead are driven by high rates of post-settlement mortality (Penin et al. 2010). Understanding rates of recruitment, as well as post-settlement growth and survival will be key for determining bottlenecks to recovery (Chong-Seng et al. 2014; Doropoulos et al. 2015; Sarribouette et al. 2022; Speare et al. 2025). Additionally, the lack of fine-scale hydrological, oceanographic, and genetic data limits understanding of coral connectivity (but see van Oppen et al. 2008; Choukroun et al. 2010; Hoey et al. 2020; Marzonie et al. 2023), which is crucial for assessing recovery potential in these isolated reefs, especially in the face of climate change (Cheung et al. 2021; Figueiredo et al. 2022).

Chapter 4 highlights taxon- and size-based differences in bleaching susceptibility, with juveniles appearing more resistant. However, tracking of individual colonies through tagging or photogrammetry (Meiling et al. 2020; Kopecky et al. 2023) is needed to determine lethal and sublethal effects (e.g., reduced growth and partial mortality; Gold and Palumbi 2018; Leinbach et al. 2021; Burn et al. 2022), which may alter structure and functions (Pisapia et al. 2020; Madin et al. 2023). Small colonies, which may predominate after bleaching, may play a key role in recovery (Doropoulos et al. 2022; Speare et al. 2022; Winslow et al. 2024), but shifts toward smaller colonies due to mortality could reduce reef complexity and fecundity, with cascading effects on reef ecosystems (Graham and Nash 2013; Graham and van Woesik

2013; Hughes et al. 2019a; Álvarez-Noriega et al. 2023). Ongoing surveys, coupled with demographic assessments of colony size, growth, partial mortality, and recruitment, are critical to understanding coral recovery trajectories and informing reef management strategies in the face of climate change (Holbrook et al. 2018; Jones et al. 2023; Morais et al. 2023).

6.3 Conclusions

Australia's Coral Sea Marine Park holds ecological, cultural, and economic significance, harbouring diverse habitats including sea mounts, expansive abyssal plains, islands, and coral reefs (Stoeckl et al. 2010; Ceccarelli et al. 2013). The research presented in this thesis has (i) provided an important update on the contemporary state of coral assemblages throughout the CSMP, (ii) provided new insight into the recovery potential of isolated reefs within the CSMP, (iii) quantified which coral colonies were most susceptible to coral bleaching during the severe 2020 marine heat wave, and (iv) assessed how susceptibility to bleaching translated into changes in coral cover and community composition in the aftermath. This research highlights the extreme vulnerability of isolated coral assemblages, despite their relative distance from many of the chronic pressures that impact more coastal reef systems (Coelho and Manfrino 2007; Sheppard et al. 2020; Baumann et al. 2022).

Owing to their remoteness, significant logistical challenges exist for research and monitoring in the CSMP, although more work is necessary to document the drivers and/or bottlenecks to recovery following this most recent bleaching event. Recurrent surveys on other remote reefs (e.g., Chagos, Scott Reef, Palmyra Atoll) have provided valuable insights on disturbance regimes, and recovery capacity. Whilst this thesis adds significantly to the body of work conducted so far in the CSMP, comparable data are still lacking. Given the vast spatial scale of the CSMP (1,000,000 km^2), annual surveys may be impractical. Instead, monitoring select reefs (representing both bright and dark spots across the three regions) every 2-5 years

would help bridge critical knowledge gaps regarding the CSMPs recovery capacity (Gouezo et al. 2021a).

Isolation also limits opportunities for management. For example, active restoration practises now common on accessible reefs (Bayraktarov et al. 2020; McLeod et al. 2022; Pancrazi et al. 2023), are not feasible on remote reefs. Instead, management will rely on designating or maintaining protected areas and no-take zones, which may enhance resilience of remote systems (Magris et al. 2017; Favoretto et al. 2020). Moreover, international co-operation and strong climate policy is needed to curb emissions, which are the root cause of the environmental change threatening even our most isolated and remote coral reefs globally (Hughes et al. 2003, 2021; Hoey et al. 2016; Cheal et al. 2017; Heron et al. 2018; Lawman et al. 2022; van Woesik et al. 2022).

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Appendix A – Supplementary materials for Chapter 2

Table S2.1: Raw percentage cover per taxon within each habitat and region of the CSMP and GBRMP in 2020. Corresponding mvabund univariate contrasts and p values are presented, where LRT (likelihood ratio test) represents relative contributions to dissimilarity in community composition among regions, and significant p values (<0.05) infer a significant contribution to differences in communities among regions.

	Mean ± SE % cover by region						Total	
Taxon	South GBRMP	Central GBRMP	North GBRMP	South CSMP	Central CSMP	North CSMP	LRT	p -value
Crest								
Tabular *Acropora*	0.0 ± 0.0	7.6 ± 1.2	2.4 ± 0.4	1.5 ± 0.2	1.3 ± 0.1	0.6 ± 0.2	71.67	0.001
Other *Acropora*	0.8 ± 0.3	13.0 ± 1.1	7.5 ± 0.9	10.0 ± 0.7	3.8 ± 0.3	2.7 ± 0.4	59.05	0.001
Staghorn *Acropora*	0.0 ± 0.0	2.8 ± 0.6	0.4 ± 0.1	2.4 ± 0.4	0.2 ± 0.1	0.0 ± 0.0	55.71	0.001
Pocillopora	0.1 ± 0.1	4.8 ± 0.7	4.7 ± 0.7	1.9 ± 0.2	4.9 ± 0.3	6.7 ± 0.7	50.56	0.001
Isopora	0.3 ± 0.1	1.3 ± 0.3	0.7 ± 0.2	7.0 ± 0.9	0.5 ± 0.1	0.6 ± 0.3	47.69	0.001
Seriatopora	0.2 ± 0.1	0.0 ± 0.0	0.1 ± 0.0	0.4 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	34.97	0.001
Favites	0.12 ± 0.1	1.3 ± 0.3	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.3 ± 0.1	33.27	0.001
Stylophora	0.3 ± 0.1	1.1 ± 0.3	0.3 ± 0.1	1.9 ± 0.2	0.9 ± 0.1	0.5 ± 0.1	15.48	0.140
Montipora	0.3 ± 0.1	1.1 ± 0.2	0.7 ± 0.2	1.4 ± 0.2	1.2 ± 0.1	2.1 ± 0.4	12.27	0.380
Goniastrea	0.3 ± 0.1	1.7 ± 0.3	0.8 ± 0.2	0.9 ± 0.2	0.7 ± 0.1	0.5 ± 0.1	11.39	0.412
Branching *Porites*	0.4 ± 0.2	0.0 ± 0.0	0.3 ± 0.2	0.3 ± 0.2	0.1 ± 0.0	0.4 ± 0.2	9.45	0.551
Massive *Porites*	1.9 ± 0.5	2.2 ± 0.3	3.1 ± 0.4	3.1 ± 0.4	3.3 ± 0.3	1.5 ± 0.2	9.26	0.551
Dipsastraea	0.0 ± 0.0	0.5 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.0	0.3 ± 0.1	8.92	0.551
Other Scleractinia	1.2 ± 0.3	2.9 ± 0.5	2.7 ± 0.3	2.0 ± 0.2	2.5 ± 0.2	2.5 ± 0.3	6.18	0.551
Astrea	0.2 ± 0.1	0.3 ± 0.1	0.1 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	4.82	0.551
Slope								
Pocillopora	0.1 ± 0.1	2.2 ± 0.4	3.0 ± 0.4	0.6 ± 0.1	3.6 ± 0.2	5.5 ± 0.6	73.50	0.001
Branching *Porites*	1.6 ± 0.5	0.2 ± 0.1	0.6 ± 0.2	0.2 ± 0.1	0.2 ± 0.1	8.8 ± 1.8	64.44	0.001
Seriatopora	0.1 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	1.0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	58.63	0.001
Montipora	0.2 ± 0.2	2.0 ± 0.3	1.1 ± 0.2	2.4 ± 0.3	1.4 ± 0.1	4.8 ± 0.6	42.30	0.001
Other Scleractinia	1.2 ± 0.4	5.8 ± 0.8	5.4 ± 0.7	3.3 ± 0.3	5.6 ± 0.3	9.1 ± 0.7	36.90	0.001
Staghorn *Acropora*	0.0 ± 0.0	1.4 ± 0.4	0.8 ± 0.2	0.4 ± 0.1	0.2 ± 0.0	0.1 ± 0.1	35.23	0.001

Goniastrea	0.2 ± 0.1	0.9 ± 0.2	0.9 ± 0.1	0.4 ± 0.1	1.3 ± 0.1	1.9 ± 0.2	34.37	0.001
Favites	0.1 ± 0.1	0.9 ± 0.2	0.3 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	1.9 ± 0.3	34.23	0.001
Isopora	0.1 ± 0.1	0.4 ± 0.2	0.1 ± 0.1	4.7 ± 0.7	0.8 ± 0.1	1.4 ± 0.4	33.42	0.001
Tabular *Acropora*	0.0 ± 0.0	2.7 ± 0.6	1.5 ± 0.3	0.5 ± 0.1	1.0 ± 0.1	0.5 ± 0.1	30.36	0.002
Other *Acropora*	0.2 ± 0.1	4.1 ± 0.6	4.6 ± 0.6	3.7 ± 0.4	2.5 ± 0.2	2.2 ± 0.4	26.16	0.002
Dipsastraea	0.1 ± 0.1	0.8 ± 0.3	0.4 ± 0.1	0.3 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	14.46	0.087
Astrea	0.1 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.4 ± 0.0	0.3 ± 0.1	11.69	0.193
Massive *Porites*	0.7 ± 0.2	2.9 ± 0.4	3.4 ± 0.4	4.1 ± 0.5	4.2 ± 0.3	4.1 ± 0.5	10.42	0.205
Stylophora	0.2 ± 0.1	1.3 ± 0.3	0.5 ± 0.1	1.0 ± 0.2	1.2 ± 0.1	0.7 ± 0.2	8.07	0.205

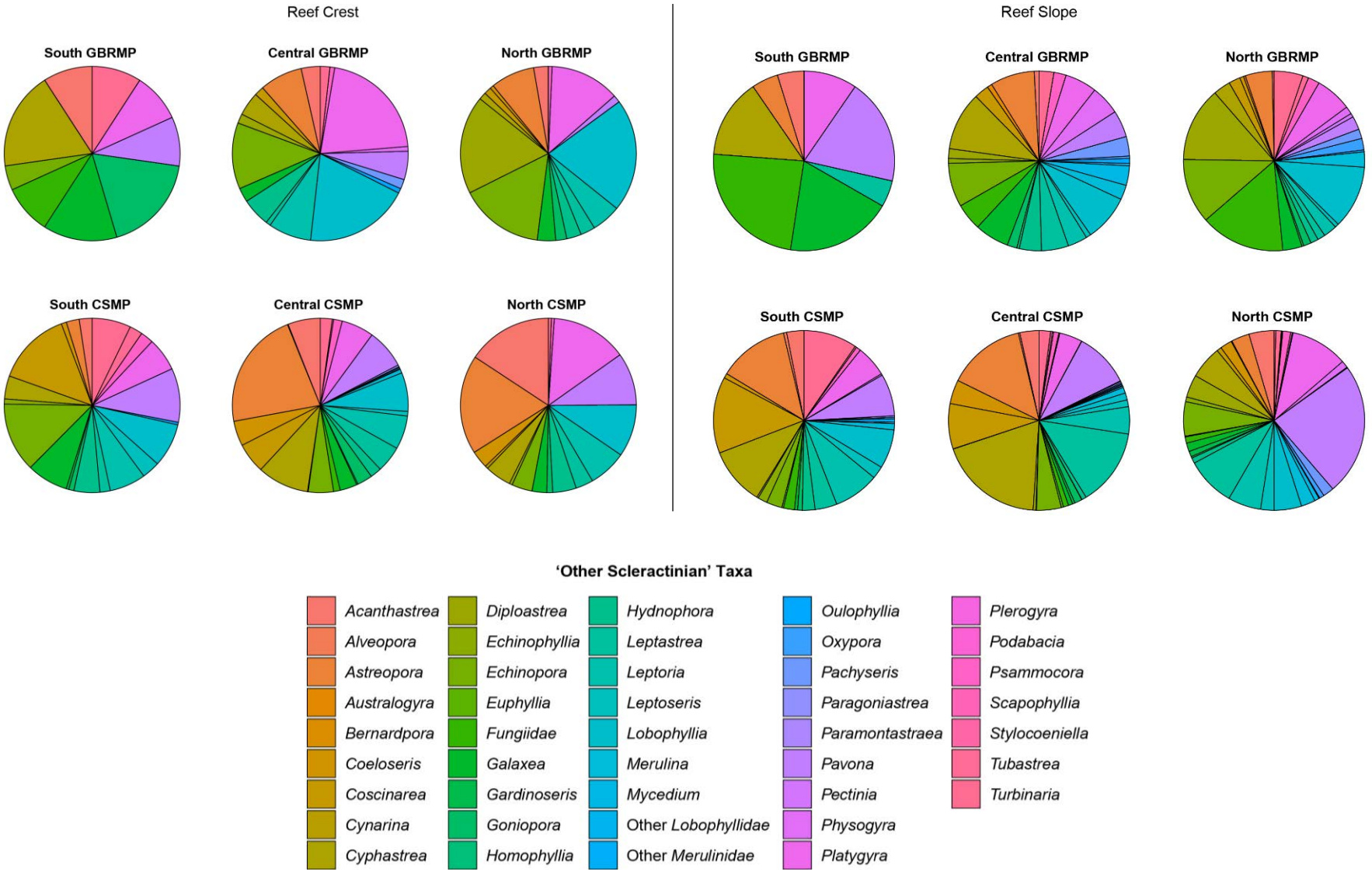


Figure S2.1: Proportions of 'other scleractinian' taxa in the coral community in habitats and regions of the CSMP and GBRMP.

Appendix B – Supplementary Materials for Chapter 3 (Burn et al. 2024)

Table S3.1 Summaries of GLMMs assessing the fixed effects of marine park, region and habitat, and their interactions on the abundance of juvenile corals belonging to four taxonomic groups: *Acropora*, *Porites*, *Pocillopora*, and remaining pooled taxa.

Response	Fixed effects	Estimate	Std. Error	Z-value	p-value
Juvenile *Acropora* Abundance	Intercept (GBRMP southern crest)	1.56896	0.75646	2.074	**0.0381**
	Marine Park CSMP	-0.09084	0.88876	-0.102	0.9186
	Region Central	1.13028	0.88011	1.284	0.1991
	Region North	0.22159	0.84474	0.262	0.7931
	Habitat Slope	-0.71924	0.33567	-2.143	**0.0321**
	CSMP: Central	-2.54580	1.05050	-2.423	**0.0154**
	CSMP: North	-0.13182	1.21687	-0.108	0.9137
	CSMP: Slope	0.03385	0.37937	0.089	0.9289
	Central: Slope	-0.46176	0.40130	-1.151	0.2499
	North: Slope	0.16999	0.38373	0.443	0.6578
	CSMP: Central: Slope	0.92350	0.45276	2.040	**0.0414**
	CSMP: North: Slope	-0.87849	0.50608	-1.736	0.0826
Juvenile *Porites* Abundance	Intercept (GBRMP southern crest)	3.66484	0.51340	7.138	**9.44e-13**
	Marine Park CSMP	-1.85034	0.59775	-3.096	**0.00196**
	Region Central	-2.92062	0.62497	-4.673	**2.97e-06**
	Region North	-1.86728	0.58963	-3.167	**0.00154**
	Habitat Slope	-0.96654	0.44673	-2.164	**0.03050**
	CSMP: Central	2.04315	0.72025	2.837	**0.00456**
	CSMP: North	0.03333	0.82073	0.041	0.96760

	CSMP: Slope	0.50376	0.50797	0.992	0.32133
	Central: Slope	1.20087	0.56011	2.144	**0.03203**
	North: Slope	0.08596	0.52827	0.163	0.87074
	CSMP: Central: Slope	-0.39486	0.62547	-0.631	0.52784
	CSMP: North: Slope	-0.05989	0.72401	-0.083	0.93408
Juvenile *Pocillopora* Abundance	Intercept (GBRMP southern crest)	0.08643	0.53528	0.161	0.87173
	Marine Park CSMP	-0.20507	0.62458	-0.328	0.74266
	Region Central	0.95052	0.62291	1.526	0.12703
	Region North	0.80894	0.59918	1.350	0.17699
	Habitat Slope	-0.68720	0.45624	-1.506	0.13200
	CSMP: Central	-0.82404	0.73119	-1.127	0.25975
	CSMP: North	0.57644	0.82367	0.700	0.48403
	CSMP: Slope	-0.74696	0.53605	-1.393	0.16348
	Central: Slope	-0.56471	0.52486	-1.076	0.28196
	North: Slope	0.14778	0.49918	0.296	0.76719
	CSMP: Central: Slope	1.98838	0.60647	3.279	**0.00104**
	CSMP: North: Slope	0.96099	0.61883	1.553	0.12044
Other juvenile taxa abundance	Intercept (GBRMP southern crest)	2.23946	0.25653	8.730	**< 2e-16**
	Marine Park CSMP	-0.66805	0.20588	-3.245	**0.001175**
	Region Central	-1.23619	0.25235	-4.899	**9.65e-07**
	Region North	-1.70140	0.30894	-5.507	**3.65e-08**
	Habitat Slope	0.09547	0.15410	0.620	0.53555
	Central: Slope	0.65482	0.18288	3.581	**0.000343**
	North: Slope	0.66840	0.23840	2.804	**0.005052**

Appendix C – Supplementary Materials for Chapter 4 (Burn et al. 2023)

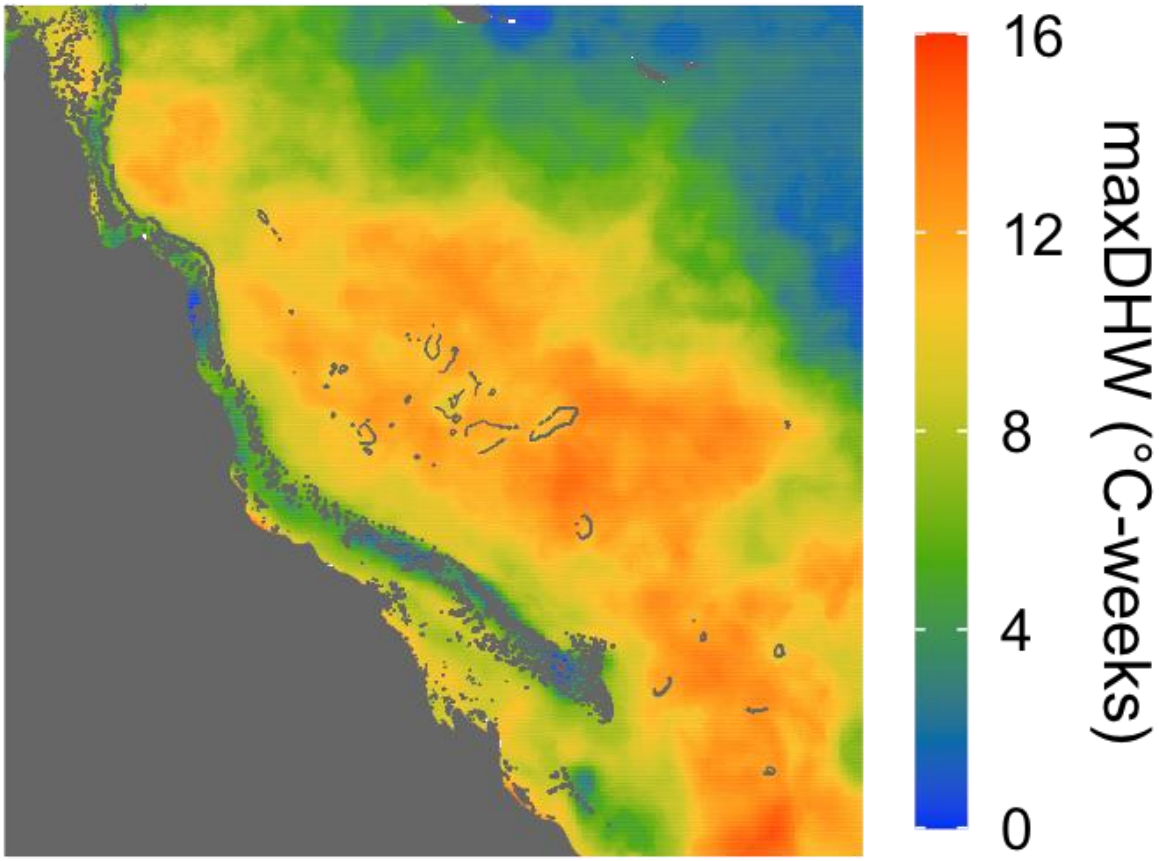


Figure S4.1: Map of heat stress (annual maximum degree heating weeks; °C-weeks) across the Great Barrier Reef and Coral Sea Marine Parks for the year 2020. The gradient of colours from blue (0 °C-weeks) to red (16 °C-weeks) indicate heat stress, whilst grey regions represent the Queensland coast and the coral reefs of the two Marine Parks. Data derived from NOAA Coral Reef Watch V3.1 5km Satellite Coral Bleaching Degree Heating Week product.

Reef-scale bleaching severity categories were determined based on proportion of colonies showing signs of bleaching. However, as the proportion of colonies showing signs of bleaching increased, so did the severity of bleaching at the colony level (Fig. S4.2). Thus, the proxy of bleaching severity used in our manuscript accounts for both incidence and severity of the bleaching response.

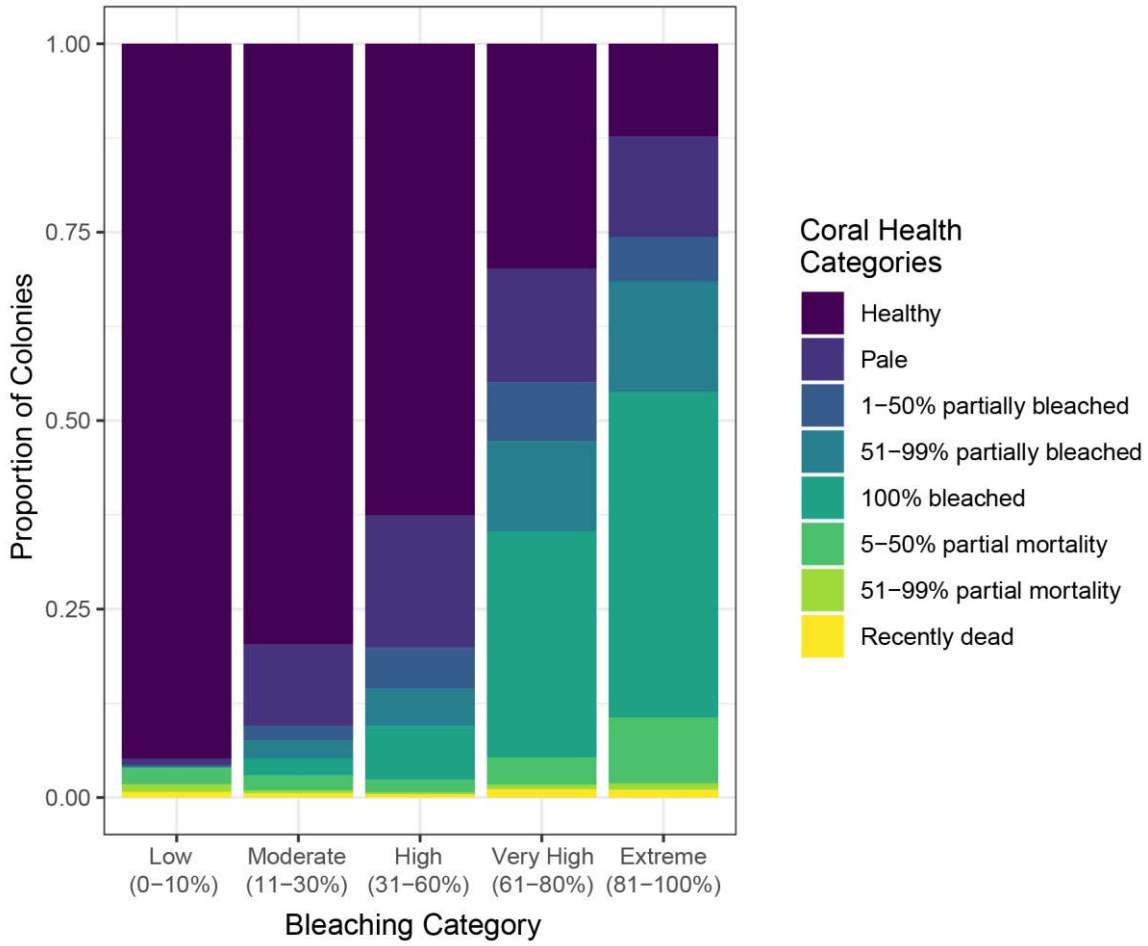


Figure S4.2: Proportion of coral colonies recorded within each of the eight health categories for each of the five reef-scale bleaching severity categories (Bleaching Category).

To determine if it was necessary to include habitat (reef crest and slope) in our analysis, a Bayesian hierarchical generalized linear model was constructed to assess the effect of habitat on bleaching susceptibility (Fig. S4.3). Two-way interactions between habitat and both taxa and reef-scale bleaching severity category were included to determine how bleaching susceptibility within these groups varied in response to habitat. Region (GBRMP vs CSMP) was included as a random factor to account for different bleaching susceptibilities between oceanic and continental shelf reefs. The model was fit against a zero-one inflated beta distribution, using weakly informative priors. Posteriors were generated via a No-U-Turn sampler (NUTS), run for 5000 iterations (excluding the first 1000 warmup samples) from each of the three chains, with a thinning rate of 10. All chains were found to be well mixed and converged (Rhat ~1) on a stable posterior. Goodness of fit was assessed statistically using leave-one-out cross-validation, ensuring all Pareto-k estimates were below 0.5, and visually using a posterior probability check.

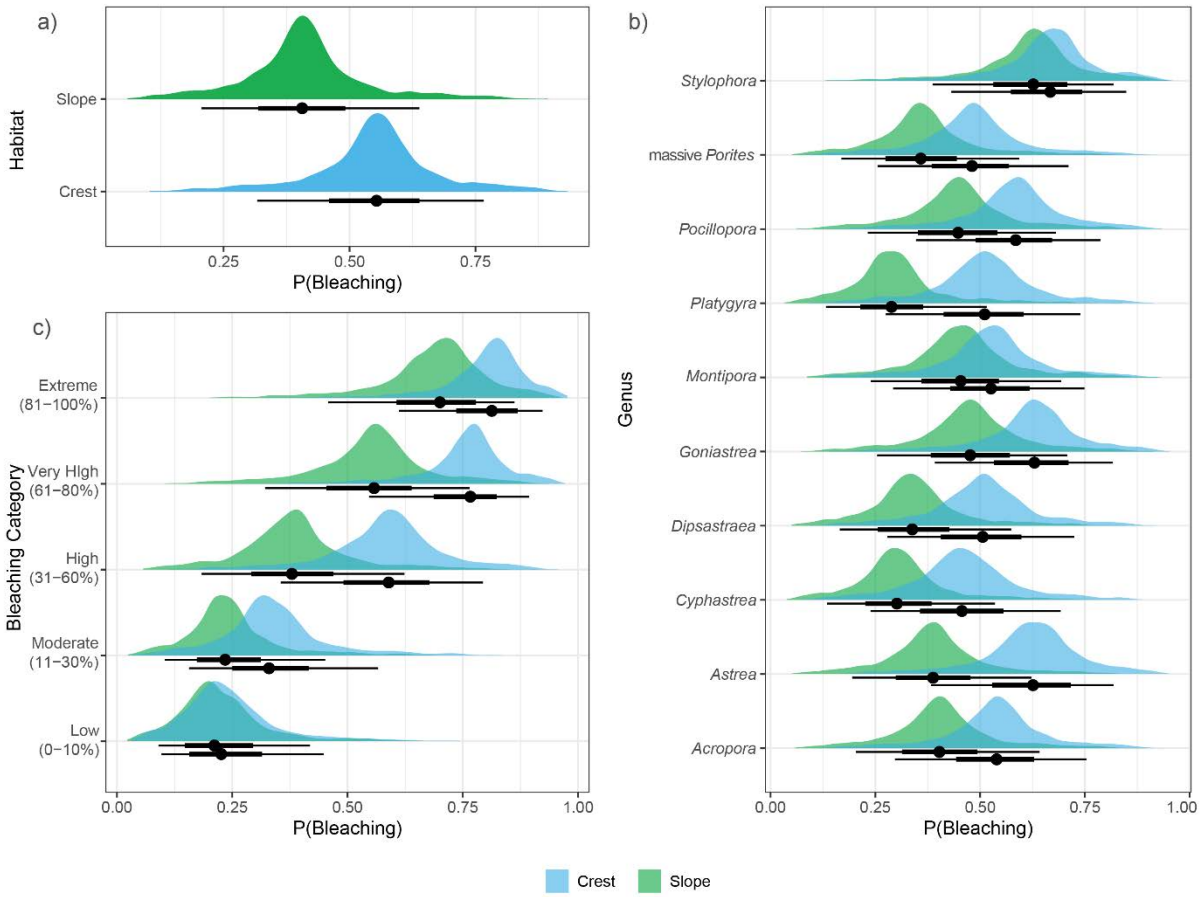


Figure S4.3: Marginal posterior distributions of bleaching susceptibility (P(Bleaching)) for each habitat (a), genus interacting with habitat (b) and reef-scale bleaching severity interacting with habitat (c). Points represent estimated marginal means, thick and thin lines represent 66% and 90% highest posterior density credible intervals, respectively.

There was strong evidence that bleaching was more likely on the reef crest compared to the reef slope (Fig. S4.3a; crest: 55% [90% Credible Intervals (CrI) 35.6 - 79.9%]; slope: 41% [CrI 15.2 - 57.9%]; contrast ratio: 1.82 [CrI 1.65 - 2.00]). There was strong evidence that bleaching was more likely on the crest than the slope for each bleaching severity category, except the Low (0-10%) category (Fig. S4.3c). This lack of statistical difference between habitats at reefs within the low severity category occurred because there were so few colonies bleached at these reefs (<10%). For all the taxa modelled, there was evidence that the likelihood of bleaching was higher on the reef crest compared to the reef slope (Fig. S4.3b). Due to the highly consistent effect of habitat on bleaching likelihood, and the lack of interaction in the model,

data across habitats was pooled to increase statistical power in the model presented in the manuscript.

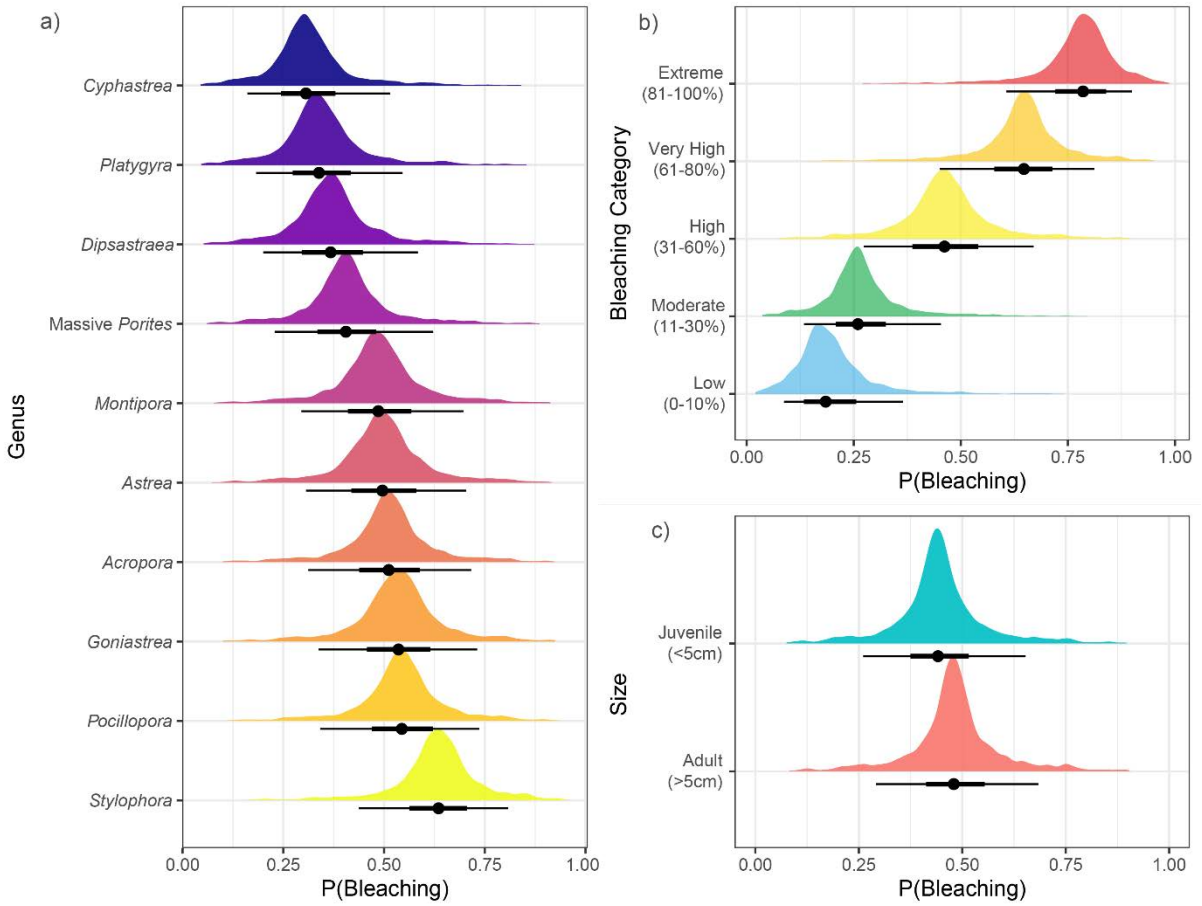


Figure S4.4: Marginal posterior distributions of bleaching susceptibility (P(Bleaching)) for genus (a), colony size (b) and reef-level bleaching severity (c). Points represent estimated marginal means, thick and thin lines represent 66% and 90% highest posterior density credible intervals, respectively.

Supplementary Tables

Tables below present pairwise comparisons of estimated marginal means for the three two-way interactions in the model presented in the main text. Where 66% and 90% highest posterior density credible intervals (CrI) are presented, they should be interpreted in the following manner. When the upper and lower bounds of the 66% CrI's do not contain 1, there is evidence of a difference in bleaching susceptibility between the contrasting variables, and where the bounds of the 90% CrI's do not contain 1, there is strong evidence of a difference in bleaching susceptibility between the contrasting variables. If both 90% and 66% CrI's do contain 1, it should be considered unlikely that there is any difference in bleaching susceptibility between the contrasting variables.

Table S4.1: Pairwise comparisons of estimated marginal means for bleaching susceptibility between size classes (adults *vs* juveniles), presented for the fixed effect and for each taxon in the interaction.

Genus	Contrast (size class)	Response	Confidence level	Lower CrI	Upper CrI	Likelihood of difference
A) Fixed effect of size class						
	Adult >5cm / Juv <5cm	1.164	0.66	1.056	1.237	Very Likely
			0.9	1.009	1.318	
B) Interaction between Taxa and Size Class						
Acropora	Adult >5cm / Juv <5cm	1.168	0.66	0.958	1.365	Unlikely
			0.9	0.805	1.527	
Astrea	Adult >5cm / Juv <5cm	1.393	0.66	1.030	1.669	Likely
			0.9	0.884	2.018	
Cyphastrea	Adult >5cm / Juv <5cm	1.222	0.66	0.936	1.487	Unlikely
			0.9	0.763	1.718	
Dipsastrea	Adult >5cm / Juv <5cm	1.240	0.66	0.909	1.508	Unlikely
			0.9	0.734	1.805	
Goniastrea	Adult >5cm / Juv <5cm	1.866	0.66	1.350	2.181	Very likely
			0.9	1.182	2.624	
Montipora	Adult >5cm / Juv <5cm	0.663	0.66	0.513	0.791	Very likely
			0.9	0.440	0.923	
Platygyra	Adult >5cm / Juv <5cm	1.586	0.66	1.200	1.910	Very likely
			0.9	1.013	2.241	

Pocillopora	Adult >5cm / Juv <5cm	0.591	0.66	0.465	0.681	Very likely
			0.9	0.414	0.789	
Massive *Porites*	Adult >5cm / Juv <5cm	1.257	0.66	1.024	1.465	Likely
			0.9	0.907	1.666	
Stylophora	Adult >5cm / Juv <5cm	1.279	0.66	1.008	1.509	Likely
			0.9	0.854	1.704	

Table S4.2: Pairwise comparisons of estimated marginal means for bleaching susceptibility between taxa for each bleaching severity category (A through E). For brevity, only contrasting taxa estimated to have a very high likelihood of a difference in their bleaching susceptibility are presented (i.e., where the 90% CrI's do not contain 1).

Contrast (taxa)	**Response**	**90% Lower CrI**	**90% Upper CrI**
A) Low Bleaching Severity (0-10%)			
Cyphastrea / Goniastrea	0.456	0.123	0.965
B) Moderate Bleaching Severity (11-30%)			
Acropora / Astrea	0.569	0.286	0.887
Acropora / Cyphastrea	2.534	1.328	3.996
Acropora / Dipsastrea	2.100	1.147	3.286
Acropora / Platygyra	2.045	1.149	3.094
Acropora / Pocillopora	0.524	0.291	0.771
Acropora / Stylophora	0.491	0.271	0.741
Astrea / Cyphastrea	4.493	2.151	7.337
Astrea / Dipsastrea	3.662	1.831	6.122
Astrea / Montipora	2.152	1.108	3.470
Astrea / Platygyra	3.600	1.930	5.884
Astrea / massive *Porites*	2.642	1.368	4.155
Cyphastrea / Goniastrea	0.436	0.218	0.705
Cyphastrea / Montipora	0.488	0.223	0.755
Cyphastrea / Pocillopora	0.203	0.104	0.327
Cyphastrea / massive *Porites*	0.585	0.319	0.939
Cyphastrea / Stylophora	0.191	0.096	0.312
Dipsastrea / Goniastrea	0.525	0.280	0.862
Dipsastrea / Montipora	0.590	0.305	0.921
Dipsastrea / Pocillopora	0.246	0.124	0.382
Dipsastrea / Stylophora	0.234	0.123	0.365
Goniastrea / Pocillopora	0.471	0.256	0.729
Goniastrea / Stylophora	0.443	0.229	0.693
Montipora / Pocillopora	0.420	0.218	0.632
Montipora / Stylophora	0.396	0.210	0.616
Platygyra / Pocillopora	0.255	0.141	0.391

Platygyra / Stylophora	0.239	0.129	0.375
Pocillopora / massive *Porites*	2.892	1.663	4.287
Massive *Porites / Stylophora*	0.327	0.176	0.490
C) High Bleaching Severity (31-60%)			
Acropora / Cyphastrea	3.913	1.874	6.026
Acropora / Dipsastrea	2.693	1.256	4.494
Acropora / Platygyra	3.176	1.678	5.180
Acropora / Pocillopora	0.575	0.317	0.867
Acropora / massive *Porites*	2.672	1.441	4.018
Acropora / Stylophora	0.426	0.226	0.641
Astrea / Cyphastrea	4.214	2.050	6.771
Astrea / Dipsastrea	2.915	1.274	5.097
Astrea / Platygyra	3.443	1.520	5.665
Astrea / Pocillopora	0.620	0.288	0.957
Astrea / massive *Porites*	2.889	1.483	4.614
Astrea / Stylophora	0.460	0.235	0.726
Cyphastrea / Goniastrea	0.256	0.121	0.414
Cyphastrea / Montipora	0.239	0.111	0.385
Cyphastrea / Pocillopora	0.148	0.075	0.231
Cyphastrea / Stylophora	0.109	0.054	0.170
Dipsastrea / Goniastrea	0.367	0.166	0.648
Dipsastrea / Montipora	0.341	0.139	0.576
Dipsastrea / Pocillopora	0.212	0.092	0.349
Dipsastrea / Stylophora	0.157	0.068	0.262
Goniastrea / Platygyra	3.220	1.508	5.465
Goniastrea / Pocillopora	0.579	0.310	0.930
Goniastrea / massive *Porites*	2.693	1.368	4.235
Goniastrea / Stylophora	0.431	0.213	0.680
Montipora / Platygyra	3.440	1.567	5.642
Montipora / Pocillopora	0.621	0.319	0.965
Montipora / massive *Porites*	2.886	1.434	4.423
Montipora / Stylophora	0.457	0.247	0.735
Platygyra / Pocillopora	0.181	0.091	0.286
Platygyra / Stylophora	0.133	0.067	0.217
Pocillopora / massive *Porites*	4.659	2.625	7.078
Massive *Porites / Stylophora*	0.160	0.090	0.246
D) Very High Bleaching Severity (60-80%)			
Acropora / Astrea	1.981	1.281	2.844
Acropora / Cyphastrea	2.954	1.901	4.203
Acropora / Dipsastrea	2.464	1.508	3.554
Acropora / Platygyra	2.877	1.853	4.138
Acropora / Stylophora	0.562	0.354	0.763
Astrea / Goniastrea	0.594	0.346	0.854
Astrea / Montipora	0.477	0.289	0.689
Astrea / Pocillopora	0.572	0.359	0.814
Astrea / massive *Porites*	0.694	0.432	0.984

Astrea / Stylophora	0.284	0.179	0.411
Cyphastrea / Goniastrea	0.395	0.234	0.565
Cyphastrea / Montipora	0.318	0.195	0.460
Cyphastrea / Pocillopora	0.380	0.252	0.542
Cyphastrea / massive *Porites*	0.462	0.310	0.658
Cyphastrea / Stylophora	0.190	0.120	0.271
Dipsastrea / Goniastrea	0.478	0.277	0.701
Dipsastrea / Montipora	0.384	0.230	0.557
Dipsastrea / Pocillopora	0.457	0.293	0.667
Dipsastrea / massive *Porites*	0.560	0.348	0.796
Dipsastrea / Stylophora	0.229	0.139	0.335
Goniastrea / Platygyra	2.472	1.503	3.552
Goniastrea / Stylophora	0.478	0.297	0.672
Montipora / Platygyra	3.058	1.796	4.404
Montipora / Stylophora	0.597	0.373	0.850
Platygyra / Pocillopora	0.391	0.238	0.546
Platygyra / massive *Porites*	0.476	0.300	0.666
Platygyra / Stylophora	0.194	0.113	0.276
Pocillopora / Stylophora	0.497	0.333	0.692
Massive *Porites / Stylophora*	0.407	0.277	0.565
E) Extreme Bleaching Severity (80-100%)			
Acropora / Stylophora	0.489	0.219	0.876
Astrea / Goniastrea	0.510	0.201	0.912
Astrea / Stylophora	0.422	0.166	0.743
Cyphastrea / Goniastrea	0.414	0.155	0.762
Cyphastrea / Stylophora	0.346	0.133	0.619
Dipsastrea / Stylophora	0.537	0.200	0.960
Goniastrea / Platygyra	2.700	1.042	4.906
Montipora / Stylophora	0.404	0.161	0.741
Platygyra / Stylophora	0.308	0.121	0.558
Pocillopora / Stylophora	0.346	0.148	0.604
Massive *Porites / Stylophora*	0.435	0.182	0.737

Table S4.3: Pairwise comparisons of estimated marginal means for the bleaching susceptibility between colony sizes for each bleaching severity category. Upper and Lower highest posterior density credible intervals are shown at both the 66% and 90% confidence level.

Bleaching Severity	Contrast (size class)	Response	Confidence level	Lower CrI	Upper CrI	Likelihood of difference
Interaction between Severity and Size Class						
0-10%	Adult >5cm / Juv <5cm	2.114	0.66	1.561	2.581	Very Likely

			0.9	1.247	3.043	
11-30%	Adult >5cm / Juv <5cm	1.429	0.66	1.221	1.599	Very Likely
			0.9	1.092	1.750	
31-60%	Adult >5cm / Juv <5cm	1.165	0.66	0.974	1.308	Unlikely
			0.9	0.883	1.459	
61-80%	Adult >5cm / Juv <5cm	1.030	0.66	0.904	1.127	Unlikely
			0.9	0.845	1.228	
81-100%	Adult >5cm / Juv <5cm	0.589	0.66	0.469	0.680	Very likely
			0.9	0.418	0.781	

Table S4.4: Pairwise comparisons of estimated marginal means for the bleaching susceptibility between colony sizes (juvenile <5cm vs Adults >5cm) for each taxon within each bleaching severity category (A through E). For brevity, upper and lower highest posterior density credible intervals are shown at the 90% confidence level.

Taxon	**Response**	**Lower CrI**	**Upper CrI**	**Likelihood of difference**
A) Low Bleaching Severity (0-10%)				
Astrea	2.125	1.125	3.256	Very Likely
Cyphastrea	2.525	1.198	4.082	Very Likely
Dipsastrea	2.220	1.120	3.607	Very Likely
Goniastrea	2.246	1.151	3.804	Very Likely
Montipora	3.357	1.725	5.454	Very Likely
Platygyra	1.198	0.591	1.900	
Pocillopora	2.877	1.380	4.613	Very Likely
Massive *Porites*	1.074	0.573	1.671	
Stylophora	2.272	1.230	3.521	Very Likely
Acropora	2.324	1.235	3.672	Very Likely
B) Moderate Bleaching Severity (11-30%)				
Astrea	1.431	0.944	1.965	
Cyphastrea	1.717	0.979	2.513	
Dipsastrea	1.500	0.896	2.240	
Goniastrea	1.525	0.881	2.302	
Montipora	2.290	1.358	3.322	Very Likely
Platygyra	0.814	0.501	1.167	
Pocillopora	1.941	1.177	2.824	Very Likely
Massive *Porites*	0.723	0.482	1.020	
Stylophora	1.547	1.003	2.109	Very Likely
Acropora	1.576	0.990	2.185	
C) High Bleaching Severity (31-60%)				
Astrea	1.166	0.721	1.594	
Cyphastrea	1.398	0.841	2.074	
Dipsastrea	1.222	0.734	1.786	
Goniastrea	1.239	0.673	1.898	

Montipora	1.872	1.113	2.778	Very Likely
Platygyra	0.661	0.397	0.969	Very Likely
Pocillopora	1.576	0.912	2.319	
Massive *Porites*	0.590	0.362	0.814	Very Likely
Stylophora	1.257	0.831	1.768	
Acropora	1.274	0.836	1.818	
D) Very High Bleaching Severity (61-80%)				
Astrea	1.035	0.716	1.402	
Cyphastrea	1.238	0.748	1.776	
Dipsastrea	1.083	0.687	1.577	
Goniastrea	1.104	0.620	1.644	
Montipora	1.654	0.980	2.336	
Platygyra	0.588	0.370	0.826	Very Likely
Pocillopora	1.405	0.848	1.984	
Massive *Porites*	0.524	0.364	0.713	Very Likely
Stylophora	1.116	0.761	1.497	
Acropora	1.136	0.723	1.538	
E) Extreme Bleaching Severity (31-60%)				
Astrea	0.592	0.354	0.833	Very Likely
Cyphastrea	0.707	0.378	1.064	
Dipsastrea	0.622	0.335	0.929	Very Likely
Goniastrea	0.628	0.348	0.986	Very Likely
Montipora	0.943	0.536	1.449	
Platygyra	0.336	0.186	0.498	Very Likely
Pocillopora	0.799	0.442	1.197	
Massive *Porites*	0.301	0.181	0.438	Very Likely
Stylophora	0.639	0.380	0.919	Very Likely
Acropora	0.644	0.381	0.958	Very Likely

Appendix D – Supplementary Materials for Chapter 5

Table S5.1: Annual maximum degree heating weeks measured at each site from the NOAA Coral Reef Watch 5km product (Version 3.1) NetCDF archived data. Reefs and sites are ordered from north to south, and respective regional categories are noted. Purple and yellow text represent highest and lowest DHW values, respectively, to match heat map (Fig. 5.1)

Region	Reef, site	latitude	longitude	°C-weeks
South				
	Saumarez_03	-21.9178	153.5845	11.35
	Saumarez_07	-21.9119	153.5912	11.35
	Saumarez_05	-21.75	153.7697	12.25
	Wreck_03	-22.1867	155.1705	**12.83**
	Wreck_02	-22.1781	155.1767	**12.83**
	Wreck_01	-22.1927	155.3341	12.58
	Kenn_01	-21.2476	155.7662	10.23
	Kenn_02	-21.2532	155.7622	10.39
	Kenn_04	-21.2046	155.7724	10.23
	Frederick_01	-21.0111	154.351	12.72
	Frederick_02	-21.0104	154.3474	12.54
	Frederick_04	-20.9384	154.3974	12.51
Central				
	Marion_07	-19.2951	152.2378	11.37
	Marion_06	-19.1213	152.3999	11.38
	Flinders_05	-17.8616	148.4665	10.5
	Flinders_06	-17.8309	148.5135	10.57
	Flinders_01	-17.7136	148.4371	10.6
	Flinders_02	-17.7022	148.4666	10.75
	Flinders_07	-17.5368	148.5511	12.07
	Herald_04	-16.9725	149.1287	11.96
	Herald_06	-16.9919	149.1308	11.96
	Herald_01	-16.9435	149.1857	11.92
	Chilcott_02	-16.9396	149.9964	9.68
	Chilcott_04	-16.936	149.9984	9.68
	Lihou_01	-17.5971	151.4896	11.12
	Lihou_02	-17.5907	151.5003	11.25
	Lihou_07	-17.3742	155.8431	11.48
	Lihou_09	-17.1302	151.8393	11.4
	Lihou_04	-17.1253	151.8254	11.4
	Lihou_05	-17.1211	151.8294	11.4
	Willis_04	-16.2826	149.9657	12.19
	Willis_02	-16.2873	149.9593	12.19
	Willis_07	-16.117	149.971	12.22

	Holmes_06	-16.419	147.9898	11
	Holmes_07	-16.4269	147.9844	11
	Holmes_05	-16.5053	147.9675	10.93
	Holmes_01	-16.5261	147.807	10.51
	Holmes_10	-16.5214	147.8377	10.51
	Holmes_02	-16.5118	147.84	10.51
North				
	Bougainville_04	-15.5067	147.1123	11.15
	Bougainville_01	-15.4927	147.0864	11.11
	Bougainville_05	-15.5008	147.0989	11.26
	Osprey_07	-13.8885	146.5594	**9.25**

Table S5.2 Average percent coral cover for each taxon in 2020 and 2021, and their absolute and relative change within each region and habitat. Averages based on 50m point intercept transects (north: n = 12 per habitat; central: n =. 81 per habitat; south: n = 36 per habitat)

Taxon	**Mean % Coral cover 2020 (± se)**	**Mean % Coral cover 2021 (± se)**	**Absolute Change**	**Relative Change**
North				
crest				
Acanthastrea	0.5 (0.3)	0.5 (0.2)	0.0	0.0
Astreopora	0.4 (0.3)	0.6 (0.4)	0.2	40.0
Dipsastrea	0.2 (0.1)	0.2 (0.1)	0.0	0.0
Favites	0.3 (0.1)	0.1 (0.1)	-0.2	-66.7
Goniastrea	0.3 (0.1)	0.9 (0.3)	0.7	266.7
Massive *Porites*	0.4 (0.3)	0.3 (0.2)	-0.1	-20.0
Montipora	0.6 (0.3)	0.8 (0.3)	0.2	28.6
Other *Acropora*	2.3 (1.1)	1.1 (0.8)	-1.2	-51.9
Platygyra	0.3 (0.1)	0.7 (0.3)	0.4	166.7
Pocillopora	9.3 (1.5)	8.9 (1.4)	-0.3	-3.6
slope				
Branching *Porites*	9.6 (4.8)	9.2 (3.4)	-0.4	-4.4
Echinopora	1.5 (0.6)	0.6 (0.3)	-0.9	-61.1
Favites	5.5 (1.0)	0.3 (0.2)	-5.3	-95.5
Goniastrea	4.1 (0.9)	3.6 (0.8)	-0.5	-12.2
Isopora	1.1 (1.0)	0.7 (0.4)	-0.4	-38.5
Massive *Porites*	2.0 (1.0)	2.6 (0.7)	0.6	29.2
Montipora	8.2 (2.0)	6.0 (1.5)	-2.2	-26.5
Pavona	6.0 (1.5)	3.6 (1.1)	-2.4	-40.3
Platygyra	2.6 (1.0)	1.7 (0.7)	-0.9	-35.5
Pocillopora	9.5 (2.0)	7.0 (1.4)	-2.5	-26.3
Central				
crest				

Astreopora	0.5 (0.1)	0.8 (0.1)	0.3	56.4
Cyphastrea	0.3 (0.1)	0.1 (0.0)	-0.2	-52.2
Goniastrea	0.7 (0.1)	0.9 (0.2)	0.2	20.3
Isopora	1.2 (0.4)	0.7 (0.3)	-0.4	-32.2
Massive *Porites*	4.9 (0.8)	1.9 (0.5)	-3.0	-61.5
Montipora	1.7 (0.2)	0.9 (0.1)	-0.9	-50.0
Other *Acropora*	6.5 (0.7)	2.0 (0.4)	-4.5	-69.8
Pocillopora	5.5 (0.5)	4.0 (0.3)	-1.5	-27.4
Stylophora	0.9 (0.2)	0.1 (0.0)	-0.8	-90.0
Tabular *Acropora*	1.2 (0.2)	0.2 (0.1)	-1.0	-81.8
slope				
Astreopora	0.8 (0.1)	0.7 (0.1)	-0.1	-11.1
Cyphastrea	0.9 (0.1)	0.4 (0.1)	-0.4	-47.8
Goniastrea	1.4 (0.2)	1.0 (0.2)	-0.4	-28.3
Isopora	1.2 (0.3)	0.5 (0.2)	-0.7	-61.1
Leptastrea	1.1 (0.2)	0.8 (0.1)	-0.4	-31.5
Massive *Porites*	5.8 (0.9)	2.3 (0.4)	-3.5	-59.9
Montipora	2.2 (0.3)	1.8 (0.2)	-0.4	-18.3
Other *Acropora*	3.3 (0.3)	1.4 (0.2)	-1.9	-58.6
Pocillopora	3.9 (0.5)	2.5 (0.3)	-1.4	-35.7
Stylophora	1.5 (0.2)	0.3 (0.1)	-1.2	-79.7
South				
crest				
Branching *Porites*	0.9 (0.5)	0.2 (0.1)	-0.7	-81.3
Goniastrea	1.3 (0.3)	0.9 (0.2)	-0.4	-29.2
Isopora	4.8 (1.0)	3.3 (0.7)	-1.5	-30.6
Massive *Porites*	1.7 (0.6)	0.8 (0.4)	-0.9	-55.7
Montipora	1.3 (0.4)	1.1 (0.3)	-0.2	-16.7
Other *Acropora*	12.7 (1.4)	10.3 (1.7)	-2.4	-19.2
Pocillopora	2.9 (0.5)	2.0 (0.3)	-0.9	-31.7
Staghorn *Acropora*	1.3 (0.5)	1.4 (0.4)	0.1	10.6
Stylophora	2.1 (0.4)	0.3 (0.1)	-1.8	-84.4
Tabular *Acropora*	1.2 (0.2)	1.0 (0.2)	-0.2	-18.2
slope				
Astreopora	0.7 (0.2)	0.3 (0.1)	-0.4	-60.0
Goniastrea	0.7 (0.2)	0.2 (0.1)	-0.5	-73.1
Isopora	3.9 (1.1)	1.7 (0.6)	-2.3	-57.8
Massive *Porites*	3.3 (0.8)	1.4 (0.3)	-1.9	-58.5
Montipora	2.3 (0.5)	1.2 (0.3)	-1.1	-48.8
Other *Acropora*	4.3 (0.8)	2.1 (0.4)	-2.3	-52.3
Pocillopora	0.8 (0.2)	0.6 (0.2)	-0.3	-30.0
Seriatopora	1.0 (0.3)	0.1 (0.0)	-0.9	-94.4
Stylophora	0.8 (0.2)	0.5 (0.1)	-0.3	-40.0
Tabular *Acropora*	0.6 (0.2)	0.3 (0.1)	-0.4	-56.5

Appendix E – Other scientific contributions during this candidature

Pratchett, M.S., Nadler, L.E., **Burn, D**., Lang, B.J., Messmer, V., Caballes, C.F (2021) Reproductive investment and fecundity of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) on the Great Barrier Reef. *Marine Biology* 168:87 doi: 10.1007/s00227-021-03897-w

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Galbraith, G., McClure, E.C., Barnett, A., Creswell, B., **Burn, D**., Huertas, V., Pratchett, M.S., Hoey, A.S (2022) Diving into the deep: the unique deep habitats of the coral sea marine park. Report prepared for Parks Australia.

Chandler, J.F., **Burn, D**., Caballes, C.F., Doll, P.C., Kwong, S.L.T., Lang, B.J., Pacey, K.I., Pratchett, M.S (2023) Increasing densities of Pacific crown-of-thorns starfish

(*Acanthaster* cf. *solaris*) at Lizard Island, northern Great Barrier Reef, resolved using a novel survey method. *Scientific Reports*, 13(1): 19306

Chandler JF, Figueira WF, **Burn D**, Doll PC, Johandes A, Piccaluga A, Pratchett MS (2024) Predicting 3D and 2D surface area of corals from simple field measurements. *Scientific Reports* 14: 20549

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