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Differential susceptibility of corals to major *versus* routine disturbances in Australia's Coral Sea

Thesis submitted by
Deborah Burn B.Sc.
James Cook University in November 2020

For the degree of Master of Philosophy
ARC Centre of Excellence for Coral Reef Studies
James Cook University

Statement of Contribution of others

Nature of Assistance	Contribution	Names, Titles (if relevant) and Affiliations of Co-Contributors
Intellectual support	Proposal Writing Editorial Assistance	Morgan Pratchett ¹ Andrew Hoey ¹ Hugo Harrison ^{1,2}
	Data Analysis Statistical Support	Sam Matthews ¹ Morgan Pratchett ¹
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Data Collection	Research Assistance	Morgan Pratchett ¹ Russell Kelly ¹ Cassandra Thompson ²

¹ARC Centre of Excellence for Coral Reef Studies, James Cook University, Queensland 4814, Australia

²Australian Institute of Marine Science, Townsville QLD, Australia

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Abstract

Sustained coral loss and the corresponding degradation of coral reef ecosystems is often attributed to the increasing incidence of major acute disturbances, such as mass coral bleaching, which cause considerable coral mortality. However, routine and background disturbances (e.g., predation and competition) also contribute to ongoing coral mortality and may undermine the health and condition of individual corals, potentially increasing their vulnerability to, and limiting recovery from, major acute disturbances. Aside from causing overall declines in the abundance of corals, differential susceptibility of corals to varying disturbances may also lead to strong directional shifts in population and community structure. With increasing frequency, severity and diversity of disturbances affecting reef ecosystems and coral assemblages, research on the specific effects of routine and acute disturbances is critical to document and predict changes in coral assemblages, which will have far reaching impacts on the structure and function of reef ecosystems. My research is presented as two independent, but strongly related, studies which consider the effects of recent disturbances on shallow-water coral assemblages throughout Australia's remote and understudied Coral Sea, with comparable surveys also conducted on offshore reefs of the Great Barrier Reef (GBR). The first of these studies (Chapter 2) compares incidence of recent coral mortality before versus during widespread mass-bleaching that occurred in 2020, while Chapter 3 focusses explicitly on the 2020 mass-bleaching and documents differential patterns of bleaching susceptibility among coral taxa and colony sizes over large spatial scales where there were marked gradients in bleaching severity.

Acute and chronic disturbances both play an important role in structuring coral assemblages, whereby differential mortality will drive changes in population and community structure. In reality, few studies directly quantify instantaneous mortality that occurs during major disturbances, nor do they account for background levels of mortality, and especially partial

mortality, that occurs independently of major disturbances. Chapter 2 compares incidence of recent coral injury at >30 reefs in the Coral Sea and Great Barrier Reef before versus during the 2020 mass-bleaching. I explicitly tested for differential incidence of recent injury (including both partial and whole colony mortality) across corals from different taxa (distinguishing among major genera and growth forms) and size classes (<5cm, 5-40cm, and >40cm diameter), expecting to record greatly increased incidence of recent injury during the mass-bleaching. Contrary to expectations, overall incidence of recent injury was very consistent and low (<5%) both before and during the mass-bleaching. However, some taxa (most notably, massive *Porites*) did exhibit higher incidence of recent injury during widespread mass-bleaching in February-March 2020 compared to pre-bleaching surveys. Conversely, *Acropora* and *Pocillopora* exhibited lower incidence of recent injury during mass-bleaching compared to pre-bleaching surveys. This resulted in marked inter-annual changes in the taxonomic hierarchy for incidence of recent injury. Incidence of recent injury also increased with increasing colony size, highlighting the vulnerability of large colonies, which may lead to shifts in community size structure. Whilst recent injury was more prevalent in the Coral Sea compared with the Great Barrier Reef, and on the reef crest compared to the reef slope, spatial or habitat-related differences in the incidence of recent injury were much more pronounced than taxonomic and size-based differences. Importantly, this research highlights the need to account for background levels of coral mortality that occur independently of major disturbances, which are likely to have a major influence on the structure of coral assemblages and influence vulnerability to major disturbances.

Climate-induced coral bleaching represents one of the foremost threats to coral assemblages globally, and differential bleaching susceptibility and subsequent mortality will cause marked shifts in population and community structure. However, the selectivity of mass-bleaching is likely to be dependent on overall bleaching severity and inversely related to overall levels of

coral mortality. Chapter 3 examines variation in the bleaching susceptibility of scleractinian corals, within and among taxa, at 33 reefs across the Great Barrier Reef and Coral Sea during widespread mass-bleaching in February-March 2020. The overall proportion of corals bleached was averaged across all sites at each reef and then each reef was placed in one of five categories (low, <10%; moderate, 10-30%; high, 30-60%; very high, 60-80%; and extreme, >80%) used as a proxy for bleaching severity. To test for changes in bleaching susceptibility with increasing reef-scale bleaching severity, we compared bleaching incidence among 20 coral taxa (common genera). These data were also used to explore size-based differences in bleaching susceptibility, comparing among three size classes (<5cm, 5-40cm, and >40cm diameter) of colonies. Whilst *Stylophora*, *Goniastrea*, and branching *Acropora* were consistently among the worst affected, and *Leptastrea* and *Lobophyllia* the least affected, the hierarchy of bleaching susceptibility among taxa changed with increasing reef-scale bleaching severity. Similarly, the rank order of bleaching susceptibility differed among size classes of coral colonies. Juvenile (<5cm diameter) *Stylophora*, *Goniastrea*, massive *Porites*, *Favites*, *Lobophyllia* and Fungiidae were significantly less likely to bleach than larger (5-40cm diameter) congeners, whereas juvenile *Pocillopora* and *Montipora* colonies bleached more often than larger colonies. These findings suggest that colony size, as well as reef-scale bleaching severity, are important determinants of taxonomic bleaching susceptibility and should both be taken into account to ascertain likely shifts in the structure of coral assemblages with increasing incidence and/or severity of mass-bleaching.

The data presented in this thesis is novel, important and very timely, providing a baseline with which to test for changes in the incidence of coral mortality within shallow-water reef habitats throughout Australia's Coral Sea. Despite being very isolated and far removed from most direct human pressures, Coral Sea reefs are subject to intense and recurrent disturbances associated with severe tropical storms and global climate change. Indeed, incidence of recent coral

mortality was actually higher in the Coral Sea than for comparable offshore habitats on the GBR. Moreover, high levels of isolation may limit delivery and exchange of coral larvae among reefs in the Coral Sea, thereby constraining recovery and increasing vulnerability of these coral assemblages to changing disturbance regimes. Much more work is needed to understand the structure, dynamics and vulnerability of coral assemblages and reef ecosystems in the Coral Sea, but work presented herein also contributes to general understanding of the relative importance of acute versus chronic disturbances for coral reefs.

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Chapter 1. General Introduction

1.1 Changing disturbance regimes on coral reefs.

The importance of disturbances in structuring coral reef communities and habitats is well established (Karlson and Hurd 1993; Connell 1997). However, there is considerable and growing interest in the individual and cumulative effects of different disturbances (e.g., Ortiz et al. 2018; Gilmour et al. 2019; Mellin et al. 2019a; Cramer et al. 2020; Vercelloni et al. 2020), partly reflecting the increasing incidence, severity and diversity of disturbances affecting corals and coral reef ecosystems (Nyström et al. 2000; Bellwood et al. 2019). There is also an obvious and concerning link between incidence and severity of disturbances versus rates of coral loss occurring across most major reef systems (Bellwood et al. 2004; Gardner et al. 2015; Adjeroud et al. 2009; De'ath et al. 2012; Pisapia et al. 2019). Most notably, the pervasive and increasing effects of human-induced climate change (and corresponding changes in both baseline conditions and environmental variability) are compounding upon pre-existing disturbances and greatly accelerating the degradation of coral reef ecosystems worldwide (Alvarez-Filip et al. 2009; Hoegh-Guldberg et al. 2017; Hughes et al. 2017a; Riegl et al. 2018; Bellwood et al. 2019).

Although disturbances were historically considered to be rare and extreme events within natural ecosystems, contemporary ecological definitions of disturbance have been extended to include any extrinsic factors (environmental or biological) that cause changes in the condition or state of an individual, population, community or ecosystem (White 1979; Rykiel 1985). The wide variety of disturbances affecting coral and coral reefs has been represented using various frameworks, often distinguishing between natural versus anthropogenic disturbances (Nyström et al. 2000; Wong et al. 2018; Cramer et al. 2020), small-versus large-scale disturbances (Ferrigno et al. 2016; Bruno et al. 2019), or acute versus chronic disturbances (Ortiz et al. 2018; Pratchett and Hoogenboom 2019; Mellin et al. 2019b). There

is large variation in the spatiotemporal scale of different types of disturbances (Nyström et al. 2000; Bellwood et al. 2019), which has important consequences for the necessary scale and potential effectiveness of management responses. The frequency, duration and spatial extent of different disturbances also influences their apparent importance and ecological effects. Long-term declines in the abundance or cover of reef-building corals, which are apparent in many reef systems (e.g., Gardner et al. 2005; Adjeroud et al. 2009; Harris et al. 2010; De'ath et al. 2012; Pisapia et al. 2019), are almost universally attributed to temporally distinct (acute) and large-scale disturbances that cause noticeable increases in the rates of coral mortality, such as population irruptions of crown-of-thorns starfish (*Acanthaster* spp.), severe cyclonic storms, and mass coral bleaching (Osborne et al. 2011; De'ath et al. 2012; Sheppard et al. 2017; Madin et al. 2018; Vercelloni et al. 2019). However, sustained coral loss and the corresponding degradation of coral reef ecosystems is at least partly attributable to highly prevalent, but localised and discrete biotic disturbances (e.g., predation and competition), as well as insidious changes in baseline environmental conditions (Stimson 1985; Wakeford et al. 2008; Pratchett et al. 2013a; Ortiz et al. 2018). These chronic disturbances may not necessarily cause apparent or widespread coral mortality, but undermine the health and condition of individual corals (Pisapia et al. 2014), thereby increasing vulnerability to large-scale and acute disturbances (Hughes et al. 2007; Bruckner and Hill 2007; Wooldridge and Done 2009) and reducing recovery capacity in the aftermath of major disturbances (Ortiz et al. 2018).

Major acute disturbances undoubtedly can, and do, result in extensive coral mortality, which is evident based on punctuated declines in the local abundance (or cover) of living corals coinciding with population irruptions of crown-of-thorns starfish, severe cyclonic storms, and/or mass coral bleaching (Traçon et al. 2011; Kayal et al. 2012; Gilmour et al. 2013; Hughes et al. 2018a). In Moorea, French Polynesia, for example, there have been two discrete population irruptions of *A. cf. solaris* since the late 1970's (1979-1986 and 2005-2010), and average

annual rates of coral loss recorded during these events were much higher than recorded during either cyclonic storms or mass coral bleaching (Kayal et al. 2011; Traçon et al. 2011). Moreover, population irruptions of crown-of-thorns starfish have occurred on many reefs throughout the Indo-Pacific (Pratchett et al. 2014), and typically represent one of the foremost causes of coral loss (Bruno and Selig 2007; Osborne et al. 2011; De'ath et al 2012), especially where there are persistent or recurrent population irruptions.

Compared to population irruptions of crown-of-thorns starfish, other major acute disturbances are much less protracted in their duration and impacts. Disturbances to coral assemblages caused by cyclonic storms and mass coral bleaching, for example, are linked to extremes in environmental conditions (Knutson et al. 2010; Oliver et al. 2018), which typically last days to weeks. Corals can generally withstand a wide range of hydrodynamic forces, but often succumb to the most extreme wave generated forces (Madin and Connolly 2006), such as those that occur during severe cyclonic storms. The mechanical damage caused by cyclonic storms (e.g., dislodgement and displacement of massive coral colonies, and generation of extensive rubble banks) can be extensive and visually striking (Fabricius et al. 2008; Beeden et al. 2015). Moreover, damaging waves may occur over very large distances (up to 800km) from the direct path of very large, severe and slow moving cyclonic storms (Puotinen et al. 2020). In recent years, severe (category 4-5) cyclonic storms have impacted more than 50% of the entire extent of Australia's Great Barrier Reef (Cheal et al. 2017), and were considered to be the leading cause of coral loss (Osborne et al. 2011; De'ath et al. 2012; Mellin et al. 2019a), at least up until 2016. It is also expected that the incidence of very intense cyclonic storms will increase due to climate change (Knutson et al. 2010), further exacerbating coral loss in cyclone-prone regions (Cheal et al. 2017; Puotinen et al. 2020).

Despite apparent and often significant effects of population irruptions of crown-of-thorns starfish, severe cyclonic storms and also mass coral bleaching (which is discussed later),

the cessation of biological and environmental conditions that contribute to elevated rates of coral mortality may allow for relatively rapid subsequent recovery (Fong and Lirman 1995; Golbuu et al. 2007; Baker et al. 2008; Linares et al. 2011; Graham et al. 2011; Gilmour et al. 2013; Adjeroud et al. 2018). Notably, most disturbances have disproportionate effects on erect, branching corals (mainly *Acropora*; Loya et al. 2001; McClanahan et al. 2004; Madin and Conolly 2006; Pratchett et al. 2008), and these corals are capable of very rapid recovery, owing to high rates of recruitment (Fong and Lirman 1995) and rapid growth (Linares et al. 2011; Pratchett et al. 2015). Increasing frequency of disturbances may therefore, favour corals with traits that allow for rapid recovery and recolonisation of available spaces in aftermath of punctuated disturbances, as was originally highlighted by Connell (1978). Accordingly, there are several studies that have documented increased predominance of *Acropora* corals, and other susceptible coral species, following major disturbances (Kayanne et al. 2002; Linares et al. 2011; van Woesik et al. 2011). However, there are instances where the high incidence of selective disturbances has caused long-term shifts in the structure of coral assemblages towards massive and robust corals, such as *Porites* (Alvarez-Filip et al. 2011; Burt et al. 2011; Riegl et al. 2017, 2018). Such changes in the composition of coral assemblages will have significant consequences for the structure and function of coral reef ecosystems (Alvarez-Filip et al. 2009; Pratchett et al. 2020a; McWilliam et al. 2020).

Coral-dominated habitats can recover in the aftermath of major disturbances, whereby coral cover can return to pre-disturbance levels quite rapidly even if coral composition is not restored (Halford et al. 2004; Berumen and Pratchett 2006; Sheppard et al. 2008; Diaz-Pulido et al. 2009; Gilmour et al. 2013). Nonetheless, many long-term data sets (or meta-analyses) reveal distinct downward trends in overall coral cover (Sheppard 1999; Gardner et al. 2003; Bruno and Selig 2007; Green et al. 2008; Dea'th et al. 2012; Bellwood et al. 2019). This is mostly taken to indicate that the increased incidence and/or severity of major acute

disturbances has overwhelmed the recovery capacity of coral populations, whereby the limited interval between successive disturbances does not allow sufficient time for effective recovery (Oliver et al. 2018; Hughes et al. 2018a). There are however, several additional factors that may be constraining coral recovery (Baker et al. 2008; Graham et al. 2011; Ortiz et al. 2018). Firstly, major disturbances may have latent and lasting effects on coral populations, which suppress recovery for several years post-disturbance (Ortiz et al. 2018). For example, individual coral colonies that withstand significant periods of heat stress may have significantly depressed regeneration, growth and/ or reproductive output for several years thereafter (Cantin and Lough 2014; Howells et al. 2016; Bonesso et al. 2017). Secondly, large-scale and severe disturbances may have sufficiently widespread impacts so as to effectively suppress the reproductive capacity of potential source populations, and thereby constrain overall levels of coral recruitment (Bauman et al. 2014; Hughes et al. 2019a). Such effects are likely to be particularly pronounced in small and isolated reef systems (Gilmour et al. 2013). Thirdly, recovery may be impeded by chronic disturbances (Ortiz et al. 2018) and/ or persistent changes in the structure and function of coral reef organisms (Hughes et al. 2007; Graham et al. 2011, 2015). Ortiz et al. (2018) showed that recovery rates of corals on Australia's Great Barrier Reef are declining and particularly low in areas of chronic environmental degradation, which is attributed to deleterious effects of poor water quality on growth, recruitment and partial mortality of corals. The proliferation of macroalgae in areas with high fishing pressure and corresponding low biomass of herbivorous fishes, may also prevent recruitment and recovery of corals in the aftermath of major disturbances (Hughes et al. 2007; Graham et al. 2015).

1.2 Chronic disturbances and background levels of coral mortality

While acute disturbances can cause elevated rates of whole colony mortality, thereby contributing to loss of coral cover (e.g., Pratchett 2010; Álvarez-Noriega et al. 2018), background rates of coral mortality (in the absence of acute disturbances) may also be

considerable (Wakeford et al. 2008; Pratchett et al. 2013a; Pisapia and Pratchett 2014). Wakeford et al. (2008) showed that rates of coral mortality during years with no obvious acute disturbances were as much as 50% of the mortality rates recorded during acute disturbances (including severe cyclones and populations irruptions of crown-of-thorns starfish). High rates of background coral mortality are attributed to chronic and routine disturbances (e.g., competition among corals and sustained levels of coral predation), as well as senescence, which account for high rates of natural turnover, especially among fast growing and short-lived coral taxa (Stimson 1985; Wakeford et al. 2008; Pratchett et al. 2013a). Most often, these chronic and routine disturbances cause injuries (or partial mortality) rather than killing whole colonies outright (Meesters et al. 1997; Nugues and Roberts 2003; Pisapia et al. 2016a; Madin et al. 2020). However, high incidence and severity of partial mortality has a major bearing on the individual condition and fitness of coral colonies (Rinkevich 1996; Meesters et al. 1994; Madin et al. 2020), with consequences for growth and fecundity and therefore, population and community dynamics. Importantly, much of the discourse regarding coral loss and reef degradation focusses on major acute disturbances (De'ath et al. 2012; Baird and Marshall 2002), with limited consideration given to background levels of coral mortality. Establishing background levels of coral injury and mortality is important in understanding the susceptibility of corals to major acute disturbances, as well as recovery potential in the aftermath of such disturbances (Wakeford et al. 2008; Pisapia et al. 2016b). Such data would benefit modelling efforts to project impacts of disturbances and to assess the validity of restoration activities.

The incidence and severity of background levels of coral injury and mortality vary among taxa (Bythell et al. 1993; Bruckner 2012; Lirman et al. 2014; Pratchett et al. 2013a; Pisapia et al. 2014) due to taxonomic variation in susceptibility to chronic and routine disturbances, but also differences in energetic investment and capacity for tissue repair (Meesters et al. 1997). Moreover, the appearance and accumulation of injuries depends on coral

growth and longevity (Meesters et al. 1996; Denis et al. 2011). Reported incidence of background levels of coral mortality, and especially partial mortality, tends to be highest (typically >90%) for slow-growing massive corals (e.g., massive *Porites*; Pisapia et al. 2015, 2016), which is counter to taxonomic hierarchies of susceptibility to disturbance. Fast-growing corals, including branching *Acropora* spp., as well as encrusting *Montipora* spp., tend to be among the most susceptible corals to a broad range of different disturbances (Meesters et al. 1996; Loya et al. 2001; Cole and Pratchett 2011; Madin et al. 2014), but also have exceptional regenerative capacity (Diaz-Pulido et al. 2009) and invest significantly in tissue repair following localised injuries (e.g., Okubo 2008). High levels of physiological integration and increased vulnerability to fragmentation further increase the likelihood that these corals will persist as discrete colonies with limited incidence of tissue loss or damage (Meesters and Bak 1995). However, the smaller discrete colonies will be much more susceptible to whole colony mortality (Riegl 1999; Madin et al. 2014). At the other extreme, massive *Porites* are very resistant to whole colony mortality (Glynn et al. 2009), which increases with colony size (discussed below). However, these corals experience high levels of partial mortality due to major acute disturbances (Glynn et al. 2009) and chronic or routine disturbances (e.g., predation by parrotfishes: Bonaldo et al. 2011; Welsh et al. 2015). Moreover, injuries that damage or expose the underlying skeleton of massive *Porites* corals are repaired very slowly, if at all, and mainly due to eventual overgrowth by surviving parts of the colony (Done 1987; Bonaldo et al 2011; Roff et al 2014). Apparent differences in the incidence of injuries may therefore, be related to differential regeneration and recovery, as well as susceptibility or resistance to chronic or routine disturbances (Meesters et al. 1996, 1997), especially when considering the accumulation of injuries throughout the lifetime of corals.

Aside from taxonomic differences, mortality schedules also vary with coral colony size (Madin et al. 2020), reflecting size-based differences in both inherent exposure to, and the

capacity to withstand, different disturbance (Henry and Hart 2005; Hughes and Jackson 1985). While the probability of whole colony mortality decreases with increasing colony size (Madin et al. 2020), the incidence and extent of partial mortality increases in larger colonies (Hughes and Jackson 1980; Hughes and Jackson 1985; Lewis 1997; Meesters et al 1997; Madin et al. 2014). Any given disturbance is less likely to result in whole colony mortality with increasing colony size, but will have apparent effects on colony condition and subsequent fate (Jayewardene et al. 2009; Madin et al. 2014). Despite this, many empirical studies fail to detect variation in the incidence or severity of injuries with colony size (Bak and Meesters 1998; Meesters et al. 1994; Nugues and Roberts 2003; Pisapia et al. 2014). Some studies have even shown that injuries are more prevalent among smaller corals (e.g., Wesseling et al. 2001; Pisapia and Pratchett 2014), which might be explained by differences in regeneration capacity, whereby larger corals are expected to have greater energetic reserves (Loya 1976). The inherent trade-off between colony growth and partial mortality is manifested as allometric net growth (Madin et al. 2020), whereby effective declines in the size of colonies due to partial mortality prevent colonies from realising maximum potential growth that is independent of colony size. Accordingly, partial mortality has a disproportionate effect on net growth of smaller colonies, and constraints imposed by background mortality are also greatest for slower growing species (Madin et al. 2020). There is however, a definite need for further research into taxonomic and size-based differences in susceptibility to disturbances, which may have important consequences for population structure and dynamics (Pisapia et al. 2019, 2020; Madin et al. 2020) and the responses of coral populations and assemblages to changing environmental conditions. Such data could be further used to inform ecological models and management decisions.

1.3 Climate change and coral bleaching

Given the important role of chronic and acute disturbances in structuring coral assemblages and reef ecosystems (Hughes 1989; Graham et al. 2015) it is unsurprising that global climate change is rapidly and dramatically transforming coral reefs (Hoegh-Guldberg 1999; Hughes et al. 2003, 2018b). Human-induced climate change not only imposes chronic pressures on reef-building corals and reef-associated organisms through sustained changes in environmental conditions (De'ath et al. 2009; Cantin et al. 2010), but greatly increases the frequency and severity of major acute disturbances (Heron et al. 2016, Hughes et al. 2017b, 2018a) caused by more extreme temporary excursions in key environmental parameters (Fordyce et al. 2019; Turner et al. 2020). Most notably, increasing surface temperatures are exacerbating the chronic pressures facing coral reef organisms (Buddemeier et al. 2004), but are also driving increased incidence and severity of marine heatwaves and corresponding episodes of mass-bleaching and elevated coral mortality (Heron et al. 2016; Gilmour et al. 2019; Leggat et al. 2019; Skirving et al. 2019), which are arguably one of the foremost threats to coral reefs globally (Hughes et al. 2015, 2018a).

Scleractinian corals are renowned for their symbiotic relationship with intracellular dinoflagellates (zooxanthellae, family: Symbiodiniaceae), whereby the zooxanthellae receive metabolic by-products (e.g. CO₂) from the coral host and, in return, provide up to 100% of the host's daily energy requirements through photosynthesis (Muscatine et al. 1981; Grottoli et al. 2006). Mass bleaching occurs when corals are exposed to anomalous high temperatures (Glynn and D'Croz 1990; Jokiel and Coles 1990; Hoegh-Guldberg 1999), causing oxidative stress as zooxanthellae become over-excited (Lesser 1997). To reduce oxidative stress, corals must reduce the concentrations of zooxanthellae within their tissues and/ or reduce the photosynthetic pigment and activity of entrained zooxanthellae, both of which result in the appearance of pale or white (bleached) animal tissue (Glynn 1984; Douglas 2003). While

bleaching increases the capacity of host corals to withstand short-term exposure to deleterious environmental conditions and may even allow for adaptive changes in the structure of symbiont assemblages (Baker 2001), severe or prolonged exposure to adverse environmental conditions ultimately results in high levels of host coral mortality (Hughes et al. 2018b; Eakin et al. 2019; Leggat et al. 2019). Extremely severe heatwaves, for example, can physiologically damage coral beyond repair, resulting in almost instantaneous, widespread mortality (Hughes et al., 2018b; Leggat et al. 2019).

The incidence, scale and severity of mass-bleaching episodes are increasing in direct accordance with increasing occurrence and magnitude of marine heatwaves (Heron et al. 2016; Hughes et al. 2018a; Eakin et al. 2019). Most notably, severe mass-bleaching and high rates of coral mortality were recorded throughout most major reef localities in 2016, which was the hottest year on record (Eakin et al. 2019). Unprecedented incidence of successive years of mass-bleaching were also recorded at many localities in 2016-17 (Eakin et al. 2019), including the Great Barrier Reef (GBR, Hughes et al. 2019b) and Coral Sea (Harrison et al. 2018). Overall, the interval between successive mass-bleaching episodes at a given reef location have decreased from 25-30 years in the 1980s to <6 years in 2016 (Hughes et al. 2018a), which limits opportunities for reef recovery in the aftermath of these disturbances. With continued increases in greenhouse gas emissions, mass-bleaching is expected to occur annually at virtually all reef locations by 2050 (van Hooidonk et al. 2013), whereby the onset of persistent annual mass-bleaching is expected to overwhelm the recovery and adaptive capacity of coral assemblages, resulting in inevitable degradation of reef ecosystems. In reality, coral assemblages require much more than 1-2 years reprieve from coral bleaching and other major acute disturbances for effective recovery (Gilmour et al. 2013; Johns et al. 2014; Edmunds et al. 2019; McWilliam et al. 2020), and longer in marginal or isolated locations. The current global average for the recurrence of mass-bleaching episodes (<6years; Hughes et al. 2018a)

is therefore, already contributing to widespread degradation of coral reef ecosystems, especially given significant other chronic and acute disturbances that are also impacting coral reef ecosystems.

Aside from suppressing coral cover, recurrent mass-bleaching has marked impacts on biological and physical structure of coral reef habitats (Hughes et al. 2018b), largely owing to marked interspecific differences in bleaching susceptibility among scleractinian corals (e.g., Marshall and Baird 2000; Loya et al. 2001; van Woesik et al. 2011; Grotolli et al. 2014). For the most part, erect branching corals from the families Acroporidae and Pocilloporidae appear disproportionately susceptible to elevated temperatures and mass-bleaching (but see Guest et al. 2012) and recurrent mass-bleaching can lead to declines in the abundance of these species with corresponding increases in the predominance of massive and robust corals (Alvarez-Filip et al. 2011; Riegl et al. 2017). Such shifts in coral composition affect habitat complexity (Alvarez-Filip et al. 2011), biodiversity (Wilson et al. 2006) and reef accretion (Perry et al. 2013). However, the corals that are most susceptible to coral bleaching (e.g., *Acropora* spp.) generally have greatest capacity for recovery and replenishment (Pratchett et al. 2020a), and will continue to dominate reefs so long as there is sufficient interval between major disturbances to allow for effective recovery (e.g., Gilmour et al. 2013), and there is sustained high levels of recruitment, necessary for rapid replenishment (Hughes et al. 2019a).

1.4 Australia's Coral Sea Marine Park

Australia's Coral Sea Marine Park (CSMP) is a very large (978,836 km²) multi-use marine park located immediately adjacent to the Great Barrier Reef Marine Park (GBRMP, Director of National Parks 2018). 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 15,000km² (Director of National Parks 2018). While there have been recurrent surveys of these reefs (Ayling and Ayling 1985; Oxley et al. 2004; Oxley et al. 2005; Ceccarelli

et al. 2008; Ceccarelli et al. 2009; Edgar et al. 2015; Harrison et al. 2018), 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. 2018). 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. 2018), possibly due to recurrent coral bleaching events (Oxley et al. 2005; Harrison et al. 2018) 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. 2018). In 2016, coral bleaching was restricted to central reefs, where there was a corresponding decline in the abundance *Acropora* and *Pocillopora* corals (Harrison et al. 2018). 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. 2018). This lack of fast growing coral species, will however, likely constrain the capacity for coral recovery across large parts of the central CSMP (Ceccarelli et al. 2009; Oxley et al. 2005). 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. 2016b). 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 constrains capacity for recovery (Smith et al. 2008; 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 et al. 2011). This lack of spatial and temporal scope leaves huge gaps in our knowledge and understanding of reefs in the CSMP. To better inform the sustainable management of these reefs, the current coral community structure on reefs throughout the CSMP and their susceptibility to varying disturbances must be determined.

1.5 Objectives

The purpose of the research presented within this thesis was to assess spatio-temporal patterns of recent disturbance within the CSMP, considering background levels of coral mortality during years when there were no apparent major acute disturbances, but also exploring the differential incidence and severity of mass-bleaching during a very large scale and intense marine heatwave in 2020. Given the large distances separating shallow reef environments in the CSMP, connectivity among reefs is expected to be very low (Ceccarelli et al. 2013), which will have major consequences for coral recovery and vulnerability to major disturbances. This limited biological connectivity may be partially offset by isolation from chronic and acute human disturbances, whereby the CSMP is far removed from the Australian coastline and subject to very low levels of fishing (Payet et al. 2020). If so, background levels of coral mortality and injury may be relatively low (e.g., compared to GBR reefs located much closer to the Australian coastline), providing increased capacity to withstand and recover from major disturbances. Quantitative data on the incidence of coral injuries and bleaching is therefore,

compared between the CSMP and comparable reefs within the GBRMP. The results of this research are presented in two separate chapters:

Chapter 2 quantifies incidence of recent coral injury (inclusive of whole and partial colony mortality) at reefs across the Coral Sea and GBR both during periods (2018-19) when there were no apparent major acute disturbances, and during the recent mass-bleaching (2020). Importantly, high incidence of injury could constrain growth and replenishment of coral, making coral populations even more vulnerable to major disturbances events (Pisapia et al. 2020), such as mass bleaching. As the frequency and intensity of disturbances increases (Bellwood et al. 2019), we might expect to see higher prevalence and severity of injuries, especially during years of mass disturbance, although this has never been explicitly tested. Furthermore, partial mortality of corals has only been quantified on one reef in the CSMP and incidence of background partial mortality during a routine year has never been recorded (Oxley et al. 2004). As such, my first chapter presents and discusses incidence of injury occurring on corals for 20 reefs throughout the CSMP and 27 reefs on the GBR. Susceptibility of different taxa and colony sizes is examined between a period of routine, background mortality, during which no major disturbances occurred (2018/19) and a period during which a major coral bleaching event occurred (2020). This was assessed on an extensive spatial scale, documenting variability in susceptibility among habitats, sites, reefs and marine parks.

Chapter 3 investigates susceptibility of coral assemblages to recent coral bleaching in the CSMP and GBR. This latest mass-bleaching event (in 2020) is the third large scale bleaching disturbance to have affected CSMP (and the GBR) in the last five years. Previously, bleaching susceptibility has been assessed for both parks to some extent (Harrison et al. 2018; Hughes et al. 2018b), but focus has been on the spatial extent of the bleaching, temporal variation between bleaching events and the link between bleaching severity and heat stress. As coral assemblages shift and return times between major disturbances decrease, it is important

to continually assess how coral communities respond to bleaching, to determine which corals are likely to persist into the future. Therefore, this chapter tests the effects of colony size and the level of overall bleaching severity at each reef on the bleaching susceptibility of different coral taxa. Determining the vulnerability of different corals to varying levels of reef-wide bleaching severity will help to elucidate what communities may look like as incidence and intensity of bleaching continues to increase into the future.

This thesis also includes a summative concluding chapter, which discusses the outcomes of both chapters, focussing particularly on the effect that differential susceptibility of coral taxa and colony sizes may have on community composition and size structure in the face of recurrent disturbances on relatively isolated reefs throughout the Coral Sea.

Chapter 2. Changes in the incidence of coral mortality during widespread mass-bleaching across Australia's Coral Sea and Great Barrier Reef

2.1 Introduction

Coral reef ecosystems are being rapidly degraded globally, with sustained declines in the abundance of reef-building scleractinian corals (Gardner et al. 2003; De'ath et al. 2012; Bruno and Selig 2007; Ortiz et al 2018; reviewed by Pandolfi et al. 2003). Widespread coral loss is generally attributed to increasing frequency, severity and/or diversity of acute disturbances, such as severe tropical storms or climate induced coral bleaching (De'ath et al. 2012; Bruno and Selig 2007; Hughes et al. 2018b; Bellwood et al. 2019; Gilmour et al. 2019; McWilliam et al. 2020). However, it is increasingly apparent that chronic environmental pressures, such as declining water quality, also contribute to declining coral cover (Ortiz et al. 2018; Mellin et al. 2019a), either by constraining recovery or increasing vulnerability to major disturbances. Similarly, the effects of small-scale routine, background disturbances (e.g., disease, natural predation or sedimentation) may also contribute to the declining health, resilience, and abundance of reef-building corals (Wakeford 2008; Pisapia and Pratchett 2014), but these are often overlooked. Even in the absence of major disturbances, background partial mortality can be highly prevalent among coral assemblages (Hughes and Jackson, 1985; Pisapia and Pratchett; Pisapia et al. 2015). It is important to establish baseline levels of mortality, including partial mortality, occurring in the absence of major disturbances, against which to assess effects of major disturbances (Lirman et al. 2014).

Few studies have compared incidence of full and partial coral colony mortality before and after major disturbances, with limited evidence suggesting there are significant increases in both full and partial colony mortality (collectively referred to hereafter as injuries) both

during and after major disturbances (Harriott 1985; Lirman et al. 2014). For example, Lirman et al (2014) reported baseline annual injury of eleven Caribbean coral species increased from <5% to 19.9% during a cold-water anomaly (Lirman et al. 2014). Increases in injuries were also observed several months after the 1981 mass-bleaching on Australia's Great Barrier Reef (GBR) (Harriott 1985). Whilst there was a clear increase in injuries associated with the bleaching event in 1981, there was no explicit comparison of injury rates before *versus* during the bleaching. The lack of data on coral injury during the bleaching makes it difficult to distinguish between injury caused directly by the bleaching, and injury caused by routine disturbances occurring simultaneously. More recently, Hughes et al (2018b) quantified very recent whole colony mortality of corals during the 2016 bleaching event on the GBR, clarifying which corals were most susceptible to instantaneous bleaching induced mortality, however no comparisons to routine levels of recent mortality were available. Determining incidence of recent partial and whole colony mortality during periods preceding a major disturbance will allow for more accurate understanding of the true magnitude of disturbance induced injury.

Aside from causing overall declines in the abundance of corals, chronic and acute disturbances may also contribute to changes in population and community structure of coral assemblages, owing to differential susceptibility among coral taxa and with colony size (e.g., Harriott 1985; Meesters et al. 1997; Pisapia and Pratchett 2014; Bruckner 2012; Nugues and Roberts 2003; Madin et al. 2020). For example, injury caused by sediment deposition may only affect species lacking the ability to reject fine particles (Nugues and Roberts 2003). More generally, it appears that erect branching corals are disproportionately susceptible to different sources of disturbances, including physical damage (Meesters et al. 1996, Madin and Connolly 2006), predation (Cole and Pratchett 2011) and bleaching (Loya et al. 2001). However, these corals (e.g., branching *Acropora*) tend to have lower prevalence of partial mortality, especially compared with massive *Porites* (e.g., Pisapia and Pratchett 2014; Pisapia et al. 2015). To

reconcile this mismatch in susceptibility to disturbance *versus* prevalence of partial mortality, it is important to account for taxonomic differences in tissue regeneration and repair (Meesters et al. 1997). Notably, partial mortality is likely to be very apparent and persistent on slow-growing massive and robust corals (Pisapia and Pratchett 2014; Pisapia et al. 2015). Conversely branching *Acropora* exhibit fast tissue repair (Hall 1997), but also large dead and peripheral portions of the colony are likely to erode or become dislodged reducing the appearance of persistent partial mortality (Madin et al. 2020). Nonetheless, high incidence of injuries occurring in the background influences the population dynamics of branching corals, with important ramifications for reef structure and function (Hughes et al. 2018b; 2019a; McWilliam et al. 2020).

Together with taxonomic differences, the incidence of partial mortality is typically positively related to colony size (Jackson 1979; Hughes and Jackson 1985; Meesters et al. 1994; Pratchett et al. 2013a; Madin et al. 2020; but see Wesseling et al. 2001), while the likelihood of whole colony mortality is negatively related to colony size (Bak and Engel 1979; Madin et al. 2014), although this does somewhat vary with morphology. This size-related variation is generally related to exposure to disturbances which increases with colony longevity and hence colony size (Jackson 1979), though size-based differences in the incidence of partial mortality are not always apparent (Bak and Meesters 1998; Pisapia and Pratchett 2014; Nugues and Roberts 2003). Whilst regeneration rates appear unaffected by colony size in some studies (Lirman 2000; Meesters et al. 1994), it may be that this lack of size specificity in incidence of partial mortality is due to differing regenerative capacities among size classes (Loya 1976; Hughes 1984; Kramarsky-Winter and Loya 1996). Despite this, small corals may actually be disproportionately susceptible to certain effects of major disturbances (e.g., sedimentation) that cause elevated rates of whole-colony mortality (Bak and Engel 1979; Madin et al. 2014), leading to increased preponderance of larger colonies (e.g., Bak and Meesters 1999; Dietzel et

al. 2020). More often, however, high incidence of partial mortality following disturbances reduces the effective size of larger corals, leading to a preponderance of smaller colonies (Gilmour 2004; Pisapia et al. 2019, 2020). The loss of larger, more fecund colonies will have significant impacts on future rates of recruitment and recovery (Hughes et al 2019a). It is, therefore, important to understand varying rates of whole and partial colony mortality on different taxa and colony sizes to inform our understanding of how assemblages may change following varying disturbance regimes.

This study explicitly quantified the incidence of recent injury (including whole and partial colony mortality) during the peak of the 2020 mass-bleaching on shallow water coral assemblages within Australia's Great Barrier Reef (GBR) and throughout the adjacent Coral Sea. Specifically, I compare the incidence of recent injury during the 2020 bleaching *versus* surveys conducted when there was no widespread mass bleaching (Pratchett et al. 2020b). In addition, I examine the incidence of recent injury among different coral taxa and colony sizes. This is the first study to quantify incidence and cause(s) of recent injury for shallow-water coral assemblages throughout Australia's Coral Sea, providing some insight into contemporary disturbances and recovery capacity of coral assemblages on a large spatial scale throughout this remote, poorly connected region. A hierarchy of spatial scales (between regions and among reefs, sites and habitats) is examined to determine spatial patterns in the occurrence of recent mortality in scleractinian corals. By focussing solely on recent mortality, this study helps to reconcile apparent differences in susceptibility to disturbance, rather than reflecting differences in tissue regeneration and recovery capacity (Meesters et al. 1997).

2.2 Methods

2.2.1 Study Sites

This study was conducted between 12th April 2018 and 22nd March 2020 at reefs throughout the Coral Sea Marine Park (referred to hereafter as the Coral Sea) and at select reefs (mostly outer shelf reefs) within the Great Barrier Reef (GBR) Marine Park. The Coral Sea covers a vast area (978,836 km²) and includes 34 isolated reef systems and atolls that are >160km from the Queensland coast (Fig. 2.1). Due to the remote nature of these oceanic reefs, they are far removed from land-based pressures, though connectivity between reefs is also likely to be low, potentially limiting recovery and increasing vulnerability of reef assemblages to any major disturbances (*sensu* Gilmour et al. 2013). The areal extent of the GBR is approximately one third of the size (343,699km²) of the Coral Sea, but comprises ~3000 closely positioned reefs. To determine how the incidence of recent injury on coral colonies varied between regions and survey periods (pre- and during bleaching), and among coral taxa, colony size, reefs, sites and habitats, a series of benthic surveys were conducted both prior to (2018-19) and during the 2020 bleaching event. Surveys were conducted at 140 sites, across 30 reefs (20 in the Coral Sea, 10 in the GBR), between April 2018 and March 2019 (hereafter pre-bleaching; Fig. 2.1). Surveys were also conducted at 90 sites across 33 reefs (16 in the Coral Sea, 17 in the GBR), during the peak of the 2020 mass-bleaching event (February – March 2020; Fig. 2.1). One to 13 sites were surveyed at each reef (median = 3 sites/reef), always in areas where there was continuous reef matrix with a well-defined shallow crest (~2m depth) and adjacent slope extending into deeper water.

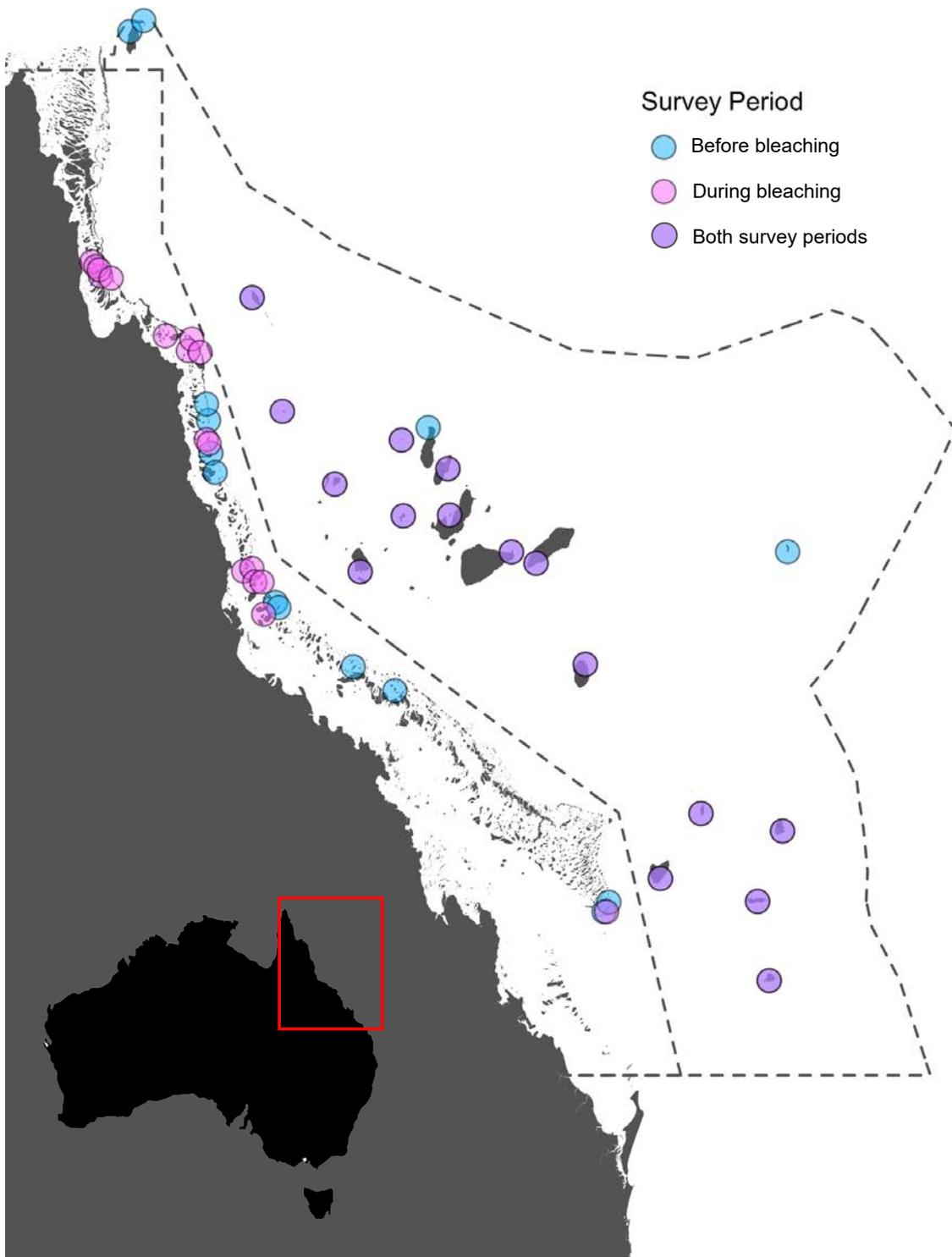


Figure 2.1: Map showing the reefs surveyed in Australia’s Coral Sea Marine Park and Great Barrier Reef Marine Park. Blue dots represent reefs surveyed pre-disturbance (2018/19; n = 14 reefs), pink dots represent reefs surveyed during the 2020 bleaching event (n = 17 reefs) and purple dots represent reefs

surveyed in both years (n = 16 reefs). Dashed lines are the boundaries of the Great Barrier Reef and Coral Sea Marine Parks.

2.2.2 Recent Mortality

To quantify incidence of recent mortality within the coral assemblage, three replicate 10 x 1 m belt transects were surveyed on the reef crest (~2m depth) and the reef slope (~8m depth) (n=6) at each site. Each transect was spaced 50m apart, laid parallel to the reef contour and at a constant depth. All scleractinian corals within each belt were identified to genus, and placed into morphological groups, where appropriate (e.g., acroporids were categorised into ‘tabular’, ‘staghorn’ and ‘other’ and poritids into ‘massive’, ‘branching’, and ‘encrusting with uprights’ (predominantly *Porites rus*). The maximum diameter of each coral was estimated and placed into one of five size classes (juveniles: <5cm, small: 5-20cm, medium: 20-40cm, large: 40-60cm and very large: >60cm diameter), which were later collapsed into three classes (juveniles: <5cm, medium: 5-40cm, and large: >40cm diameter) to increase the sample size in each class. Each colony was classified as either healthy (i.e., no injuries) or injured (including recently dead) based on the presence of >5% tissue loss with the skeletal structure still intact or recently broken (including fish bites) and little or no growth of turf algae, cyanobacteria or macroalgae present (following Lirman et al. 2014). For all injured colonies the likely cause of injury was noted and placed into one of twelve categories: 1) algal competition; 2) bleaching; 3) breakage; 4) crown of thorns starfish predation; 5) disease; 6) *Drupella* predation; 7) bio-eroding invertebrates; 8) fish predation; 9) other predation; 10) sedimentation; 11) territorial damselfish; and 12) unknown. These were based on the shape and nature of the scar (i.e., fish bites, breakage, disease or sedimentation), the presence of corallivores, bioeroders or other ecosystem engineers within the immediate vicinity (i.e. crown of thorns starfish, *Drupella* snails, excavating invertebrates and *Stegastes spp.* damselfish).

Unlike many previous studies (e.g., Pisapia et al. 2019), coral mortality recorded in this study is restricted to incidence of instantaneous or relatively recent mortality (i.e., areas of tissue loss where the skeletal structure was still intact, with little or no growth of turf algae, cyanobacteria or macroalgae). I explicitly excluded mortality where thick assemblages turf algae, cyanobacteria and/or macroalgae had colonised the coral skeleton, or where there was evidence of skeletal erosion, indicating mortality older than ~1 month (Diaz-Pulido and McCook 2002). Therefore, ramets of living tissue remaining on larger colonies that had experienced partial mortality were treated as individual colonies for the purposes of understanding more recent disturbance effects on rates of mortality. Small colonies classified here as ‘juveniles’ may therefore, represent ramets of old partial mortality.

2.2.3 Statistical Analyses

A Bayesian hierarchical generalized linear model was constructed to investigate the effects of three variables; taxa (TAXA), colony size (SIZE) and survey period (YEAR) on incidence of recent injury. Interactions between taxa and both colony size and survey period were modelled to investigate how differential incidence of injury varied temporally and with respect to colony size. Additionally, a nested random variable (random intercepts) was included with habitat zone (z) nested within site (s) nested within reef (r) within region (R) to account for variable rates of injury at different spatial scales. The probability of an individual coral colony i , from zone z , site s , reef r and region R , (π_{Rrszi}) being injured was modelled as:

$$\begin{aligned} \ln\left(\frac{\pi_{Rrszi}}{(1 - \pi_{Rrszi})}\right) \\ = \beta_0 Rrszi + \beta_1 YEAR_{Rrszi} + \beta_2 TAXA_{Rrszi} + \beta_3 SIZE_{Rrszi} \\ + \beta_4 TAXA_{riRrszi} SIZE_{Rrszi} + \beta_5 TAXA_{Rrszi} YEAR_{Rrszi} \end{aligned}$$

Effects plots with 95% credible intervals and posterior distributions were produced to show how injury varied with respect to six common taxa (*Acropora*- other, *Isopora*, *Montipora*,

Pocillopora, massive *Porites* and *Stylophora*), survey period (pre-bleaching and during-bleaching) and colony size (<5cm, 5-40cm, and >40cm colony diameter) individually as well as effects plots with 95% credible intervals to show the interactive effects, reported as log-odds ratios. Tukey's pairwise comparisons were generated using estimated marginal means to test for significant differences among the levels of the interacting factors (taxa, colony size and survey period).

To explicitly examine spatial variation in incidence of recent injury, an additional Bayesian hierarchical generalized linear model was constructed to investigate the fixed effects of habitat zone (crest vs. slope) and Marine Park (GBR vs. Coral Sea), with a nested random effect of site within reef on the probability of a coral colony to exhibit injury.

All data was analysed using R 3.5.1 (R core team 2018) using the "brms" package to fit the hierarchical models (Bürkner 2017), with the "emmeans" (Lenth 2019) and "multcomp" (Hothorn et al. 2008) packages used for pairwise comparisons of marginal means and the calculation of p-values.

Results

During this study, I recorded the incidence of recent injury (the proportion of colonies exhibiting recent whole and partial colony mortality) for a total of 103,037 coral colonies from 27 taxa across the 230 sites, with 4486 of the colonies examined showing signs of recent injury. Interestingly, the incidence of recent injury for all coral taxa combined did not differ between pre-bleaching and during-bleaching periods, however, the cause of injury changed markedly between survey periods, with the main causes before the bleaching recorded as 'unknown' followed by 'breakage', while 'bleaching' related injuries were most prevalent during the 2020 bleaching event (Fig. 2.2b). Despite the relatively consistent rate of injury between survey

periods, the incidence of recent injury and the cause of injury varied among taxa and size classes both before and during bleaching (Fig. 2.2a).

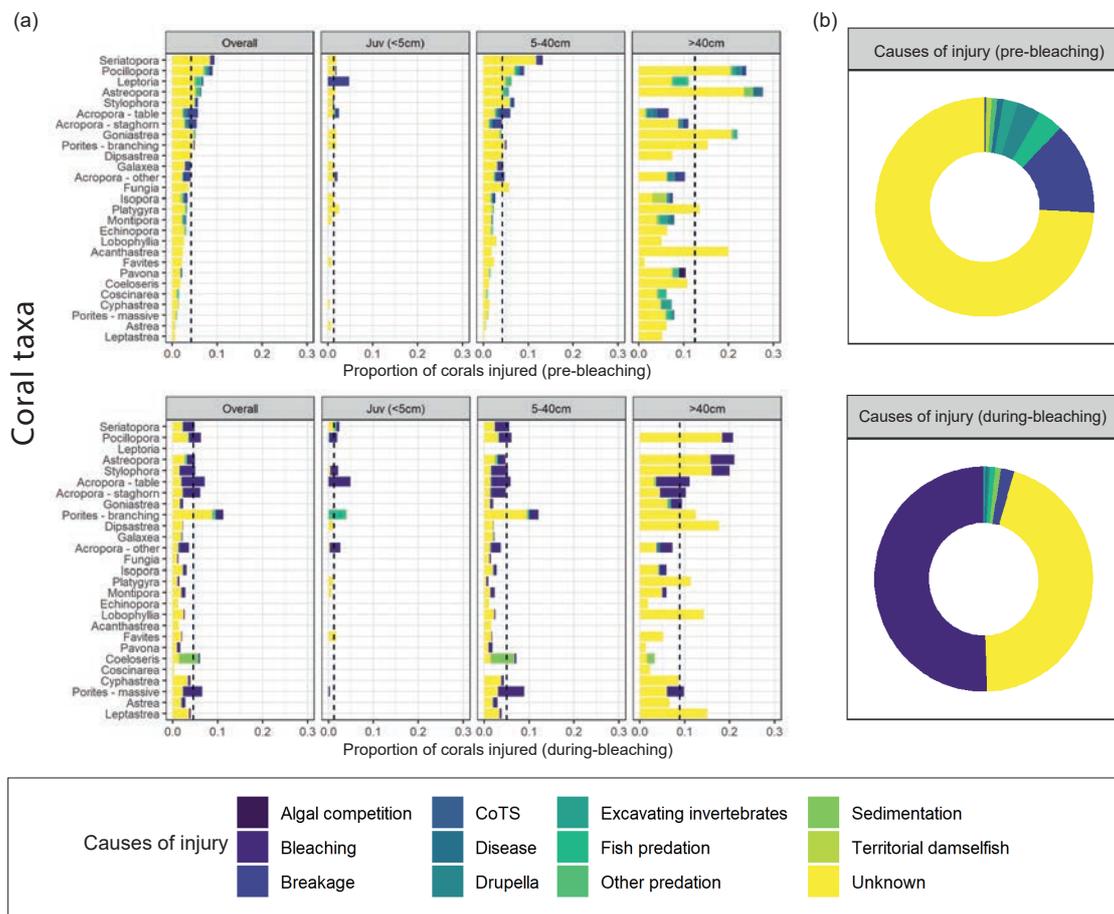


Figure 2.2: Proportional incidence of recent injury and causes for the pre-bleaching survey period (top) and during-bleaching (bottom). Bar plots (a) represent proportional incidence of recent injury (mean) for each taxon, among size classes (columns), broken down by injury category (colours) where median proportion of colonies injured is displayed by the dashed vertical line. Pie charts (b) represent the causes of injury when pooled across all taxa and colony sizes for each survey period.

Incidence of recent injury varied spatially, with more variability explained by the random effects of Reef and Site than the fixed effects of Habitat and Marine Park (Marginal $R^2 = 0.002$; Conditional $R^2 = 0.03$). Whilst this model only accounted for 3% of the variability within the assemblage, there was a significantly higher likelihood of injury occurring in corals

in the Coral Sea compared to the GBR, with these differences most pronounced when comparing between coral assemblages surveyed on the reef crest (Fig. 2.3). Results from the full model indicate that the fixed (and interactive) effects of year, size and genus accounted for 2.4% (Marginal $R^2 = 0.024$) of the variability while the spatial nested random factor (Region/Reef/Site/Zone) accounted for an additional 6% of the variability (Conditional $R^2 = 0.084$). These results indicate that incidence of injury varies more across various spatial scales than with respect to taxonomy, survey period and colony size.

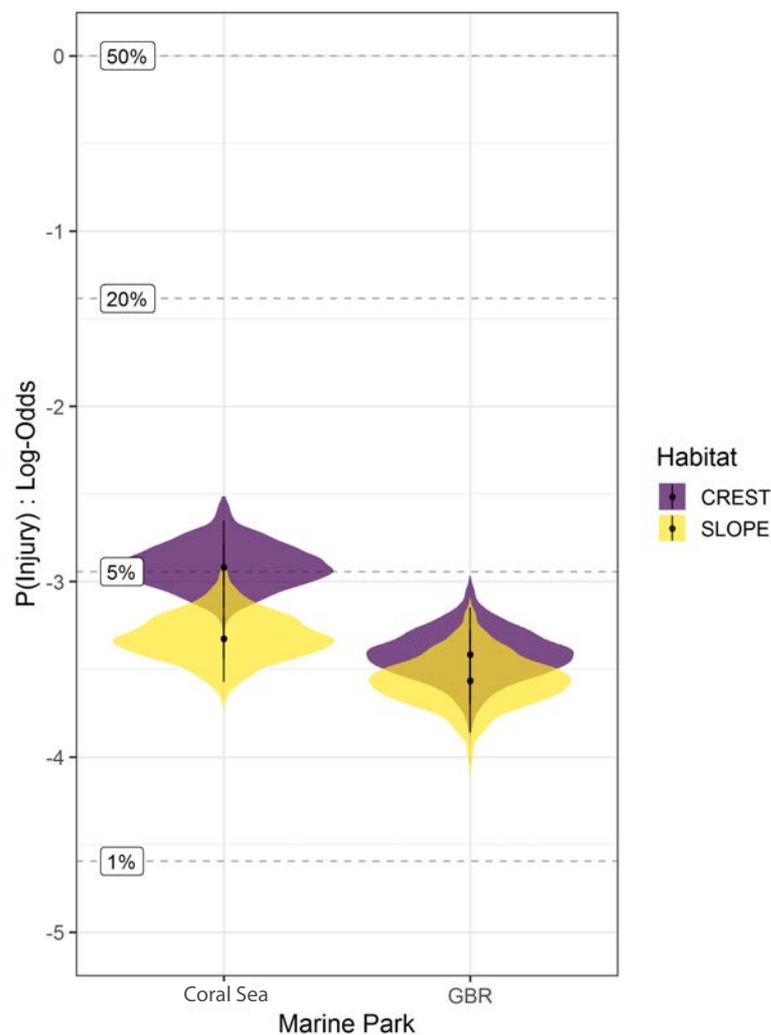


Figure 2.3: Marginal posterior distributions of incidence of recent injury (P(Injury)) for the interaction between habitat zone and marine park. Points represent estimated marginal means on the log-odds scale,

lines represent 95% quantile intervals. Boxed letters represent significant differences between variable levels obtained from Tukey pairwise comparisons. Dotted lines indicate the percentage value when back-transformed from the log-odds scale.

Despite the mass coral bleaching event occurring in 2020, the overall incidence of recent injury was statistically consistent between survey periods ($z=0.66$, $p=0.503$), increasing very slightly from 4.2% recent injury prior to the bleaching to 4.5% during the bleaching (Fig. 2.4c). However, the incidence of recent injury varied among taxa both prior to and during the bleaching. Prior to the bleaching event, the incidence of recent injury ranged from 0.7% for *Leptastrea* to 9.7% for *Seriatopora* colonies and during the bleaching event ranged from 0% for *Leptoria* to 11.2% for branching *Porites* (Fig 2.2a). Of the six modelled taxa (most commonly occurring taxa), the incidence of injury for three taxa (*Stylophora* ($z=0.479$, $p=0.632$), *Isopora* ($z=1.208$, $p=0.227$), and *Montipora* ($z=0.387$, $p=0.699$)) remained consistent between survey periods (Fig. 2.5a). But for the remaining three taxa, the incidence of injury differed between survey periods with the incidence of injury being lower for *Pocillopora* ($z=8.15$, $p < 0.0001$) and *Acropora*-other ($z=5.945$, $p < 0.0001$) during- compared to pre-bleaching, but greater for massive *Porites* ($z=17.871$, $p < 0.0001$), of such magnitude that it appeared among the most injured taxa during the bleaching (Fig. 2.5a). This change in hierarchy was not just seen among modelled taxa; ranked hierarchies of all taxa showed a re-shuffling of the most/least injury between survey periods (Fig. 2.2a). In particular, branching *Porites* (from rank 9: 5% to rank 1: 11.2% recent injury) and massive *Porites* (rank 25: 1.6% to rank 3: 6.5%) joined the ranks of taxa exhibiting the most injury during the bleaching, whilst *Leptoria* dropped from one of the most injured taxa prior to the bleaching, to exhibiting no injuries during the bleaching (rank 3 6.9% mortality to rank 27 0% mortality) (Fig. 2.2a).

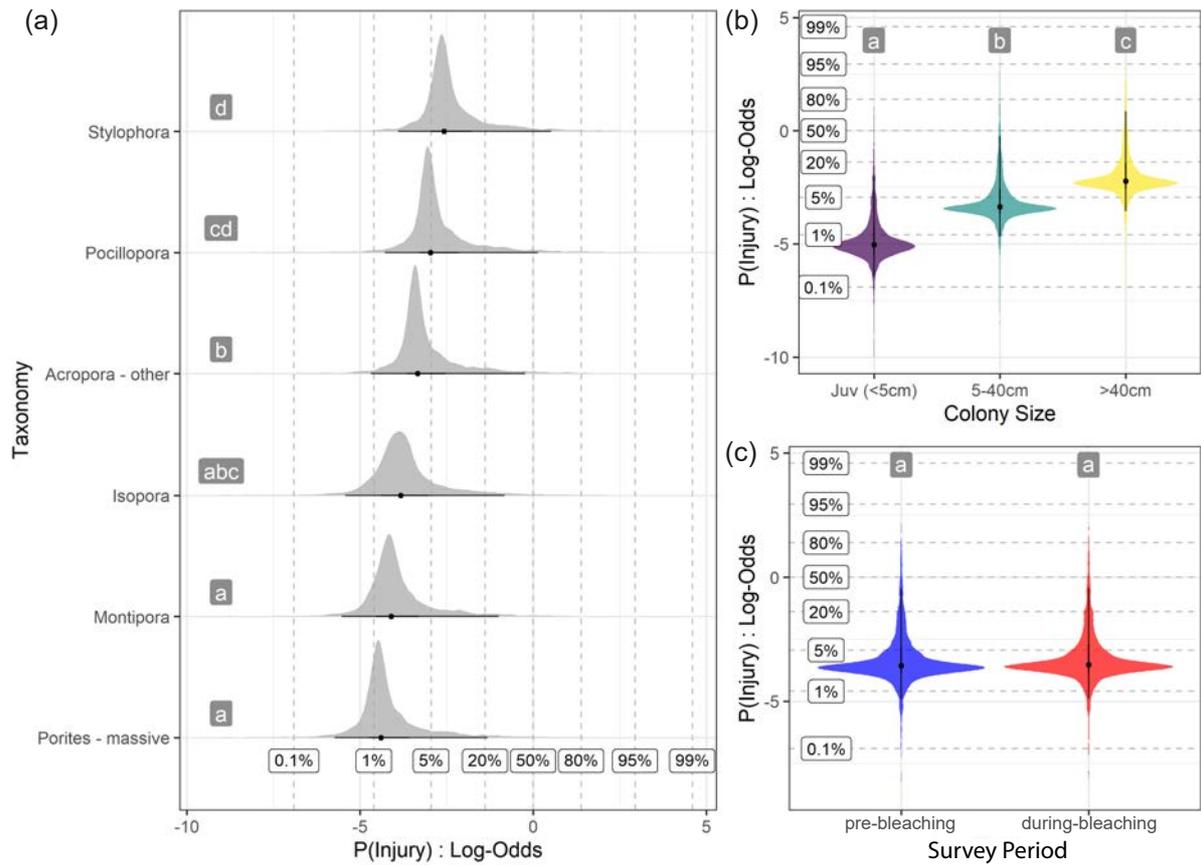


Figure 2.4: Marginal posterior distributions of incidence of injury (P(Injury)) among coral taxa (a), colony sizes (b) and between survey periods (c). Points represent estimated marginal means on the log-odds scale, and horizontal (a) and vertical (b, c) lines represent 95% quantile intervals. Boxed letters represent significant differences between variable levels obtained from Tukey pairwise comparisons. Dotted lines indicate the percentage value when back-transformed from the log-odds scale.

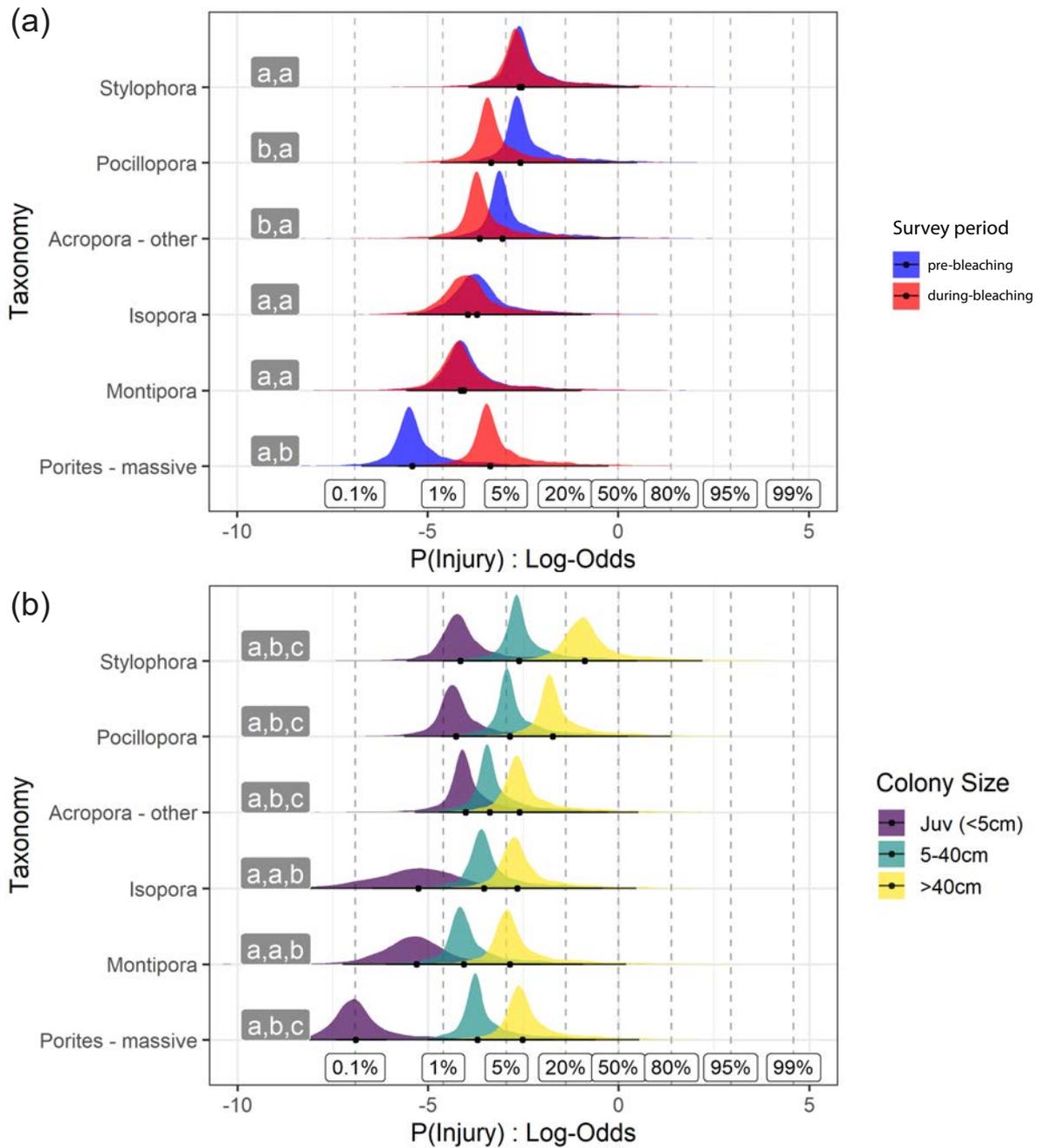


Figure 2.5: Marginal posterior distributions of incidence of injury (P(Injury)) for the interaction between taxa and survey period (a) and taxa and colony size (b). Points represent estimated marginal means on the log-odds scale, lines represent 95% quantile intervals. Boxed letters represent significant differences between variable levels obtained from Tukey pairwise comparisons. Dotted lines indicate the percentage value when back-transformed from the log-odds scale.

The proportion of injured colonies increased with increasing colony size (Fig. 2.4b). This was relatively consistent among all six taxa within the model interaction, where the largest colonies (>40cm diameter) were significantly more likely to be injured than both medium (Large – Medium: $z = 14.656$, $p < 0.0001$) and juvenile (Large – Juvenile: $z = 13.125$, $p < 0.0001$) colonies (Fig. 2.5b). In four out of the six modelled taxa, medium sized corals (5-40cm diameter) were also significantly more likely to be injured than juveniles (<5cm diameter) (Fig. 2.5b). The non-significant differences for *Isopora* ($z = 1.944$, $p = 0.137$) and *Montipora* ($z = 2.284$, $p = 0.058$) were only marginally so and reflective of more variability in the smallest size class (Fig. 2.5b). In particular, the magnitude of the difference in probability between juveniles and the next size class to exhibit injury was most apparent in massive *Porites*, when compared with other taxa (Medium (2.4%) – Juvenile (1.1%): $z = 11.149$, $p < 0.0001$) (Fig. 2.5b).

Discussion

Despite widespread and severe coral bleaching throughout the Coral Sea and GBR in 2020 (e.g., Pratchett et al. 2020b, see also Chapter 3), incidence of recent injury remained below 5% and did not differ from background levels recorded prior to the bleaching event. The levels of recent injury reported here are comparable to levels of recent injury reported at other locations (9% *Acropora cytherea* colonies in the Chagos archipelago, Pratchett et al. 2013a; <5% on coral communities in the Florida Reef Tract, Lirman et al. 2014), but lower than previous estimates from the GBR (59% - 92%, Pisapia and Pratchett 2014) outside of major disturbance events. We also recorded relatively low incidence of recent coral mortality during the mass-bleaching compared to previous major bleaching episodes on the GBR. During the 2016 bleaching on the GBR, the incidence of recent full colony mortality (Hughes et al. 2018b) was considerably higher than estimates of injury (inclusive of recent whole and partial colony mortality) recorded herein, which is likely explained by differences in the magnitude of heat

stress and corresponding severity of mass-bleaching. In 2016, Hughes et al. (2018b) recorded low incidence of recent mortality (<5%) at reefs that were exposed to 4 degree heating weeks (DHW, °C-weeks), but mortality was very high (27%) on reefs exposed to > 8 DHW (see also Leggat et al. 2019). Low levels of coral injury recorded in this study may suggest that there were consistently low levels of heat stress (DHW), though observed incidence of coral injury will also vary with the timing of the surveys relative to the peak in heat stress, differences in community composition among studies (e.g., Harrison et al. 2018), or acclimation through previous exposure to heat stress (Ainsworth et al. 2016; Fordyce et al. 2019). Severe mass-bleaching may also lead to more protracted coral mortality (e.g., Baird and Marshall 2002; Hughes et al. 2018b), requiring further follow-up surveys to assess whether this recent mass-bleaching resulted in elevated levels of coral mortality. It should also be taken into consideration that previous back-to-back mass bleaching events in 2016 and 2017 (Harrison et al. 2018) may have latent effects on the levels of injury recorded in our pre-bleaching surveys, possibly increasing the susceptibility to injury 12 months later.

Even though there was no marked change in recorded incidence of injury during surveys conducted before *versus* during the bleaching, there were shifts in the nominal cause of recent coral injury. In the recent (2020) surveys conducted during the bleaching, ~50% of all injuries recorded were attributed to immediate effects of the bleaching itself, whereas < 1% of recent injuries were attributed to bleaching in previous surveys. Prior to the bleaching, it was very difficult to establish the specific cause of observed injuries and recent colony injury. ~75% of injuries were not attributed a specific cause prior to the bleaching, but these ‘unknown’ injuries were not caused by temperature stress. It is possible however, that injuries caused by unknown entities occurring on bleached corals were wrongly attributed to the 2020 bleaching in this study, increasing the appearance of bleaching-related injuries. Alternatively, because no increase in the overall incidence of recent injury during the mass-bleaching was

recorded, it may be that bleaching induced coral mortality might occur mainly on colonies that were already compromised due to other routine or background disturbances. If so, the prevalence of bleaching-related injuries might effectively mask other causes of recent injury. This unexpected result highlights the need to further assess changes in the incidence of recent injuries before versus during major disturbances, to more accurately assess the extent to which major disturbances compound upon background rates of coral mortality and thereby lead to elevated mortality, or not. It is also possible that surveys conducted during the peak of the bleaching in this study failed to fully capture resulting injury attributable to this widespread bleaching event, which may occur up to 9 months post-bleaching (Hughes et al. 2017b). A time lapse series of observations of tagged colonies might assist with a more accurate understanding of temporal effects of disturbance (e.g., Baird and Marshall 2002), however capturing the same large sample size over the extensive spatial scale of this study would be unfeasible. It is also important to explicitly consider whether there is an overall increase in the severity of injuries during mass-bleaching, whereby moderate changes in overall incidence of recent injury might belie increased levels of whole colony mortality.

Whilst the incidence of recent injury was seemingly low (<5% of colonies) both before and during the 2020 mass-bleaching, the cumulative and longer-term effects of routine injuries could be substantial. Importantly, I restricted consideration of recent injuries to only those injuries where there was very limited apparent overgrowth of the exposed coral skeleton by algae, suggesting that these injuries occurred in just the last 4-6 weeks (*sensu* Diaz-Pulido and McCook 2002). The current surveys were conducted exclusively in summer months (November to April), and so rates of injury might be lower (or higher) at other times throughout the year, but if ~5% of colonies are subject to new injuries every month, this likely to have major effects on energy invested in regeneration and repair (Lirman 2000; Croquer et al. 2002) and/ or the accumulation of injuries on corals where injuries are never completely healed (e.g.,

Pisapia and Pratchett 2014; Pisapia et al. 2015). Both these outcomes can have significant ramifications for growth (Bak 1983; Meesters et al. 1994), reproduction (Rinkevich and Loya, 1989; van Veghel and Bak 1994) and individual colony condition (Pisapia et al. 2014). Long term implications of recent injuries could be far-reaching, particularly given that during major bleaching, incidence of injury increased for subset of taxa known to regenerate tissue at a slow rate (e.g., *Porites spp.*). Further monitoring of these injuries within the population, as well as quantification of old injuries may help further our understanding of the long-term impacts of routine and background disturbances.

Incidence of recent injury was spatially variable throughout the Coral Sea and GBR, where injury was higher in the Coral Sea, especially when comparing among coral assemblages on the reef crest. Given the relative isolation of reefs in the Coral Sea, and especially their limited exposure to chronic human pressures (Ceccarelli 2019), we expected to find much lower incidence of routine and background injury in the Coral Sea compared to reefs on the GBR (Jupiter et al. 2008). The higher incidence of recent injury recorded in the Coral Sea, and on reef crest habitats may reflect increased exposure to physical disturbances (Pisapia et al. 2014, Madin et al. 2013; Mass et al. 2011), especially during severe storms. Indeed, several major storms did pass over reefs in the Coral Sea immediately prior to several of the surveys during both survey periods. There is also the possibility that the reduced human related pressures in the Coral Sea (e.g., overfishing, Payet et al. 2020), owing to the relative distance from the coastline, has caused relative increases in abundance of excavating fishes which, in turn, may lead to increased incidence of injury in corals (Bellwood et al. 2012). However, 8.4% of variation explained in our model suggests that injuries were very random events and given that overall incidence of recent injury was <5%, whilst observed differences between habitats and regions were significant, they are relatively small.

Whilst overall incidence of injury did not change before *versus* during the 2020 bleaching event, the hierarchy of those taxa affected by injury did change. Regardless of the survey period, branching taxa (e.g., Staghorn *Acropora*, *Stylophora*, *Seriatopora*) were consistently within the top five taxa most affected by recent injury, which is unsurprising given their susceptibility to a wide range of disturbances (De'ath and Moran 1998; Loya et al. 2001; Madin et al. 2014). But interestingly, declines in the incidence of injury were observed for some taxa (e.g., *Pocillopora* and *Leptoria*) during the bleaching. This could be due to high interannual variability in the likelihood of injury, or influenced by protracted effects of previous bleaching events in 2016 and 2017, but more research is needed to understand this response. Branching and massive *Porites*, which were among the least injured taxa prior to the bleaching, exhibited significant increases in injury during the bleaching. This is somewhat surprising given the comparative insensitivity of this taxon toward bleaching elsewhere (Loya et al. 2001; Baird and Marshall 2002; Harrison et al. 2018; Hughes et al. 2017b), but aligns with the high susceptibility of these taxa to severe bleaching in 2020 (see Chapter 3). For slow-growing corals, recurrent disturbances that cause this level of recent injury are very likely to have long term ramifications for the size structure and viability of these populations (Madin et al. 2020). As the severity and intensity of coral bleaching events increase with anthropogenic climate change (Oliver et al. 2018; van Hooidonk et al. 2013) our results suggest that even the robust, slow growing taxa may be affected which, due to their limited capacity to recover, may ultimately lead to shifts in community composition (e.g., Kayanne et al. 2002; Van Woesik et al. 2011; Pratchett et al. 2020a), subsequent declines in taxonomic richness and trait diversity (McWilliam et al. 2020) and overall declines in coral cover (Babcock et al 2020).

Incidence of recent injury increased with increasing colony size for most (but not all) coral taxa. Higher incidence of partial mortality on larger coral colonies may lead to increasing shifts in community size structure, whereby reefs may become dominated by small, broken

colonies (Pisapia et al. 2019). Coral assemblages are almost universally dominated by small colonies (Bak and Meesters 1999; Bauman et al. 2013), reflecting cumulative mortality and attrition within each cohort of new recruits, and effective reductions in colony size caused by partial mortality. If however, small colonies are disproportionately susceptible to major disturbances (e.g., Dietzel et al. 2020) and/ or there are sustained declines in population replenishment (e.g., Bauman et al. 2014; Hughes et al. 2019a) coral populations and assemblages may become dominated by large colonies (Dietzel et al. 2020). Such shifts in the apparent size structure of common coral taxa have been reported for the GBR (Dietzel et al. 2020), reflecting increased vulnerability to population collapse if, or when, the remaining large colonies do succumb to chronic or acute disturbances. The current data from the Coral Sea and outermost reefs of the GBR, clearly shows increasing incidence of recent injuries with increasing colony size, which will lead to disproportionate decline in the abundance of large colonies (van Veghel and Bak 1994; Hughes et al. 2019a), with potential ramifications for the reproductive capacity of remnant populations. Changes in coral size structure may also have knock on effects for communities reliant upon the complex habitat corals provide such as reef fishes and invertebrates (Idjadi and Edmunds 2006; Darling et al. 2017). Recovery of larger size classes may be reliant upon the taxonomic composition, the frequency and intensity of both routine and acute disturbances, and the incidence of recruitment pulses (Gilmour et al. 2013). Continued assessment of changing size structures as communities recover following this most recent disturbance will be critical to ascertain the future of these remote coral assemblages.

This study has revealed that whilst increased instances of instantaneous injury did occur on some corals during the bleaching in 2020, it was not ubiquitous across taxa and did not increase the overall incidence of recent injury relative to background levels recorded during periods without widespread mass-bleaching. It is however, necessary to consider whether there

was elevated injury in the aftermath of this bleaching event, leading to overall declines in abundance, size structure or taxonomic composition of coral assemblages across the Coral Sea and outermost reefs on the GBR. Importantly, the incidence of recent injury varies among habitats and reefs, but it is relatively consistent among taxa and with colony size. Chronic levels of background mortality will constrain recovery (e.g., Pratchett et al. 2013a), and is likely to contribute to directional changes in the structure of coral populations and communities (Oliver et al. 2018; Pratchett et al. 2020a; Madin et al. 2020). Shifts in community composition and size structure have significant ramifications for reef structure and function, and in particular, worrying implications for reproduction and replenishment through the loss of large colonies combined with the increased energetic investment in repair. Replenishment may be further impaired by the already highly disturbed nature and poor connectivity of the Coral Sea (Brewer et al. 2007; Ceccarelli et al. 2013; McWilliam et al. 2020). This is the first record of recent injury (including full colony mortality) prior to, and during, a mass bleaching event for the Coral Sea and GBR and should be used as a baseline for recent injury occurring in the absence of major disturbance. Continuing to assess the incidence and, where possible, the causes of injuries occurring on these coral assemblages will further our understanding of the contemporary disturbance regimes and help to identify areas most vulnerable to future disturbance which is fundamental for the management of this large, remote and under-studied marine park.

Chapter 3. Differential bleaching susceptibility among coral taxa and colony sizes across Australia's Coral Sea and Great Barrier Reef

3.1 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. 2017b; Hughes et al. 2018a; Skirving et al. 2019). Prolonged exposure to elevated temperatures and/or extreme increases in temperature can disrupt the symbiotic relationship between corals and zooxanthellae (Symbiodiniaceae), whereby declines in intracellular concentrations or performance of zooxanthellae cause the coral to appear pale or white (bleached), and greatly constrain the capacity of the coral host to obtain energy (Glynn 1984; Douglas 2003). The incidence and severity of marine heatwaves and corresponding mass-bleaching episodes has increased markedly in the last few decades (Oliver et al. 2018; Hughes et al. 2018a; Hughes et al. 2019b), and is predicted to continue to increase under ongoing climate change (Sheppard 2003, van Hooidonk et al. 2013).

Coral taxa are widely reported to vary in their bleaching susceptibility (e.g., Baskin 1998; Loya et al. 2001). Generally, the fast growing and finely branched corals (e.g., *Stylophora*, *Seriatopora* 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. 2013b; Hughes et al. 2017b; Harrison et al. 2018; McClanahan et al. 2020) and high levels of mortality (Brown and Suharsono 1990; Fujioka, 1999; Loya et al. 2001; Baird and Marshall 2002) when exposed to marine heatwaves. 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. 2013b; Harrison et al. 2018; Hughes et al. 2017b; but see Guest et al. 2016). Contrasting bleaching responses of 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 on the GBR has resulted in dramatically altered coral communities (Johns et al. 2014; Bento et al. 2016; Hughes et al. 2018b; Hughes et al. 2019a; Pratchett et al. 2020a), with potential long-term consequences for ecosystem function (McWilliam et al. 2020). Importantly, the cumulative effects of multiple disturbances will likely incur different community responses (Hughes et al. 2019b), 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).

Colony size has also been suggested to influence bleaching susceptibility (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. 2013b; Alvarez-Noriega et al. 2018). Small corals have less resources and a smaller surface area, and are therefore more likely to be killed rather than injured by any given disturbance (Madin et al. 2014). Despite this, some studies suggest small corals may be more resistant to bleaching than larger colonies (Depczynski et al. 2013; Shenkar et al. 2005; Mumby 1999) due to favourable surface area to volume ratios and/or the diversity of symbionts they harbour. Some coral species (e.g., *Acropora tenuis*) harbour a greater variety of symbiont types during early ontogeny, possibly allowing for a more flexible bleaching response than their adult conspecifics (Abrego et al. 2008, 2009). Small colonies

also have significantly higher mass transfer rates than larger colonies, allowing for more efficient diffusion of both CO₂ 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 on the Great Barrier Reef (GBR) were reported to be more susceptible to bleaching mortality than larger congenics (>5cm diameter) during the 2016 bleaching event (Alvarez-Noriega et al. 2018), whereas small corals (<10cm diameter) of the same genus in French Polynesia during an earlier bleaching event were less susceptible to bleaching than their larger congenics (>50cm diameter, Pratchett et al. 2013b). Variability in size selectivity within taxonomic groups, among regions could be related to differences in species composition of *Pocillopora spp.*, symbiont type, genotype or the host's ability to switch or shuffle symbionts (Sampeyo et al. 2008; Goulet 2006), but the mechanisms behind this inconsistency in size-based bleaching are still unknown. Whilst 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), the persistence of juveniles may act as a buffer against shifts in community composition and aid in recovery following such disturbances (Alvarez-Noriega et al. 2018; Chong-Seng et al. 2014).

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. 2017b; 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, whereas extreme heatwaves will likely result in high incidence of bleaching and mortality across all

coral, regardless of size or species (Hughes et al. 2017b). 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. 2017b). However, differential bleaching susceptibility among corals cannot be predicted by heat stress alone, especially following concurrent disturbances (DeCarlo and Harrison 2019; McClanahan et al. 2019; McClanahan et al. 2020), whereby a suite of interacting factors (e.g., sunlight, water flow, nutrient levels) affects the susceptibility of corals to bleaching (Maina et al. 2008; Grottoli et al. 2014; Ainsworth et al. 2016; Sully et al. 2019; De Carlo et al. 2020). Moreover, variation in the specific conditions that lead to elevated temperatures (e.g., the rate of warming) may also have very different effects on corals (e.g., Fordyce et al. 2019) and potentially disrupt normal hierarchies of temperature susceptibility (e.g., Guest et al. 2016). The overall severity of conditions leading to bleaching events are rarely accounted for when determining differential susceptibility, with heat tolerance thresholds only reported for a handful of taxa (reviewed in McLachlan et al. 2020) and only in laboratory conditions.

The objective of this study was to explicitly test for variation in bleaching susceptibility among major coral taxa and colony size classes relative to the overall proportion of corals that bleached at each of 33 reefs (reef-scale bleaching severity) across the Great Barrier Reef (GBR) and Coral Sea. With accelerating climate change, and unprecedented disturbances on coral reefs, we are having to re-learn much of what we knew about the vulnerability and resilience of coral assemblages (Hughes et al. 2018b; Hughes et al. 2019b; McWilliam et al. 2020). Previous coral bleaching events combined with a suite of other acute and chronic disturbances have dramatically altered both size structure and taxonomic composition of coral assemblages (Johns et al. 2014; Hughes et al. 2018b; Mellin et al. 2019; Dietzel et al. 2020), with consequences for ecosystem function and resilience (McWilliam 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 corals are getting smaller (Pisapia et al. 2020; Dietzel 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.

3.2 Methods

3.2.1 Survey sites

This study was conducted from 16 February to 23 March 2020, during a widespread mass-bleaching event in the Coral Sea and adjacent Great Barrier Reef (GBR). Sampling was conducted at 16 reefs in the Coral Sea and 17 reefs on the GBR (Fig. 1). Between 1 and 6 sites ($n = 90$) were surveyed at each reef, with sites selected to ensure comparable habitats were sampled across reefs. Sites were generally positioned on the outer rim (i.e., avoiding lagoon habitat) of select reefs where there was continuous reef matrix with well-defined shallow crest (~2m depth) and adjacent slope extending into deeper water (as described in Chapter 2).

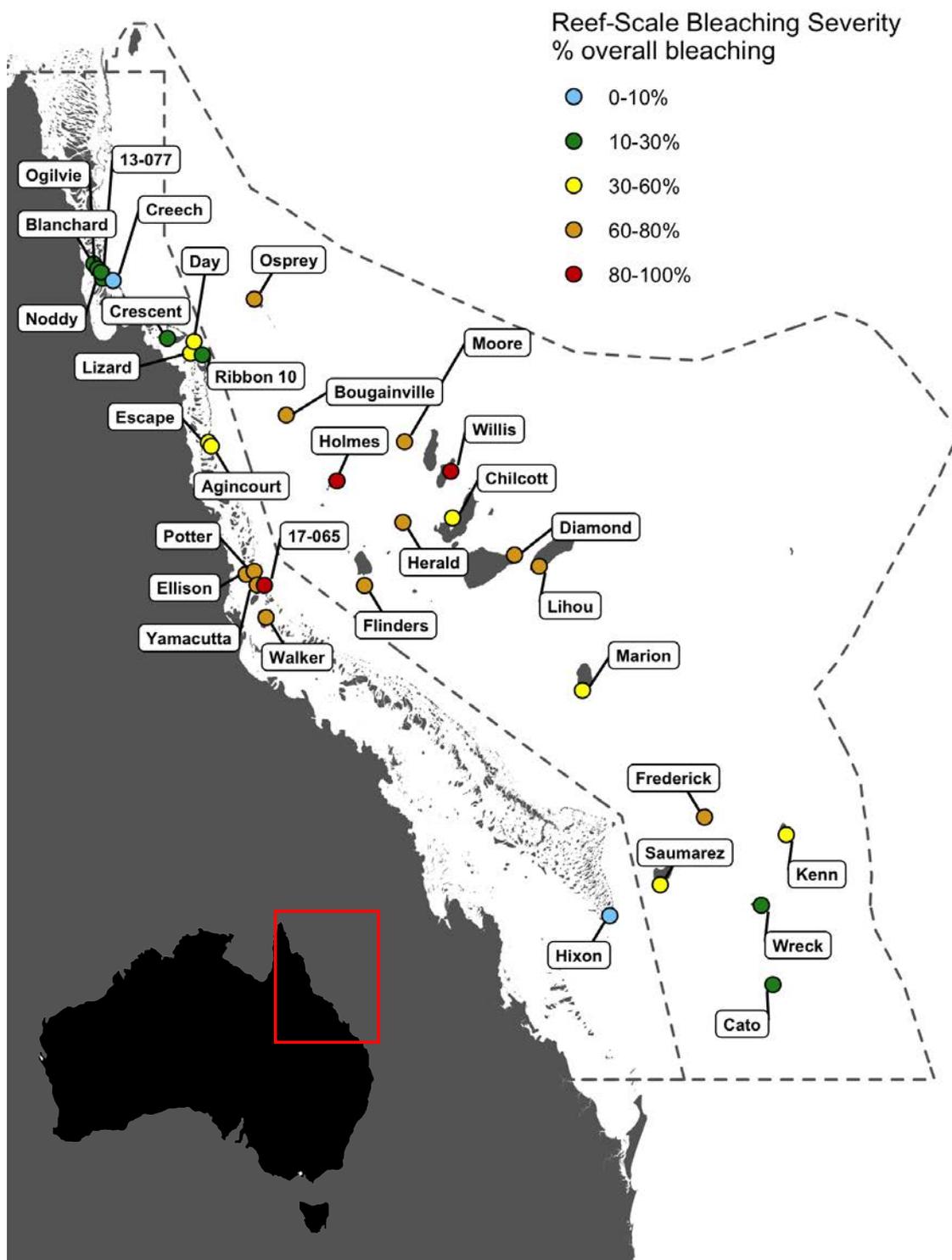


Figure 3.1: Map of 33 reefs surveyed in the Coral Sea Marine Park and Great Barrier Reef Marine Park in February-March 2020. Colours represent the reef-scale bleaching category for each reef, determined by the overall percent of corals surveyed on each reef that were bleached. Dashed lines represent marine park boundaries.

3.2.2 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 (~8m depth) and the reef crest (~2m depth), at each site. Each transect was laid parallel to the reef contour and at a constant depth. All scleractinian corals within each belt were identified to genus, and further resolved (where appropriate) into morphological groups (e.g., acroporids were further split into ‘tabular’, ‘staghorn’ and ‘other’ and poritids into ‘massive’, ‘branching’, and ‘encrusting with uprights’ (e.g., *Porites rus*)). Each coral was placed into one of five size classes based on maximum colony diameter (juveniles: <5cm, small: 5-20cm, medium: 20-40cm, large: 40-60cm and very large: >60cm diameter) and later collapsed into three classes (juveniles: <5cm, medium: 5-40cm, and large: >40cm diameter) to account for small sample sizes. Bleaching status of individual colonies was scored as either ‘bleached’ (inclusive of pale colonies through to bleaching induced recent mortality) or ‘not bleached’, to allow levels of bleaching severity to be assigned using the overall proportion of corals bleached per reef. 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, as it is difficult to discern between very old ramets and colonies which have derived from larvae and grown adjacent to a healthy conspecific (McClanahan 2008).

3.2.3 Statistical Analyses

Each of the 33 reefs were assigned to one of five categorical levels of reef-scale bleaching severity based on the overall proportion of colonies that were bleached across all sites and habitats sampled; i) ‘low’ (0-10% bleaching), ii) ‘moderate’ (10-30% bleaching), iii) ‘high’ (30-60% bleaching), iv) ‘very high’ (60-80% bleaching) and v) ‘extreme’ (80-100%

bleaching), following Hughes et al. (2017b). A Bayesian hierarchical generalized linear model was constructed to investigate the effects of three variables (reef-scale bleaching severity (BLEACH), taxa (TAXA), and colony size (SIZE)) on bleaching susceptibility. Interactions between taxa and both reef-scale bleaching severity and colony size were modelled to investigate how differential susceptibility to bleaching varied with respect to colony size and reef-level bleaching severity. Additionally, a regional random factor was included to account for different responses between Coral Sea and GBR reefs. The probability of an individual coral colony i , from region r , (π_{ri}) being bleached was modelled as:

$$\ln\left(\frac{\pi_{ri}}{(1 - \pi_{ri})}\right) = \beta_0 + REGION_r + \beta_1 BLEACH_{ri} + \beta_2 TAXA_{ri} + \beta_3 SIZE_{ri} \\ + \beta_4 TAXA_{ri} SIZE_{ri} + \beta_5 TAXA_{ri} BLEACH_{ri}$$

Effects plots with 95% credible intervals and posterior distributions were produced to show how bleaching susceptibility varied with respect to taxa, bleaching severity and colony size individually as well as effects plots with 95% credible intervals to show the interactive effects. Tukeys pairwise comparisons were conducted to test for significant differences among the levels of the interacting factors (taxa, colony size and survey period).

All data was analysed using R 3.5.1 (R core team 2018) using the “brms” package to fit the hierarchical models (Burkner 2017), with the “emmeans” (Lenth 2019) and “multcomp” (Hothorn et al. 2008) packages used for pairwise comparisons of marginal means.

3.3 Results

Of the 49,760 distinct coral colonies recorded across the 90 sites, 26,132 colonies displayed signs of bleaching. While bleaching susceptibility among coral taxa varied with reef-scale bleaching severity (Fig. 3.2a), some taxa (e.g., *Stylophora*, *Acropora* - other and *Goniastrea*) were consistently shown to be among the most susceptible coral taxa. *Stylophora* and *Goniastrea* were consistently within the top five most susceptible taxa regardless of bleaching

severity (Fig. 3.2a). Conversely, *Leptastrea* and to a lesser extent *Lobophyllia*, were among the least susceptible taxa across all levels of bleaching severity (Fig 3.2a). For other taxa however, bleaching susceptibility varied among reefs, and the overall hierarchy of bleaching susceptibility changed with increasing reef-scale bleaching severity (Fig. 3.2a). Bleaching susceptibility was particularly variable for branching *Porites* (Figure 3.2a), which was the single most susceptible taxon at lowest (0-10% bleaching) and highest (80-100% bleaching) levels of reef-scale bleaching severity, but ranked in the middle during moderate severities (Fig. 3.2a). Notably, some of the least susceptible taxa at low levels of reef-scale bleaching severity, such as massive *Porites*, were particularly susceptible at high levels of reef-scale bleaching severity (Fig. 3.2a). Conversely, some taxa (e.g., *Galaxea* and *Favites*) were relatively more susceptible during mild reef-scale bleaching than during more severe bleaching.

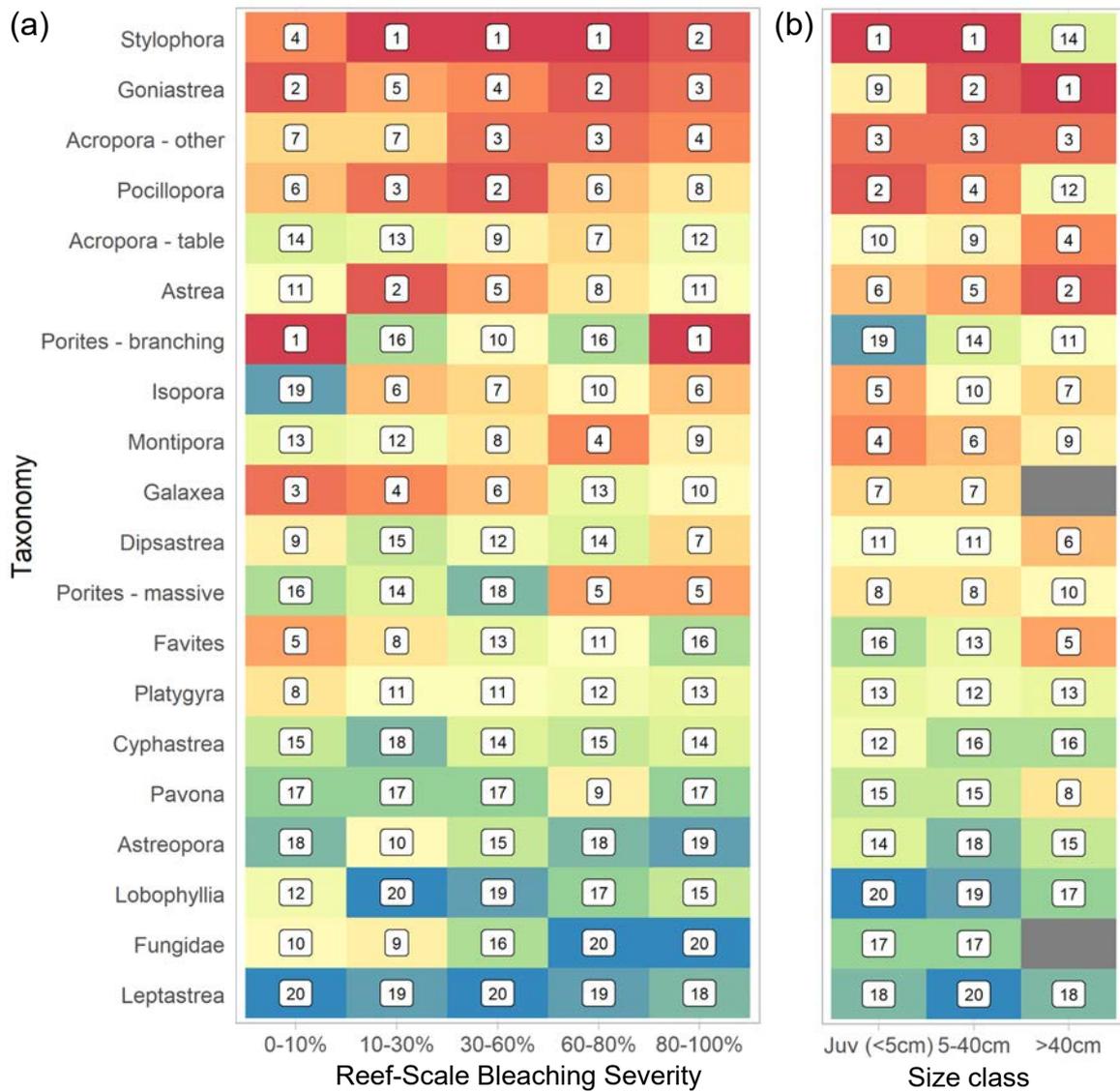


Figure 3.2 Rank order of bleaching susceptibility (proportion of observed colonies bleached) of coral taxa for each reef-scale bleaching severity category (a) and for size class (b). Boxed numbers and corresponding heat gradient colours represent rank order, with red representing the most bleached and blue the least bleached. Colonies were pooled according to the overall reef-level bleaching recorded at the reef.

The Bayesian hierarchical generalized linear model revealed high variability in bleaching susceptibility among taxa (Fig 3.3a). Estimated marginal means for *Stylophora*, *Goniastrea* and ‘other’ *Acropora* were higher than 50% of the data, indicating higher relative

susceptibility, whereas *Leptastrea*, Fungiidae and *Lobophyllia* fell lower than 50% of the data, indicating these taxa were relatively insensitive to bleaching, when compared with other taxa. Tukey’s pairwise comparisons also indicated juvenile corals (<5cm diameter) were significantly less susceptible to coral bleaching compared to larger size classes (Juveniles – Large: $z = 3.43$, $p=0.002$; Juveniles – Medium: $z= 6.04$, $p <0.0001$) (Fig. 2b) (Fig. 3.3b) and the probability of bleaching increased significantly with each increasing bleaching severity category (Fig. 3.3c).

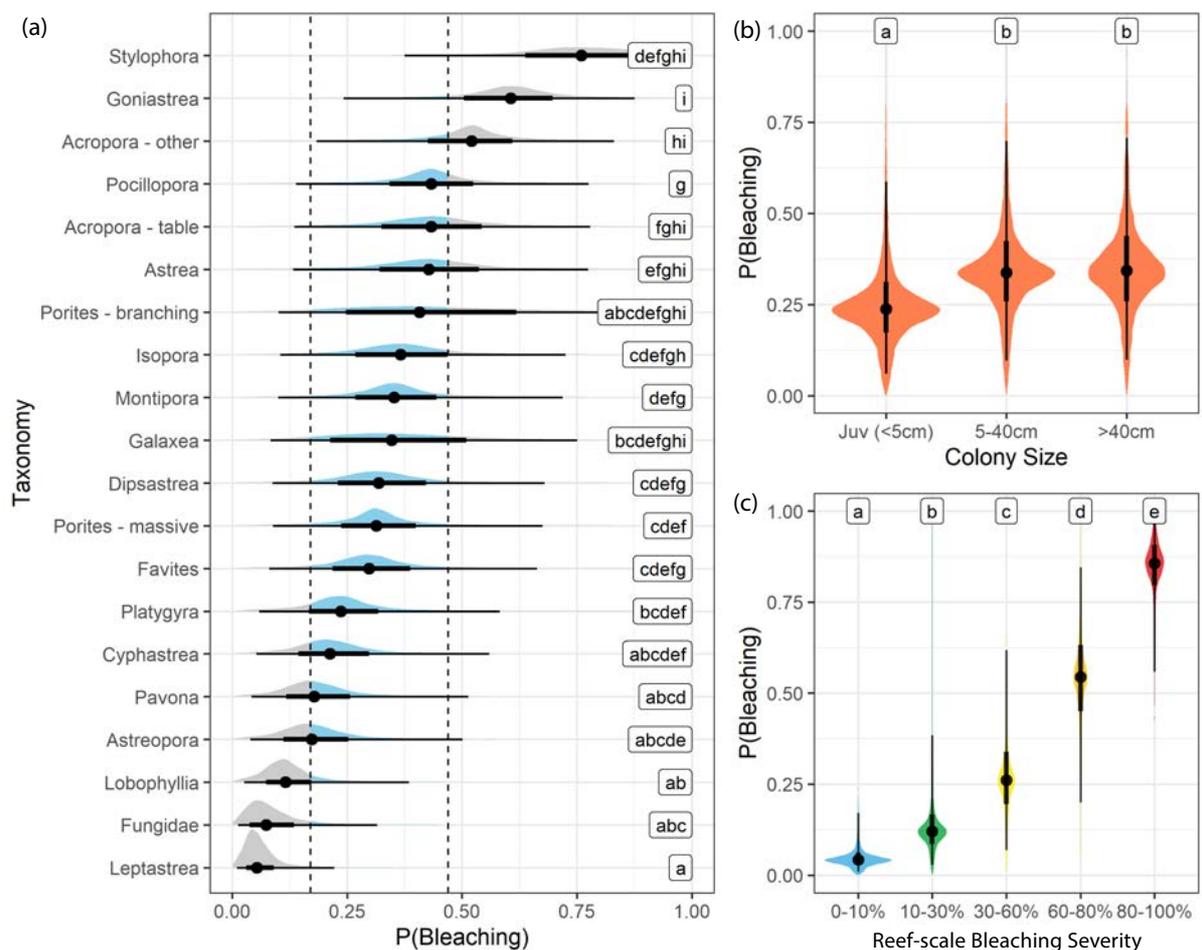


Figure 3.3: Marginal posterior distributions of bleaching susceptibility (P(Bleaching)) for taxa (a), colony size (b) and reef-level bleaching severity (c). Points represent estimated marginal means, thick and thin lines represent 66% and 95% quantile intervals, respectively. Boxed letters represent significant differences between variable levels obtained from Tukey pairwise comparisons. Vertical

dashed lines and light blue shading (a) represent the middle 50% of model estimates of bleaching susceptibility to indicate the taxa most and least susceptible to bleaching.

While the probability of bleaching increased with reef-scale bleaching susceptibility for all 20 coral taxa, the magnitude of increase differed among taxa (Fig. 3.4a). The interaction between coral taxa and reef-scale bleaching severity revealed that the likelihood of bleaching increased with each increasing severity level for the most susceptible taxa (Fig. 3.4a). This resulted in high susceptibility rankings regardless of severity level for these taxa (Fig 3.2a). However, the probability of bleaching for many of the least susceptible coral taxa (i.e. *Leptastrea*, *Fungidae* and *Lobophyllia*) did not increase significantly until bleaching severity reached 'very high' (Fig. 3.4a). In fact, the difference in the probability of a colony to exhibit bleaching among all taxa was most pronounced between reefs with high (30-60%) and very high (60-80%) bleaching severity. Further increases in bleaching severity from very high (60-80%) to extreme (80-100%) yielded fewer significant increases in bleaching probabilities (Fig. 3.4a).

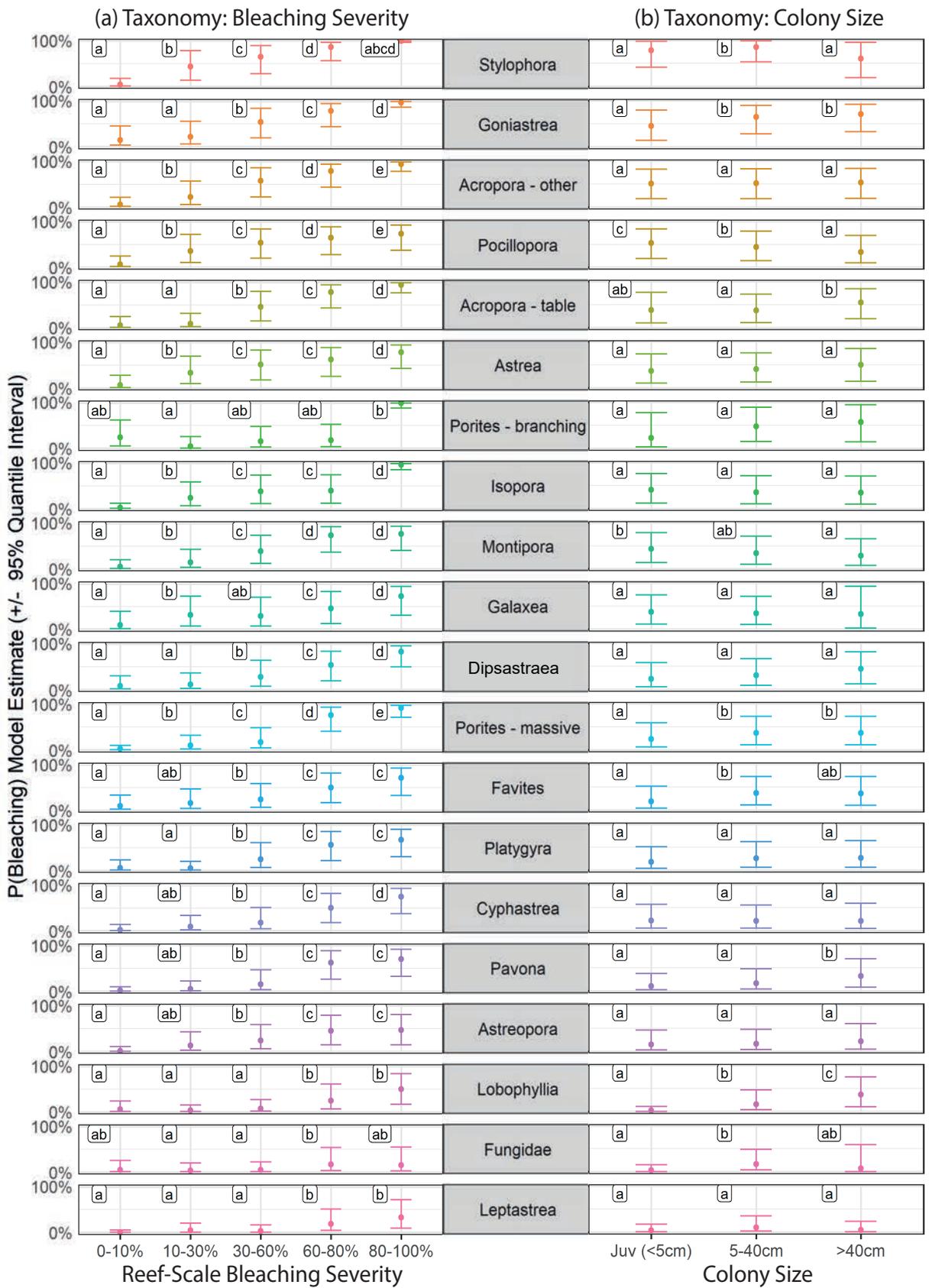


Figure 3.4: Estimated marginal means (\pm 95 % quantile intervals) for the interactions between taxa and reef-level bleaching severity (a) and taxa and colony size (b). Numbers represent significant differences between variable levels obtained from Tukey pairwise comparisons.

Bleaching susceptibility also varied with colony size. The overall incidence of bleaching was lowest (36%) among juvenile corals (<5cm diameter) and increased to 43% for colonies 5-40cm diameter, and 48% for colonies >40cm diameter, though size-based bleaching susceptibility varied among taxa (Fig. 3.4b). Analysis of the model interaction revealed that juveniles (<5cm diameter) of *Stylophora* (Juveniles – Medium: $z = 3.29$, $p = 0.003$), *Goniastrea* ($z = 3.73$, $p < 0.001$), *Porites* – massive ($z = 10.38$, $p < 0.0001$), *Favites* (-0.93 ± 0.30 , $z = 3.07$, $p = 0.006$), *Lobophyllia* ($z = 3.71$, $p < 0.001$) and Fungiidae (-1.84 ± 0.51 , $z = 3.66$, $p < 0.001$) were less likely to bleach than larger (5-40cm diameter) congeners (Fig. 3.4b). Similarly, the largest *Pavona* colonies (>40cm) were significantly more likely to bleach than smaller congeners (Large-Medium: $z = 2.82$, $p = 0.013$; Large-Juvenile: $z = 2.87$, $p = 0.011$). In contrast, juveniles (<5cm diameter) were more susceptible to bleaching than larger colonies for both *Pocillopora* ($z = 4.65$, $p < 0.001$) and *Montipora* ($z = 2.73$, $p = 0.018$). Overall, 10 out of 20 taxa exhibited significant differences in bleaching susceptibility among two or more size classes (Fig. 3.4b), with marked changes in the hierarchy of bleaching susceptibility across size classes (Figure 3.2b). Reflective of the model interactions, the hierarchy of the most/least susceptible taxa changed with colony size. Of particular note is *Stylophora*, which was the most affected taxon when colonies were <40cm diameter, one of the least affected taxa for colonies >40cm diameter (Fig. 3.2b). Conversely, *Favites* colonies <40cm diameter ranked as relatively insensitive to bleaching (rank 16 and 13 for <5cm and 5-40cm colony diameter, respectively), but larger colonies (i.e., >40cm) were one of the five most susceptible taxa to bleaching (Fig. 3.2b).

3.4 Discussion

The incidence of bleaching recorded during recent (2020) mass-bleaching on the GBR and throughout the Coral Sea Marine Park 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. 2013b; 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, which is likely linked to the magnitude and duration of temperature stress (Hughes et al. 2018a; McClanahan et al. 2019; McClanahan et al. 2020). Rather, the rank order of the bleaching susceptibility was dependent on bleaching severity (see also Hughes et al. 2017b) with different coral taxa being disproportionately affected during low versus high levels of reef-scale bleaching severity. For example, *Favites* and *Galaxea* were among the most susceptible taxa at reefs with very low levels of overall bleaching severity but were relatively less susceptible at high levels of bleaching severity (Fig. 3.2a). This suggests that *Favites* and *Galaxea* are very sensitive to moderate or initial increases in seawater temperature, but incidence of bleaching doesn't necessarily increase in proportion to the increasing magnitude of temperature stress or increasing bleaching severity. In contrast, massive *Porites* exhibited very low incidence of bleaching on reefs where overall bleaching severity was low-high (i.e., <60% of colonies bleached), but was among the most susceptible taxa at reefs with very high (60-80% of colonies bleached) and extreme (>80% of colonies bleached) bleaching severity (Fig. 3.2a). Massive *Porites* are generally considered to be among the least susceptible coral taxa to temperature stress (Loya et al. 2001; Hughes et al. 2017b), 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). Our data suggest that massive *Porites* are disproportionately

affected during severe bleaching, such that increasingly severe marine heatwaves 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. 2020a).

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 more mild events, it appears a subset of sensitive taxa will always be disproportionately more affected than others. For those taxa that are consistently among the worst affected during mild to severe mass-bleaching events, our results are consistent with those of other studies where fast growing, branching taxa (e.g., *Stylophora*, *Seriatopora* 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. 2013b; Harrison et al. 2018; Hughes et al. 2018b). However, there were some notable exceptions. *Goniastrea* was among the most susceptible in our study, similar to findings from Thailand and the GBR (Brown et al. 2014; Hughes et al. 2017b). In contrast, *Goniastrea* was reported to be among the more tolerant taxa following the 1998 bleaching in Japan (Loya et al. 2001), however this study recorded change in coral cover and abundance rather than incidence of bleaching. 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 (van Woesik et al. 2011).

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 most susceptible to bleaching to be the primary target

of other dominant disturbances occurring on the reef (Keesing et al. 2019; Madin et al. 2018). This is however, dependent on incidence of bleaching translating to colony mortality, which for lower severity bleaching may take several months (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 differential recovery or mortality, rather than differential bleaching susceptibility (Leggat et al. 2019; Pratchett et al. 2020a). Moreover, the poor connectivity among reefs in the Coral Sea and hence replenishment of coral populations may exacerbate shifts, especially if disturbances are frequent and severe (Gilmour et al. 2013). Further monitoring of these populations will give important insights into possible shifts in community structure.

Whilst other 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. 2013b), we found the differential susceptibilities of those thermally sensitive taxa in the present study are much the same as those reported in past studies from the GBR and CS (Marshall and Baird 2000; Hughes et al. 2017b; Harrison et al. 2018). Further work should be conducted to determine if any temporal changes exist in taxonomic bleaching susceptibility in the CS and GBR 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 (36%) than medium-sized (43%) and large (>40cm diameter) colonies (48%). Lower bleaching susceptibility in juvenile corals has been documented previously (Hoeksema 1991; Mumby et al. 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 (Alvarez-Noriega et al. 2018; Loya et al. 2001; Brandt 2009) and we show herein, that the specific response is taxon-dependent. Transformations in coral size structure and topographic complexity may be exacerbated by susceptibility of specific colony size classes. 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*, *Goniastrea*, *Porites* – massive, *Favites*, *Lobophyllia* and Fungidae) 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 (which is strongly influenced by the magnitude and duration of temperature stress) and colony size. Differing severities among locations and events will therefore, be likely to result in different community compositions, with moderate stress events highlighting the ‘winners’ and ‘losers’ more clearly than extreme events, where almost all zooxanthellate corals are likely to be susceptible to bleaching. Furthermore, our study highlights the need to take size structure of a coral assemblage into account when determining bleaching susceptibility, where differential susceptibility of certain colony sizes may lead to shifts in size structure for some taxa. In the Anthropocene, where bleaching events are becoming more frequent, it is likely that genera with high tolerance for heat stress, such as *Leptastrea*, *Lobophyllia*, Fungiidae, *Cyphastrea*, *Favites* and *Dispastrea* will be selected for (Alvarez-Noriega et al. 2018; Hughes et al. 2019a), but if bleaching events become more severe, it is likely that the abundance of even these robust 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 winners and losers. Future research should aim to understand how bleaching severity affects size-based susceptibility and 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 is the third major bleaching event in five years on reefs in the GBR and Coral Sea, 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 4. General Discussion

4.1 Major disturbances affecting coral assemblages in the Coral Sea

Australia's Coral Sea Marine Park is an environmentally significant region recognised for its exceptional biological and habitat diversity (Ceccarelli et al. 2013), while being relatively unaffected by increasing anthropogenic disturbances and pressures that are causing accelerated degradation of comparable marine environments (McKinnon et al. 2014). However, remote and isolated marine systems are not immune from major or acute disturbances (Gilmour et al. 2013; Bruno and Valdivia 2016; Juhel et al. 2018). Rather, isolated coral reefs may be particularly vulnerable to pervasive effects of climate change (Gilmour et al. 2013) and other human pressures (Graham et al. 2010), owing to inherent constraints on recovery and resilience. Poor connectivity among widely separated reefs increases reliance on self-recruitment, such that large-scale disturbances, which cause significant coral loss across the entire extent of individual reef systems, may limit population replenishment and recovery (Ayre and Hughes 2004; Graham et al. 2006; Gilmour et al. 2013). At Scott Reef, an isolated reef off the north-west Australian shelf, Gilmour et al (2013) showed that there was negligible coral recruitment and corresponding coral recovery in the immediate aftermath of catastrophic coral bleaching in 1998. This suggests that there was very limited input of coral recruits from other reef systems, whereby the nearest reef was located >250km away (Gilmour et al. 2013). Alternatively, large-scale disturbances (such as widespread mass bleaching; Moore et al. 2012; Hughes et al. 2018b; Eakin et al. 2019) may be sufficient to suppress coral cover and reproduction across all relevant source populations (e.g., Hughes et al. 2019a).

Large-scale, acute disturbances, including severe cyclonic storms (Puotinen et al. 2016) and marine heatwaves (DeCarlo et al. 2019; Harrison et al. 2018) are known to have impacted coral reefs in the Coral Sea throughout the last few decades, though their specific effects on

coral assemblages are poorly understood, owing to limited recurrent sampling at relevant scales (Oxley et al. 2005; Brewer et al. 2007; Harrison et al. 2018). However, coral cover and composition vary markedly among different reefs and regions of the Coral Sea (Ceccarelli 2019; Harrison et al. 2018; Hoey et al. 2020), potentially reflecting the differential exposure to major disturbances. Notably, coral cover is much lower on mid-latitude reefs (e.g., Flinders, Herald and Lihou), compared to reefs in northern and southern Coral Sea (Hoey et al. 2020), and is also lower on smaller and more exposed reefs (Ceccarelli 2019), which is attributed to increased exposure to damaging waves, especially during severe storms. The regional impacts of severe storms may have been further compounded by marine heatwaves and corresponding coral bleaching (Oxley et al 2005, DeCarlo et al. 2019), though back-to-back bleaching in 2016 and 2017 is reported to have caused limited coral mortality on Coral Sea reefs (Harrison et al. 2018).

Recurrent sampling presented in this thesis did capture recent mass-bleaching in 2020, which was extremely widespread across both the GBR and Coral Sea (Pratchett et al. 2020b). The overall extent of bleaching recorded was highly variable (Figure 3.1), but very severe at some reefs (especially Willis Island) where >80% of coral colonies were bleached. However, surveys conducted during the bleaching revealed only very moderate incidence (<5%) of recent coral mortality, which was not significantly different to overall levels of recent injuries and coral mortality recorded during surveys conducted prior to the bleaching. It is possible that recent bleaching may have more significant longer-term effects on local coral assemblages, with coral mortality occurring weeks to months after the onset of bleaching (Baird and Marshall 2002; Hughes et al. 2018b). However, this represents the third marine heatwave and mass-bleaching event in just 5 years, and prior exposure to elevated temperatures and bleaching may moderate responses (Guest et al. 2012; DeCarlo et al. 2019; Harrison et al. 2018; Hughes et al. 2019b), either by acclimatization of individual colonies or prior removal of highly susceptible

phenotypes. That said, the taxonomic hierarchy of bleaching susceptibility recorded during the 2020 mass-bleaching was largely consistent with previous reports (*cf.* Guest et al. 2012), and varied mostly in accordance with spatial variation in overall levels of bleaching severity. Testing for evidence of acclimatization for coral assemblages in the Coral Sea will require comparisons of bleaching incidence and mortality across each of the recent bleaching episodes, while specifically accounting for both taxonomy and variation in the magnitude of heat stress at individual reefs. The immediate priority however, will be to undertake follow-up surveys within coming months to quantify the proportion of corals that actually died in the aftermath of the most recent mass-bleaching, based on changes in the size and abundance of corals at specific sites surveyed in February-March 2020.

4.2 Chronic disturbances and background levels of coral mortality

A key contribution of my overarching research was to move beyond the traditional and limited focus on large scale, acute disturbances (e.g., Traçon et al. 2011; Kayal et al. 2012; Gilmour et al. 2013; Hughes et al. 2018a), and consider the role of major disturbances within the context of other chronic and routine disturbances. Importantly, the status and trends in coral cover and coral compositions at many reef locations cannot be explained solely based on changing incidence and severity of major acute disturbances, but are strongly influenced by other chronic pressures and disturbances (Wakeford et al. 2008, Ortiz et al. 2018), which moderate both vulnerability and recovery of coral populations and communities (Hughes et al. 2007; Bruckner and Hill 2007; Wooldridge and Done 2009; Pisapia et al. 2014). Most highly degraded reef systems have been subject to sustained human pressures over many decades and centuries, including fisheries exploitation (Pandolfi et al. 2003) and land-based sources of nutrients and pollutants (Cooper et al. 2009). The relative importance of chronic versus acute disturbances in structuring coral populations and communities may therefore, differ between coastal *versus* oceanic reefs (e.g., Fabricius et al. 2005; Gilmour et al. 2013; Mellin et al. 2019b). Moreover,

we'd expect remote coral reefs, such as those in the Coral Sea, to experience lower levels of background mortality relative to comparable reefs located closer to shore and more exposed to direct human pressures.

Limited exposure to perennial and increasing direct human pressures (e.g., fisheries exploitation and pollution) is expected to increase resilience among more remote coral reefs (Sandin et al. 2008; Halford and Caley 2009; Gilmour et al. 2013), reducing vulnerability of individual corals and promoting recovery in the aftermath of major disturbances. One of the key factors that might be expected to provide for such resilience among coral populations and communities is lower incidence of routine disturbances and ongoing injuries (Wakeford et al. 2008; Pisapia et al. 2014). Pisapia et al. (2014) showed for some coral species, colonies subject to lower levels of background mortality have improved physiological condition and higher energy reserves, which is expected to increase their ability to withstand major disturbances. Contrary to expectations, I found significantly higher incidence of recent injury and coral mortality among coral colonies surveyed at relatively remote reefs across the Coral Sea relative to coral colonies surveyed in comparable habitats on the GBR (Chapter 2). Surveys conducted on the GBR were intentionally conducted mainly at outermost reefs, such that these reefs are themselves well removed from most human and coastal pressures (Mellin et al. 2019b). Observed differences in the incidence of recent injuries may therefore, relate more to variation in exposure to oceanic conditions than coastal and human pressures. Depending on the specific cause(s) of injuries, it is also possible that higher incidence of coral injuries may actually be an indicator of improved reef health and ecosystem function (Bellwood et al. 2003, 2012). For example, *Bolbometopon muricatum* is the foremost excavating parrotfish that feeds on live corals, and is highly vulnerable to fisheries exploitation (Bellwood et al. 2012). Accordingly, rates of bioerosion and coral predation are much higher on remote coral reefs (Bellwood et al. 2012).

Discerning the specific cause of recent injuries and coral mortality recorded across the Coral Sea and GBR was very difficult. In the majority of cases (~75%) outside of the mass-bleaching, I was unable to clearly attribute the observed injury or coral mortality to any specific biological or physical disturbance. This makes it difficult to assess whether the recorded incidence of injuries in the Coral Sea is representative of relatively pristine and functionally intact reef ecosystems, or how ongoing rates of injury and coral mortality might change with increasing human pressures and environmental change. It was clear, however, that ongoing incidence of coral injuries and background mortality can be substantial even within relatively remote reef systems, with potentially important consequences for the vulnerability and recovery of corals subject to major acute disturbances (e.g., Pisapia and Pratchett 2014). Moreover, this study highlights the critical importance of accounting for background levels of injuries and coral mortality when assessing the specific impacts of major disturbances, such as coral bleaching. These data could be used to support modelling efforts that project consequences of disturbance or assess restoration activities. In general, major disturbances would be expected to increase overall rates of coral mortality by adding to background rates of coral mortality caused by ongoing chronic and routine disturbances (Wakeford et al. 2008). In my study, however, there was no apparent change in the incidence of recent mortality in surveys conducted before versus during widespread mass-bleaching (in 2020). Rather, bleaching-related injuries appeared to mask other causes of recent mortality, possibly because corals that were already injured by routine disturbances were more susceptible to bleaching. It is nonetheless important to explore confluence of routine and acute disturbances, and consider their impacts not only on overall coral abundance, but changes in coral composition and size-structure.

4.3 Taxonomic differences in susceptibility to disturbance

Regardless of whether we consider major acute disturbances (e.g., coral bleaching, Chapter 3, Loya et al. 2001) or routine background disturbances (e.g., breakage, predation, Chapter 2, Madin et al. 2014, Keesing et al. 2019), branching and other morphologically complex corals appear to be disproportionately susceptible to ongoing injury and mortality. The trade-off between fast growth and high mortality rates for these taxa (Madin et al. 2020) may allow for relatively rapid regeneration and/ or recolonisation following disturbances (Pratchett et al. 2020a). However, major disturbances with highly selective effects and short return times will likely drive shifts in coral communities (e.g., Dornelas et al. 2014; Pratchett et al. 2020a), resulting in increased predominance of corals that are generally resistant to major and acute disturbances, combined with overall reductions in coral cover. Taxonomic variation in susceptibility to major disturbances is however, inherently linked to disturbance severity, whereby increasingly severe disturbances have major effects across all taxa. Moreover, there is increasing evidence that the hierarchy of taxonomic susceptibility may itself change with disturbance severity (Hughes et al. 2017b; Chapter 3). During the 2020 mass-bleaching in the Coral Sea and on the GBR, I found that some taxa (e.g., *Favites* and *Goniastrea*) were disproportionately affected on reefs with less severe bleaching, whereas other taxa (mostly massive *Porites*) were disproportionately affected during severe bleaching. These data are however, based on the bleaching susceptibility or the proportion of colonies that exhibited bleaching, and it remains to be seen whether these patterns translate to differential rates of overall mortality, which ultimately drive changes in the structure of coral assemblages (van Woesik et al. 2011; Hughes et al. 2018b).

Observed and projected increases in the occurrence of coral bleaching and mortality (Oliver et al. 2018; Hughes et al. 2018a) are expected to have a major influence on coral assemblages and benthic reef habitats in coming years and decades (Alvarez-Filip et al. 2009;

McWilliam et al. 2020). The cumulative impacts of increasing climatic disturbances and other perennial disturbances and pressures are expected to cause further declines in coral cover, especially in relatively pristine areas that are relatively unaffected by more direct human pressures (Bruno and Valdivia 2016). Despite apparent vagaries in the taxonomic susceptibility to disturbances, overall increases in the incidence of major disturbances are most likely to have disproportionate effects on branching and complex corals, such as *Stylophora* and *Acropora* (Marshall and Baird 2000; Loya et al. 2001; Baird and Marshall 2002; Pratchett et al. 2013b; Hughes et al. 2017b; Harrison et al. 2018; McClanahan et al. 2020). If branching corals are effectively lost, or increasingly replaced by massive and robust coral species, as shown or suggested by previous studies (Riegl and Purkis 2009; Darling et al. 2012; Riegl et al. 2013) this will have important consequences for reef structure and function (Alvarez-Filip et al. 2013; McWilliam et al. 2020). Notably, comprehensive loss of branching and complex corals and corresponding declines in topographic complexity of reef habitats will lead to marked reductions in coral reef biodiversity and productivity (Graham et al. 2006; Pratchett et al. 2008) even if coral cover is maintained above critical thresholds (Wilson et al. 2008). There is also the real possibility that increasing incidence and severity of disturbances will lead widespread coral loss and associated transformation of coral reef ecosystems (Done 1992; Norström et al. 2009; Graham et al. 2015), as even the most resilient coral species are lost and replaced by alternative habitat-forming organisms, such as sponges or macroalgae.

Shifts in coral composition due to selective mortality may be moderated or reinforced by taxonomic differences in population replenishment (e.g., Pratchett et al. 2011; Bauman et al. 2014), whereby widespread declines in the abundance of highly susceptible taxa may ultimately constrain reproduction and recruitment (Hughes et al. 2019a). Such effects are likely to be more pronounced on small and isolated reef systems where population replenishment is largely contingent on the local abundance and reproductive output of adult conspecifics (e.g.,

Gilmour et al. 2013). At Moorea, in French Polynesia, recurrent disturbances have resulted in sustained declines in the local abundance of *Acropora* corals and corresponding increases in the predominance of *Pocillopora* corals (Pratchett et al. 2011, Tsounis and Edmunds 2016). This shift in community structure is being compounded by very low recruitment levels for *Acropora*, especially compared to *Pocillopora* (Tsounis and Edmunds 2016; Holbrook et al. 2018), meaning that there is very limited prospect of community reassembly (Pratchett et al. 2011). These data highlight the need to consider both taxonomic differences in coral mortality and recovery capacity, in order to predict likely shifts in community structure (e.g., Baker et al. 2008; Pratchett et al. 2020b). A logical extension of the research presented in this thesis is therefore, to quantify taxonomic differences in rates of coral recruitment and growth across the Coral Sea and outer GBR. This will not only help to establish the likely transformation in coral communities, but establish the overall vulnerability and resilience of these systems to current and changing disturbance regimes.

4.4 Size-based differences in susceptibility to disturbance

The size of individual coral colonies can vary enormously, and has major ramifications not only for individual demography and fate (Hughes and Jackson 1985; Álvarez-Noriega et al. 2016; Dornelas et al. 2017; Pisapia et al. 2020), but also habitat structure and ecosystem function (e.g., Noonan et al. 2012; McWilliam et al. 2020). Importantly, larger coral colonies are important for sustaining high abundance and diversity of coral-associated organisms (Noonan et al. 2012; Darling et al. 2017; Richardson et al. 2017), and make a disproportionate contribution to reproduction and resilience (Dornelas et al. 2017; Edmunds and Burgess 2016). Potential declines in relative abundance of larger colonies and corresponding declines in mean coral size (Riegl et al. 2012; Pisapia et al. 2020), are therefore, very concerning. Reported declines in coral growth (Pratchett et al. 2015), high rates of partial mortality (Pisapia and Pratchett 2014) and size-based differences in the susceptibility of corals to major disturbances

(Álvarez-Noriega et al. 2018; Chapter 3) all point to a shift towards an increased predominance of small colonies. Declines in the size and fecundity of coral colonies is particularly concerning for remote reefs, where there is limited capacity for supplementary recruitment from other reefs (Gilmour et al. 2013).

Large corals are generally less susceptible to whole colony mortality (Madin et al. 2020), but are more likely to experience partial mortality (Madin et al. 2014). Accordingly, I found that the incidence of recent injuries increased with increasing coral size in the Coral Sea and GBR (Chapter 2). These data are important because they show that increased incidence of injuries in large corals reflects higher exposure to ongoing and routine disturbances, and not simply the long-term accumulation of injuries on long-lived colonies that make limited investment in regeneration and repair (Meesters et al. 1996). Conversely, smaller corals are expected to be more likely to die (whole colony mortality) when subject to disturbances (Bak and Engel 1979; Madin et al. 2014), given they have much more limited energetic reserves to withstand and absorb disturbances. Size-based differences in the sensitivity of corals to elevated temperatures is further complicated by declines in mass transfer efficiency with increasing size (Wooldridge 2014), which may account for lower incidence of bleaching in small and juvenile corals (e.g., Mumby 1999; Loya et al. 2001; Depczynski et al. 2013). There is however, conflicting information regarding the relative bleaching susceptibility of small *versus* large coral colonies, which appears to vary among coral taxa (Pratchett et al. 2013b; Álvarez-Noriega et al. 2018; Chapter 3). Notably, juvenile *Pocillopora* corals were more susceptible to bleaching than larger congeners in the Coral Sea and GBR, as shown by Pratchett et al (2013b) at Moore Reef, French Polynesia. Similarly, Álvarez-Noriega et al. (2018) reported a disproportionate decline in the abundance of juvenile *Pocillopora* compared to adults following mass-bleaching in the northern GBR in 2016. By comparison, *Acropora* corals were highly susceptible to bleaching across all size classes (see also Pratchett et al.

2013b; Álvarez-Noriega et al. 2018). The mechanisms responsible for taxon-specific size-based differences in susceptibility to bleaching and subsequent mortality are yet to be adequately assessed, but clearly identifying such patterns is an important precursor to this research. Furthermore, identifying how corals of differing life history traits, such as brooders and spawners, are affected by such mechanisms would be useful for predicting community dynamics following bleaching events.

Elevated levels of overall coral mortality, combined with high incidence of partial mortality, is expected to lead to net declines in the size of corals (Pisapia et al. 2020). There is however, limited empirical data available to explicitly test for long-term (decadal) changes in the size-structure of coral assemblages, despite the fact that colony size is one of the easiest traits to measure (Pisapia et al. 2020). Available data from marginal reef environments (e.g., Persian Gulf: Riegl et al. 2017; Caribbean: Edmunds 2015) does reveal sustained long-term declines in the abundance of larger corals and a corresponding increase in predominance of small corals. However, comparable analyses from the GBR (Dietzel et al. 2020) indicate that there has been a disproportionate decline in the abundance of smaller corals following mass-bleaching on the GBR in 2016 and 2017, leading to effective increases in colony size for many coral taxa. These shifts in size-structure do however, belie marked declines in the overall abundance of corals, and likely represent only a temporary condition (Dietzel et al. 2020). Data collected as part of this study does provide an important baseline with which to test for temporal changes in coral size, though coral assemblages across much of the central Coral Sea appear to have been impacted by recent or sustained disturbances, and it is possible that coral size may actually increase in coming years if coral assemblages are spared from further major disturbances and the have the opportunity to recover. It will also be potentially very insightful to explicitly compare the size structure of corals across different regions of the Coral Sea, and

between the Coral Sea and GBR, to assess whether coral size is higher or lower in areas where coral cover is suppressed.

4.5 Conclusions

The research presented in this thesis was conducted as part of an extensive assessment of coral reef health in Australia's Coral Sea (Hoey et al. 2020), providing important insights into the current condition of shallow reef environments, which were highly variable across the broad extent of the Coral Sea. It is however difficult to reconcile apparent differences in coral cover and reef condition given limited insights into the history of disturbances that may have structured these coral populations and communities. As such, my research provides important baseline information on the incidence of recent injuries and coral mortality, to test for further spatio-temporal variation in the impacts of chronic and acute disturbances. While it was expected that routine and background disturbances would be negligible at remote reefs across the Coral Sea (see also Gilmour et al. 2013), the incidence of recent and ongoing injuries was higher than recorded on comparable reefs on the GBR, and fairly consistent among Coral Sea reefs. These findings highlight the critical need to better understand rates and causes of background coral mortality in different reef environments, which is particularly important in assessing vulnerability and recovery of coral populations and communities subject to increasing major disturbances.

Environmental change is the foremost cause of recent coral loss in most major reef regions, and is now considered to be the single greatest threat to coral reef ecosystems globally (Hughes et al. 2018a; Bellwood et al. 2019; Bruno et al. 2019; Anthony et al. 2020; Hickey et al. 2020). The effects of ongoing environmental change were all too apparent in the Coral Sea, whereby the recent (2020) mass-bleaching represents the third such event in just the last 5 years (Harrison et al. 2018; Pratchett et al. 2020b). The ecological impacts of this latest bleaching event will not be fully appreciated until after follow-up surveys are completed, but data

presented in this study highlights the potentially important role of this event in further structuring of local coral assemblages. Marked differences in size-based and taxonomic susceptibility to disturbance will lead to strong directional shifts in population and community structure. The apparent selectivity in the effects of major disturbances, and especially coral bleaching, has been reported previously (e.g., Loya et al. 2001; Depczynski et al. 2013), though my research shows that the hierarchy of bleaching susceptibility is somewhat dependent on the overall severity of bleaching. The severity of mass-bleaching and corresponding coral mortality is likely to further increase with projected increases in ocean temperatures (Frölicher et al. 2018; Leggat et al. 2019), leading to declines in the abundance of previously insensitive taxa (e.g., massive *Porites*), which have very limited capacity for recovery. Increasing incidence and severity of disturbances is also expected to result in overall declines in the size of corals, with further effects on reproduction and recovery.

While findings of this research are most relevant to understanding and managing the Coral Sea Marine Park, the scale and extent of data collected during this study provides considerable opportunity to contribute to general understanding of coral demography, and particularly the role of disturbances in structuring coral populations and communities. Most critically, this research reinforces the need for increased demographic information (see also Edmunds and Riegl 2020) and specific discrimination among coral taxa and size-classes when assessing vulnerability to chronic and acute disturbances. Ongoing research at relatively remote coral reef systems is also important to distinguish global impacts of environmental change from more localised impacts of sustained human pressures (Bruno and Valdivia 2016). My research helps to highlight that remote coral reefs are not immune from impacts of environmental change, and may actually be even more vulnerable to such disturbances owing to inherent constraints of isolation on subsequent recovery. There is therefore, considerable scope and

critical need for further and ongoing research and monitoring of coral assemblages across the Coral Sea.

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Appendix – Other scientific contributions during candidature

Other papers published during my candidature:

Pisapia C, **Burn D**, Pratchett MS (2019) Changes in the population and community structure of corals during recent disturbances (February 2016- October 2017) on Maldivian coral reefs. Sci Rep 9:8402

Burn D, Matthews S, Caballes C, Chandler J, Pratchett MS (2020) Diurnal behaviour of *Acanthaster planci* versus *Acanthaster* cf. *solaris*. PLoS One 15(2): e0228796 [doi:10.1371/journal.pone.0228796]