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JAMES COOK
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Spatial, temporal and taxonomic variation in the

incidence of partial mortality among reef-building corals

Thesis submitted by

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Statement on the contribution of others

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Abstract

Until now, most studies of coral reef degradation have focused on catastrophic mortality associated with acute disturbances (e.g., coral bleaching and outbreaks of crown-of-thorns starfish), but even in the absence of major disturbances corals are consistently subject to high levels of background mortality. In particular, corals are regular subject to high levels of partial mortality (or injuries) caused by chronic or persistent disturbances, which can have critical influence on population dynamics and resilience of coral populations. Spatial, temporal and taxonomic differences in injury regimes are important for understanding vulnerability and resilience of scleractinian corals to acute disturbances and environmental change. This thesis explicitly assesses variation in rates of background mortality, and mostly partial mortality, at both small (between adjacent colonies) and large (between locations in different ocean basins) scales.

To establish baseline levels of partial mortality among common reef-building corals, I first quantified prevalence (proportion of colonies with injuries) and severity (areal extent of injuries on individual colonies) of injuries across four common coral taxa (massive *Porites*, encrusting *Montipora, Acropora hyacinthus* and branching *Pocillopora*) on the Great Barrier Reef, Australia. A total of 2,276 adult colonies were surveyed annually over three years across three latitudinal sectors, nine reefs and 27 sites along the Great Barrier Reef. The prevalence of injuries was very high (>83%) for all coral taxa, but especially high for *Porites* (91%) and *Montipora* (85%). Within individual taxa, there was significant temporal or spatial variation in prevalence of partial mortality in *Montipora* and *Pocillopora*. Severity of partial mortality on injured colonies ranged from 5% for *A. hyacinthus* up to 21% for *Montipora*, and varied both spatially and temporally. These findings confirm that background levels of partial mortality are high even in the absence of major disturbances, and are likely to significant influence

differential vulnerability of colonies, populations and coral species to other more acute disturbances.

Building on my initial studies on the Great Barrier Reef, I then compared rates of background mortality (including both partial and whole colony mortality) between Lhaviyani Atoll, Maldives and the northern Great Barrier Reef, Australia. Comparisons were made for four dominant and widespread coral taxa (*Porites*, *Montipora*, *Acropora hyacinthus* and *Pocillopora*), which were surveyed across multiple reefs and sites at each location. Prevalence of partial mortality was consistently higher on the GBR (99.4% of colonies in *Porites*, 66% in *Acropora hyacinthus* and 64% in *Pocillopora*) than at Lhaviyani Atoll (92.4% in *Porites*, 47.5% in *A. hyacinthus* and 44% in *Pocillopora*). Conversely, severity of partial mortality was higher for *A. hyacinthus* and *Porites* (9.6% and 12.2%, respectively) at Lhaviyani Atoll than on the GBR (7% in *A. hyacinthus* and 9.6% in *Porites*). However, marked differences in severity of partial mortality were most apparent at the smallest spatial scale (e.g., among colonies located on the same transect within the same habitat). This suggests that corals in different geographical locations are consistently subject to high levels of background mortality, but the specific effects are highly patchy and likely contribute to significant inter-colony variation in susceptibility of corals to major disturbances (e.g., bleaching).

After investigating spatial variation in tissue loss, I tested the specific effects of injuries on colony condition. Intraspecific variation in physiological condition was measured, based on total lipid content and zooxanthellae density, in adult colonies of two common and widespread coral species (*Acropora spathulata* and *Pocillopora damicornis*). Importantly, these corals were subject to different levels of biological and physical disturbances and marked intraspecific variation in the physiological condition of *A. spathulata* was clearly linked to differences in local disturbance regimes. Conversely, *P. damicornis* exhibited very limited intraspecific variation in physiological condition, despite marked differences in the severity of

partial mortality. This study shows that the physiological condition of individual coral colonies is influenced by differences in injury regimes, at least for some coral taxa. Moreover, these differences in physiological condition are likely to have important effects on the fate and fitness of individual colonies, and especially their vulnerability to subsequent disturbances.

Overall, my PhD research shows that the prevalence of coral injuries is consistently high (>80% of colonies have visible injuries) across different coral taxa and among reef locations spanning 10 degrees of latitude and in different ocean basins. The severity of injuries meanwhile, varies greatly among individual colonies within the same habitat and site, which may have important ramifications for susceptibility to acute disturbances and environmental change. Much more research is needed to understand the major causes of routine injuries to reef building corals, but studies on the effects of acute disturbances on coral populations and/ or communities should not discount background levels of mortality, and the extent to which this might further increase susceptibility to, and prevent recovery from, acute disturbances.

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Chapter 1.   General Introduction

1.1. Disturbance regimes of coral reefs

Coral reefs are highly dynamic ecosystems, naturally subject to a wide range of disturbances (Nyström and Folke 2001), which operate at different temporal and spatial scales, ranging from chronic predation by polyp-feeding butterflyfishes (Cole and Pratchett 2011), to simultaneous mortality of corals across entire ocean basins, caused by climate-induced mass-bleaching events (e.g., Baker et al. 2008). There is widespread concern however, that coral reef ecosystems are becoming increasingly subject to more frequent and more severe disturbances, owing to emerging effects of global climate change as well as sustained increases in more direct anthropogenic disturbances (Hoegh-Guldberg et al. 2007). Accordingly, the long-term trajectories for coral cover in many different locations are consistently downwards (Gardner et al. 2003; Death et al. 2012). Causes of widespread declines in coral cover are generally attributed to acute disturbances, such as outbreaks of crown-of-thorns starfish (Death et al. 2012), cyclones, and climate-induced coral bleaching (Hoegh-Guldberg et al. 2007), which can cause high levels of instantaneous mortality, change habitat structure and may have strong selective pressures on community structure and functions (White and Pickett 1985). However, it is important to realize that acute disturbances operate against a backdrop of more persistent or chronic disturbances, which can exert significant influence on demographic rates and outcomes of biological interactions (Connell et al. 1997; Death et al. 2009), thereby affecting susceptibility to, and recovery from, acute disturbances (Andres and Witman 1995).

Most of the literature pertaining to coral reef degradation is fixated on acute disturbances (e.g., De'ath et al. 2012), whereas there is significant capacity for less apparent, but nonetheless critically important effects of chronic disturbances on ecosystem state and

processes (e.g., Hughes et al. 2015). With increasing effects of climate change, not only are acute disturbances (e.g., severe episodes of coral bleaching) predicted to increase in frequency and intensity (Hoegh-Guldberg et al. 2007; Mendelsohn et al. 2012; IPCC 2013), but chronic disturbances may also increase in incidence and importance. For instance, sedimentation rates on the reef, especially on the Great Barrier Reef (GBR) are predicted to increase (Hughes et al. 2015). Similarly, ocean acidification is becoming more severe, with declines in coral calcification rates with declining pH (Hoegh-Guldberg et al. 2007). De'ath et al. (2009) has already documented slower growth in massive *Porites* associated with chronic increases in temperature and declining pH. Chronic disturbances may therefore, have a critical role in undermining the capacity of corals to recover from major acute disturbances.

Coral assemblages can recover in the aftermath of major disturbances (e.g., Halford et al. 2004; Linares et al. 2011), as long as there is i) sufficient time between major disturbances, ii) adequate proximity or connectivity to viable source populations, and iii) maintenance of suitable substrates for settlement and subsequent survival of coral recruits (e.g., Connell et al. 1997). For instance, recovery is generally faster through the growth of remnant corals rather than through settlement and subsequent growth of new recruits (Halford et al. 2004; Gilmour et al. 2013). On Scott Reef on the Great Barrier Reef (GBR), rates of coral recovery following acute disturbances were relatively fast (ca 12 years) due to the growth of remnant corals (Halford et al. 2004; Gilmour et al. 2013). However, recovery also depends on the extent to which corals are subject to chronic disturbances or sub-lethal effects of changing environmental conditions. Importantly, chronic disturbances result in background levels of mortality, which can ultimately affect colony fitness and consequently growth and reproduction (Hughes and Connell 1987; Lasker 1990; Babcock 1991) and limit recovery rates between subsequent major disturbances (Wahle 1983, 1985; Done 1988; Dikou and Van Woesik 2006; Wakeford et al. 2008; Bruckner 2012a; Lirman et al. 2013).

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1.2. Partial mortality

Corals are modular (or colonial) organisms, made up of repeated units (polyps), each of which is physiologically capable of independent living (Hughes and Jackson 1980). As such, coral colonies can survive levels of injury (or partial mortality) on a scale far beyond the regenerative capacity of most solitary organisms (Hughes and Jackson 1980). However, partial mortality effectively reduces the number of polyps that make up a colony, which does nonetheless affect the fate and fitness of the colony. Importantly, smaller colonies tend have lower survivorship, growth and reproductive output (Highsmith 1982; Hughes and Jackson 1985; Henry and Hart 2005). For example, larger colonies produce more eggs per unit area and make a disproportionate contribution to population replenishment (Hall and Hughes 1996). Similarly, the probability of whole-colony mortality generally decreases with increasing colony size (Hughes and Jacskon 1985, but see Madin et al. 2014).

Coral colonies that have been subject to partial mortality not only experience reduced fitness due to declines in tissue area, but also divert a portion of their energy to tissue repair, further reducing energy expenditure on growth (Bak 1983; Meesters et al. 1994)**,** reproduction **(**Kojis and Quinn 1985**)** and/ or other metabolic functions (Bak and Criens 1981; Kojis and Quinn 1985; Rinkevich and Loya 1989; Manfred 1994; Henry and Hart 2005). Small injuries tend have very localized effects, causing declines in growth (Bak 1983) and reproduction (e.g Van Veghel and Bak 1994) among polyps immediately adjacent to the injury. However, larger injuries (> 10% of the colony) may lead to significant declines in growth and/ or reproduction across the entire colony (Rinkevich and Loya 1989; Meesters et al. 1994), though the extent of this energy translocation will depend upon the characteristics of injury (e.g. extent, type, timing) and the type of coral. Since energy reserves are often limited, significant commitments to tissue repair and regeneration can strongly impact on growth (Guzman et al. 1994; Meesters

et al. 1994; Lirman 2000). Similarly, polyp fecundity and egg volume per polyp (mm^3) can also decline following major injuries (Hall 1998). Injured colonies often invest in future reproduction through the development of new polyps (growth) at the cost of current reproductive output (Szmant and Gassman 1990; Hall 1998; Weil et al. 2009a).

Partial mortality can, in some instances, have positive outcomes for coral colonies and/ or populations (Hughes and Jackson 1985). For colonies, partial mortality enables individuals to absorb effects of disturbances without actually dying (Hughes and Jackson 1985). Where injuries lead to fragmentation and multiple daughter colonies, this may spread the risk of future whole-colony mortality and also contributes to localised increases in population size (Bruckner 2012a; Toh and Chou 2013). It is clear however, these benefits are often offset by extensive loss of overall tissue area, such that extensive partial mortality (which may or may not lead to fission) are generally regarded as negative events in the life-history of corals (Hughes and Jackson 1985).

Despite the importance of partial mortality for the fate and fitness of individual colonies, few studies (e.g., Hughes and Jackson 1985; Hall 1998; Cumming 2002; Dikou and Van Woesik 2006; Bruckner 2012a; Williams and Miller 2012; Lirman et al. 2013) have actually documented natural rates of injuries. Most of these studies provide a single, static measure of partial mortality and often at very small spatial scales. For instance, Hall (1998) documented rates of injury in select coral species around Lizard Island in Australia, based on a single survey of 673 colonies in 1994. Hall (1998) found that the incidence of pre-existing injuries varied greatly among taxa, which was attributed to taxonomic differences in regeneration rates more so than differential susceptibility to injury. It is important therefore, to explore patterns of injury over time (Hall 1998), to distinguish between corals that are highly susceptible to injuries versus those that invest little in regeneration and thereby, accumulate injuries through time. This thesis explicitly tested for changes in injury rates through time,

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following individual corals over three years, and hence provides an important data to test for differences in regeneration rates versus susceptibility to chronic disturbances.

Partial mortality is very common not only in corals, but in all other modular organisms and regeneration of such injuries is widespread. The capacity for regeneration and rates of repair vary greatly among species (Liddle and Kay 1987; Liddle 1991; Meesters et al. 1997b; Oren et al. 1997), mainly due to inherent differences in energy allocation, but also depends upon the local environment, disturbance history (Henry and Hart 2005), as well as the size and type of injury (Bak and Steward-Van Es 1980; Palumbi and Jackson 1982, Hall 1997). Some plants and gorgonian octocorals respond to partial mortality with vigorous regrowth called overcompensation (Sánchez and Lasker 2004). This process is a growth response to injury that exceeds the normal performance. More specifically, individuals exceed normal growth after partial mortality and/or breaking of the apical dominance (Huhta et al. 2000). For example, in plants overcompensation may be due to grazing or clipping (Huhta et al. 2000). Conversely, bryozoans, sponges and corals often do not regenerate large injuries showing signs of undercompensation (Bak and Steward-Van Es 1980; Henry and Hart 2005), while they can fully regenerate small injuries (Palumbi and Jackson 1982; Hall 1997). The ability to regenerate is important in modular organisms since lack of regeneration can result in declines in individual fitness.

1.3. Background mortality

While much of the literature on disturbances to coral assemblages is focussed on large-scale and acute disturbances (e.g., cyclones, mass-bleaching events and outbreaks of crown-of-thorns starfish), there are potentially high rates of coral mortality even during intervening periods with no acute disturbances. Importantly, most studies on acute disturbances tend to attribute 100% of observed injuries or coral mortality to the associated disturbance (e.g., Baird

and Marshall 2002; Sweatman et al. 2011; Death et al. 2012; McClanahan et al. 2012), whereas at least a portion of the observed mortality is likely to be caused by sustained and ongoing chronic disturbances (e.g., Wakeford et al. 2008). There are also no periods free of disturbances on coral reefs, as is the case for most ecosystems (Lugo and Scatena 1996; Lewis et al. 2004; Wakeford et al. 2008; van Mantgem et al. 2009). Wakeford et al. (2008) documented high levels of chronic disturbances that caused background mortality between major acute disturbances. Similarly Madin et al. (2014) showed high rates of whole colony mortality in a period free of major acute disturbance such as cyclones or bleaching (between 12 and 15% of whole colony mortality: Wakeford et al. 2008; Madin et al. 2014). For instance, in Barbados, tissue loss in a period without any major acute disturbances ranged from 37.8% to 48.9% in *Siderastrea siderea* (Lewis 1997), while during a bleaching event on the Great Barrier Reef it was 43 ± 6.6 % and 11 ± 1.1 % in *Platygyra daedalea* and *Porites lobata* respectively (Baird and Marshall 2002). *Acropora palmata* in Florida Keys showed a 63% decline in live area during 7 years mainly due to background mortality drivers (Williams and Miller 2012). Importantly, many studies (Table 1.1) documented a lack of recovery or a decline in coral cover even when major acute disturbances did not occur. In the Virgin Islands, hard coral cover showed a 4% decline between 1989 and 2002, while in Florida the decline was even more severe (from 7.3 to 43.9%) between 1989 and 1991 (Porter and Meier 1992), all in the absence of any major disturbances.

Background mortality (whole organism mortality) has also been documented in both temperate and tropical forests (5%year^{-1}) (Lugo and Scatena 1996; Lewis et al. 2004; van Mantgem et al. 2009). In temperate forests, tree background mortality rates have increased rapidly in recent decades due to regional warming and consequent increase in water deficits (van Mantgem et al. 2009).

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Comparative studies of coral recovery and resilience typically assume no background mortality, but it becoming increasingly clear that corals are routinely subject to significant rates of injuries and indeed, whole colony mortality (Madin et al. 2014). To account for this, some studies (e.g., Done 1988; Wakeford et al. 2008) assume consistently high levels of background mortality within and among reefs. However, rates of background mortality are likely to vary in accordance with a number of environmental gradients, including sedimentation (Guzman et al. 1994; Nugues and Robert 2003), predation (Cumming 2002; Williams and Miller 2012), and disease (Williams and Miller 2012), and will also depend on a number of intrinsic factors (Kramarsky-Winter and Loya 2000) including colony size (Hughes and Jackson 1985; Bak and Meesters 1998), age (Bak and Engel 1979), genotype (Knowlton et al. 1992) and colony morphology (Jackson 1979). For instance, small and senescent colonies generally have lower regeneration rates potentially resulting in high rates of injury. Similarly, branching corals appear much more vulnerable to breakage and injuries than massive corals but also have more rapid regenerative capacity, leading to seemingly lower levels of background partial mortality (Meesters et al. 1996).

Background mortality is very common and generally >60% of colonies have significant injuries (Bak and Luckhurst 1980; Harriot 1985; Bythell et al. 1993; Wakeford et al. 2008; Pratchett et al. 2013), However, whether it may vary spatially is still poorly understood and likely to be important in better understanding spatial variation in recovery capacity. Spatial variation in rates of tissue loss may partly explain spatial differences in population dynamics (Hughes et al. 1999; Trapon et al. 2013). Hughes et al. (1999) documented that adult abundance is relatively homogeneous among reefs and sectors, despite substantial differences in recruitment (highest in the northern GBR). The lack of conformity between adult abundance and recruitment implies variation in growth (post-recruitment processes). More specifically, this study infers that there must be underlying variation in the

growth and survivorship of corals along the length of the Great Barrier Reef, but this has never been tested.

1.4. Objectives

The overarching objective of my PhD was to quantify rates of background mortality (including both partial and whole colony mortality) at a range of spatial scales from adjacent colonies within the same reef habitat to colonies in geographic disparate locations, and to investigate the ecological consequences of injury and regeneration on colony condition. While several previous studies (e.g., Bak and Luckhurst 1980; Stimson 1985; Lewis 1997; Hall 1998; Dikou and van Woesik 2006; Wakeford et al. 2008; Lirman et al. 2013) have quantified and compared rates of background mortality and injuries across small scales (mostly, within a single reef), this study provides specific opportunity to assess the variation in rates of background mortality at geographic scales (e.g., between Northern Great Barrier Reef and Lhaviyani Atoll Maldives) and along the Great Barrier Reef. Hughes et al. (1999) documented that abundance of adult corals was relatively homogeneous along the length of Australia's Great Barrier Reef despite significant declines in rates of coral recruitment at higher latitudes. This suggests that high levels of population replenishment at higher latitudes are offset by higher rates of mortality and/ or injury. If there are important differences in background mortality at very large spatial scales, then there will also be latitudinal difference in the capacity of corals to recover from increasing acute and anthropogenic disturbances. Moreover, it is the first study to investigate the ecological consequences of injury and regeneration, which are likely to be important in understanding intraspecific variation in susceptibility and recovery capacity of colonies to acute disturbances.

While most of the research on coral reef resilience has been directed towards community-level responses to disturbances, in order to investigate phase shifts from coral-dominated to

other alternate states (Nystrom and Folke, 2001; Aronson et al. 2002; Bellwood et al. 2004), this thesis focuses on resilience at the scale of individual coral colonies. Phase-shifts at a community level occur following very severe and protracted disturbances, such that there are very limited opportunities for management once this happens (Hughes et al. 2010). It is likely however, that individuals and populations will respond much more quickly (compared to communities), maximizing opportunities to address underlying causes in the loss of resilience.

The overarching aims were addressed in a series of four separate studies, presented as distinct chapters. To investigate spatial variation in background partial mortality, prevalence (proportion of injured colonies versus uninjured per site) and severity of injury (extent of dead tissue per colony) were quantified at a hierarchy of spatial scale along most of the Great Barrier Reef based on both instantaneous (Chapter 2) and repeated (Chapter 3) measures of observable injuries. We expected to show significant variation in background mortality at the largest scales (between sectors) given that Hughes et al. (1999) showed that high population replenishment did not correspond with high number of adult colonies along the Great Barrier Reef, and suggested that spatial variation in underlying rates of background mortality (and/or reduced growth rates) may be responsible for differences between recruitment and adult populations. Specifically, recruit abundance in the northern and central sectors (in proximity of Lizard Island and Trunk Reef respectively) was twofold compared to adult abundance, while in the southern sector (in the proximity of Heron Island) adult abundance was more than double that of recruit abundance. Based on these marked latitudinal differences in population replenishment (highest in the northern GBR), despite similarities in adult abundance, it was expected background rates of mortality would be highest in the northern GBR and lowest in southern GBR.

Prevalence and severity of observable injury were also compared between different geographic locations (the Northern GBR, Australia and Lhavihany Atoll, in the Maldives,

Indian Ocean) (Chapter 4). Given broad regional differences in environmental conditions and management structures between the Northern GBR, and Lhavihany Atoll, it was expected that there would be marked differences in the prevalence and severity of coral injuries at these two locations.

After investigating spatial variation in tissue loss, it was critical to test the effects of observable and non-observable injuries on colony condition. Colony condition was assessed based on symbiont density and total lipid content, which are good proxies of coral health and have been shown to vary with changes in environmental conditions (Rowan et al. 1997; Jones 1997; Fagoone et al. 1999; Anthony et al. 2009). To investigate the ecological response of corals to partial mortality, the influence of observable and non-observable injury on colony condition was quantified (Chapter 5).

Importantly, this PhD investigated injury dynamics in both natural environments (Chapter 2,3,4,5) and using a series of experiments in the field and in the lab (Chapter 5). These studies (Chapter 2,3,4,5) were critical to investigate spatial and temporal patterns of natural injury, and were useful for better understanding the ecological consequences of injury.

Chapter 2. Spatial variation in background mortality among dominant coral taxa on Australia's Great Barrier Reef[*]

Abstract

Even in the absence of major disturbances (e.g., cyclones, bleaching), corals are consistently subject to high levels of partial mortality, which undermines individual fitness and resilience of coral colonies. This study quantified the proportion of colonies with conspicuous injuries (prevalence) as well as the areal extent of injuries (severity) across four common coral taxa; massive *Porites*, encrusting *Montipora*, *Acropora hyacinthus* and branching *Pocillopora*. A total of 2,276 adult colonies were surveyed across three latitudinal sectors, nine reefs and 27 sites along the Great Barrier Reef, Australia. The prevalence of injuries was very high, especially for *Porites* spp (91%) and *Montipora* encrusting (85%) and varied significantly, but mostly at small spatial scales (e.g., among colonies positioned <10-m apart). Similarly, severity of background partial mortality was surprisingly high (between 5% and 21%) but varied greatly among colonies within the same site and habitat. This study suggests that intraspecific variation in partial mortality is greatest between adjacent colonies than among latitudinal sectors or reefs. Differences in the prevalence and severity of background partial mortality have significant ramifications for coral capacity to cope with increasing acute disturbances, such as climate induced coral bleaching. These data are important for understanding coral responses to increasing stressors, and in particular for predicting their capacity to recover between subsequent disturbances.

2.1 Introduction

Disturbances play an important role in structuring natural communities (Hughes et al. 2003; Worm et al. 2006), especially in coral reef ecosystems, which are being subject to increasing frequency, severity and diversity of acute disturbances (Hughes et al. 2003; Karlson and Hurd 1993). Importantly, climate-related disturbances are compounding numerous pre-existing natural and anthropogenic disturbances (Hughes et al. 2003; Jackson et al. 2001; Gardner et al. 2003), contributing to extensive coral loss and associated degradation of coral reef habitats (Gardner et al. 2003; Bellwood et al. 2004; Bruno and Selig 2007; De'ath et al. 2012). Coral reefs are highly dynamic ecosystems, naturally subject to a wide range of disturbances operating at different temporal and spatial scales, ranging from widespread mass bleaching events to chronic localised removal of live coral tissue by corallivores (Nyström and Folke 2001). However, increasing effects of global climate change and other more direct anthropogenic disturbances appear to be increasing rates of coral mortality beyond those which can be sustained (Hoegh-Guldberg et al. 2007). It is also possible that the capacity of corals to recover from successive disturbance events is declining, due to sustained declines in coral growth or reproductive output (De'ath et al. 2012).

Coral assemblages can recover quite quickly in the aftermath of major disturbances (e.g., Halford et al. 2004; Linares et al. 2011), as long as there is i) sufficient time between major disturbances, ii) adequate proximity or connectivity to viable source populations, and iii) maintenance of suitable substrates for settlement and subsequent survival of coral recruits (Connell et al. 1997). Given increasing incidence of major disturbances (e.g., cyclones, bleaching or outbreaks of crown-of-thorns starfish), the interval between these events is often less than five years (Trapon et al. 2010, exceeding the time needed for effective recovery (Tanner et al. 1994). Moreover, the increasing spatial extent of disturbances (e.g., climate-induced coral bleaching) is causing comprehensive mortality over very large areas, further

undermining the capacity for recovery (but see Gilmour et al. 2013). The capacity for coral assemblages to recover can also be negatively affected by smothering or overgrowth by macroalgae, in instances where there is insufficient grazing by herbivorous fishes (Hughes et al. 2007), and by a range of factors that potentially limit the early post-settlement growth and survivorship of corals (Trapon et al. 2013).

While acute disturbances (e.g., cyclones, bleaching or outbreaks of crown-of-thorns starfish) often have very conspicuous effects on corals, causing high levels of whole colony mortality, chronic disturbances (e.g., predation, competition and disease) can have equally important effects on coral communities, further increasing susceptibility to major disturbances (Harvell et al. 2002) and greatly reduce recovery and resilience (Wakeford et al. 2008). Wakeford et al. (2008) attributed low coral cover recorded at Lizard Island, in northern Great Barrier Reef (GBR) to chronic disturbances and high rates of background mortality. Accordingly, coral assemblages at very isolated reefs (e.g., Scott Reef, off the north-west shelf), which are largely isolated from chronic anthropogenic disturbances, may recover quite rapidly even after very severe acute disturbances (Gilmour et al. 2013). In the absence of major disturbances, corals are continually subject to a range of chronic, often small-scale disturbances that can cause relatively high rates of mortality (Stimson 1985; Connell 1997; Wakeford et al. 2008; Pratchett et al. 2013). These chronic disturbances are a normal part of the natural dynamics and turnover in coral populations and communities (Hughes and Jackson 1985; Knowlton et al. 1990; Bythell et al. 1993), but may be increasing in prevalence and severity, thereby undermining the capacity for recovery (annual background mortality rates can generally vary from 1 to 30%: Bak and Luckhurst 1980; Harriot 1985; Bythell et al. 1993; Wakeford et al. 2008; Pratchett et al. 2013). If for example, background mortality rates are increasing, the rate of recovery will be reduced, requiring an even longer period for complete recovery between successive major disturbances.

Corals are modular organisms and can survive extensive injury (loss of polyps) or partial mortality, on a scale far beyond the regenerative capacity of most solitary organisms (Hughes and Jackson 1980). However, partial mortality and declines in the total number of polyps that make up a colony, result in smaller colony size, which can greatly affect individual fitness (Hughes and Jackson 1985; Hall and Hughes 1996; Bruckner and Hill 2009). Colonies suffering from partial mortality must divert energy towards tissue repair, leading to a reduced energy expenditure towards growth, reproduction and other metabolic functions (Meesters et al. 1994). Very high prevalence and severity of partial mortality may therefore, have a stronger bearing on the fitness and fate of coral colonies and/ or populations, than even colony size or other commonly used metrics of population structure. There are very few studies that have systematically quantified the prevalence or severity of partial mortality across a range of different corals or at a range of locations (Bruckner 2012a; Lirman et al. 2013). It is very likely however, that rates of injury will vary spatially, with greatest variation likely to occur at relatively small scales (Pratchett et al. 2013). On the GBR, for example, midshelf reefs are subject to frequent and severe acute disturbances, mostly associated with outbreaks of crown-of-thorns starfish (Osborne et al. 2011; Sweatman et al. 2011), whereas offshore reefs are relatively less affected by such disturbances. However, even more apparent is the patchy nature of most disturbances, such that some reefs may be severely impacted, whereas other nearby reefs are unaffected (Karlson and Hurd 1993).

The aim of this study was to quantify the prevalence and severity of partial mortality across four dominant coral taxa (*Acropora hyacinthus*, branching *Pocillopora*, massive *Porites* spp and encrusting *Montipora*) at a hierarchy of spatial scales (among sectors, among reefs and among sites within reefs) on midshelf reefs on the Australia's GBR. Biotic and abiotic agents of partial mortality can vary in frequency, intensity and spatial scale and can therefore have different impacts on coral colonies at different scales (Karlson and Hurd 1993). By

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measuring the prevalence and severity of partial mortality across a hierarchy of different spatial scales we hope to provide insights into local versus global causes of partial mortality. Quantifying rates of tissue loss along the entire GBR is critical for understanding spatial variation in the recovery capacity and resilience of reef-building corals. More specifically, this study tests the hypothesis that background rates of partial mortality decrease with latitude, thereby accounting for apparent discrepancies in rates of population replenishment versus overall abundance of adult corals (Hughes et al. 1999). Similar levels of adult abundance despite much higher levels of recruitment in the northern GBR imply that there must be higher levels of background mortality. The greatest variation was expected between latitudinal sectors, however, since chronic background disturbances are recurrent patchy stressors, prevalence and severity of partial mortality were also expected to vary at smaller scale (reef and site). If so, then this may have significant ramifications for the capacity of corals to cope with increasing acute disturbances associated with global climate change.

2.2 Materials and Methods

2.2.1 *Study sites*

This study was conducted in 2011 on the Great Barrier Reef, Australia. Sampling was undertaken at a hierarchy of spatial scales. At the largest scale, three distinct latitudinal locations, separated by at least 500km, were considered: the northern sector in the vicinity of Lizard Island (14° 41'S, 145° 28'E), the central sector, in vicinity of Trunk Reef (18 25'S, 146 °47'E), and the southern sector, in the vicinity of Heron Island (23° 27'S. 155° 55'E) (Figure 2.1). At each location, sampling was conducted at 2-3 reefs, and a total of nine different sites. Sites were separated by up to 2 km along the exposed (south-east) margin (Figure 2.1). To avoid any effect of cross shelf variation, only mid-shelf reefs were sampled. Similarly, sampling was confined to reef crest habitats, between 3-5m depth. At each site, sampling was

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conducted along three replicate 10 x 5m belt transects orientated parallel to, and positioned within 5-10m of, the reef crest. Due to the high frequency and intensity of disturbances (such as predation) on the reef crest, prevalence and severity of partial mortality were expected to be higher in this habitat compared to the flat and slope.
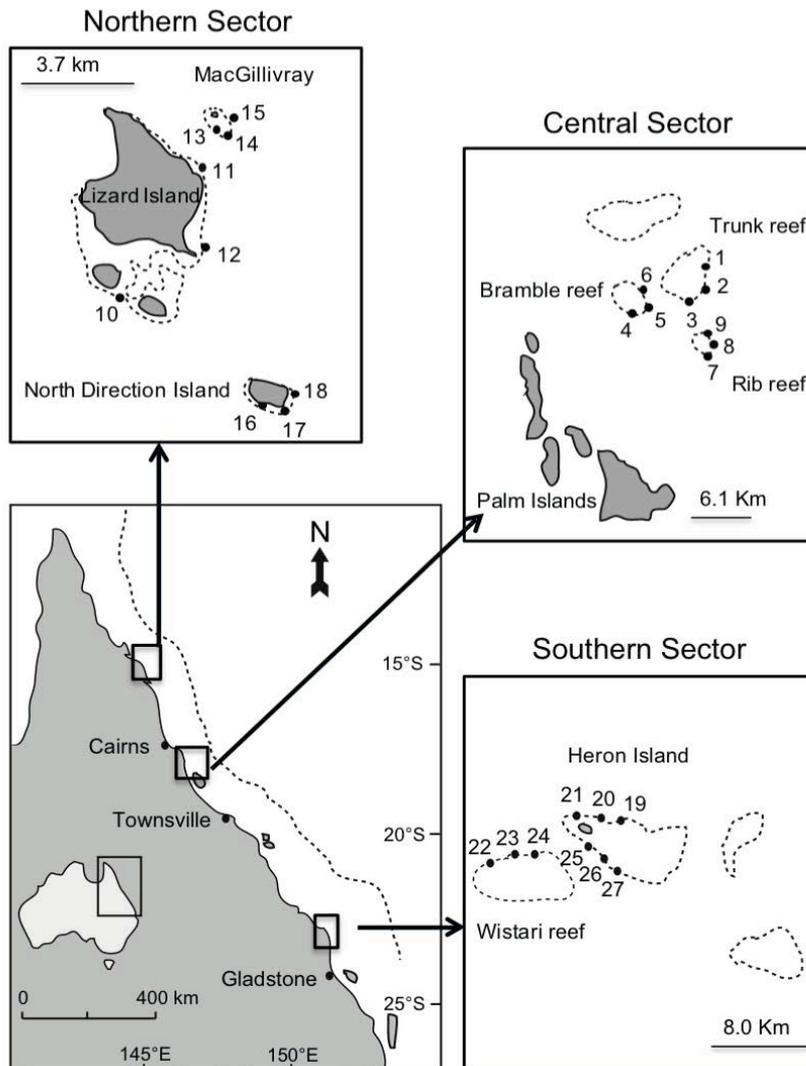
Figure 2.1 Map of the three study sectors (northern, central and southern) along the Great Barrier Reef, Australia**.** Within each latitudinal sector, three mid-shelf reefs, each with three sites on the exposed reef crest, were sampled. Figure adapted from Trapon et al. 2013.

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2.2.2 *Survey of partial mortality*

This study considered four dominant coral taxa; *Acropora hyacinthus*, branching *Pocillopora*, massive *Porites* spp and encrusting *Montipora*. These four coral taxa are not only among the most common along the GBR (Veron and Wallace 1984), but represent contrasting morphologies and life-history strategies (Darling et al. 2012). To compare the prevalence and severity of partial mortality within coral taxa, all relevant colonies located with the area of the each transect were surveyed and photographed. Each colony was photographed from the top with appropriate scale references, and all images were processed using the software Image J, to quantify the planar areal extent as a measure of colony size. The prevalence and severity of injuries were however, recorded *in situ* due to difficulties in capturing the full extent of injuries (especially on the sides and base of colonies) in a single photograph. The severity of partial mortality on individual colonies ranged from zero (no injury) to close to 100%. According to data from AIMS Long-term monitoring program, during the study period the major acute disturbances that affected the three latitudinal sectors were cyclone Hamish in 2009 (southern GBR) and cyclone Yasi in 2011 (central and northern GBR). Since cyclones have a distinctive and identifiable effect on corals, such as dislodgment and breakage of colonies, it was easy to identify this agent of disturbance and exclude it from the survey. To reduce bias, broken or dislodged colonies , as well as colonies visibly eaten by crown-of-thorns starfish, were not included in the surveys, this ensured that partial mortality recorded during the survey was due to chronic rather than acute stressors.

2.2.3 *Data analysis*

The effect of colony size on both prevalence and severity of tissue loss, regardless of spatial scales, was tested with two linear regressions for each species, using the proportion of injured colonies and arcsine partial mortality as dependent variables and colony size as

predictor. Separate 1-way ANOVAs were then conducted for each of the four different taxa for both prevalence and severity of injuries. For prevalence of injuries, we analysed the proportion of colonies at each site that had any evidence of injury, and thereby compared prevalence of injury among sectors and among reefs (nested within sectors). For severity, mean colony percentage of partial mortality (which was arcsine transformed to meet the assumptions) was analysed among sectors, reefs, and sites (site nested within reef and reef nested within site). Variation in proportional mortality among size classes was analysed using size-frequency distributions, which were calculated based on estimates of the surface area of each colony. More specifically, size classes were determined *a priori* and were consistent across all coral taxa. The specific categories used correspond with log10 transformed surface area in cm^2 of each colony following Bak and Meesters (1998), and Adjeroud et al. (2007). Variation in both prevalence and severity of partial mortality (specifically, the proportional extent of dead versus living components of each colony) among the four coral taxa (*A. hyacinthus*, branching *Pocillopora*, massive *Porites* spp and encrusting *Montipora*) were analyzed using two separate hierarchically-nested ANOVAs, with transects (3 per site) nested within site, sites (3 per reef) nested within reef, and reefs (3 per sector) nested within latitudinal sectors (3 sectors). Proportional mortality for each colony was arcsine-square root transformed prior to analysis. Due to the unbalanced design, the F-statistic and p-values resulting from the Type III sum of square were reported. Variance components were also calculated for each coral taxa to assess whether the most important scale at which variation occurs is consistent across taxa with fundamentally different life-history dynamics. A Tukey's HSD post hoc test was used to identify where differences among group means occurred. All analyses were performed using STATISTICA 7.0 (StatSoft) software.

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2.3 Results

A total of 2,276 colonies were surveyed during this study, including 862 colonies of *A. hyacinthus*, 301 colonies of massive *Porites*, 505 colonies of branching *Pocillopora* and 608 colonies of encrusting *Montipora*. Prevalence of partial mortality or injuries was very high across all taxa, averaging 71% for *Acropora*, 59% for branching *Pocillopora*, 85% for encrusting *Montipora* and 92% for *Porites* across all sectors, reefs and sites (Table 2.1). The number of colonies with no injury, low, medium and high extent of injury was relatively similar among size classes in all four species (Figure 2.2, 2.3). This may explain why the regressions showed that both prevalence and severity of injury were generally independent of colony size in all the coral taxa (Table 2.2). Importantly, the r^2 values were very low for all coral species indicating that colony size explained only a very small proportion of the total variation (Table 2.2). Colony size was a predictor of severity of partial mortality only in *Pocillopora* (r^2=0.31, n=294, p=0.002), with smaller colonies having proportionately more injury (Table 2.2). The One-way ANOVA results for tests of the regressions, investigating the relationship between prevalence of injury and severity of injury and colony size were not statistically significant in any of the coral taxa.

Table 2.1 Number of injured colonies versus number of total colonies surveyed at each site, within each reef and sector for the four coral species.

Sector	Reef	Site	*Acropora hyacinthus*	*Montipora* encrusting	*Porites* massive	Branching *Pocillopora*
North	Lizard Island	1	9/16	56/56	16/16	10/13
North	Lizard Island	2	44/68	13/13	15/15	15/23
North	Lizard Island	3	0/0	14/14	41/43	12/24
North	Mac	1	9/14	6/6	28/28	21/38
North	Mac	2	34/50	9/9	12/12	3/4
North	Mac	3	30/60	37/37	17/17	20/34
North	North Direction	1	13/20	26/26	19/19	34/44
North	North Direction	2	16/19	40/42	32/32	35/62
North	North Direction	3	39/51	7/8	28/28	59/87
Central	Trunk	1	75/81	15/15	0/0	6/9
Central	Trunk	2	39/45	30/30	0/0	0/0
Central	Trunk	3	33/33	20/20	0/0	0/0
Central	Rib	1	60/60	3/3	15/15	10/10
Central	Rib	2	20/58	2/2	10/10	3/5
Central	Rib	3	12/40	9/9	10/10	2/3
Central	Bramble	1	19/21	10/10	9/15	2/3
Central	Bramble	2	35/60	32/32	19/19	8/20
Central	Bramble	3	21/23	10/10	0/0	6/11
South	Wistari	1	9/15	11/14	0/2	10/35
South	Wistari	2	12/18	8/13	2/2	2/3
South	Wistari	3	20/20	1/5	0/0	1/4
South	South Heron	1	11/24	9/15	10/10	20/20
South	South Heron	2	10/16	1/6	0/0	0/4
South	South Heron	3	27/37	33/66	0/0	2/21
South	North Heron	1	13/13	60/60	0/0	2/3
South	North Heron	2	0/0	17/27	5/5	25/25
South	North Heron	3	0/0	51/51	3/3	0/0
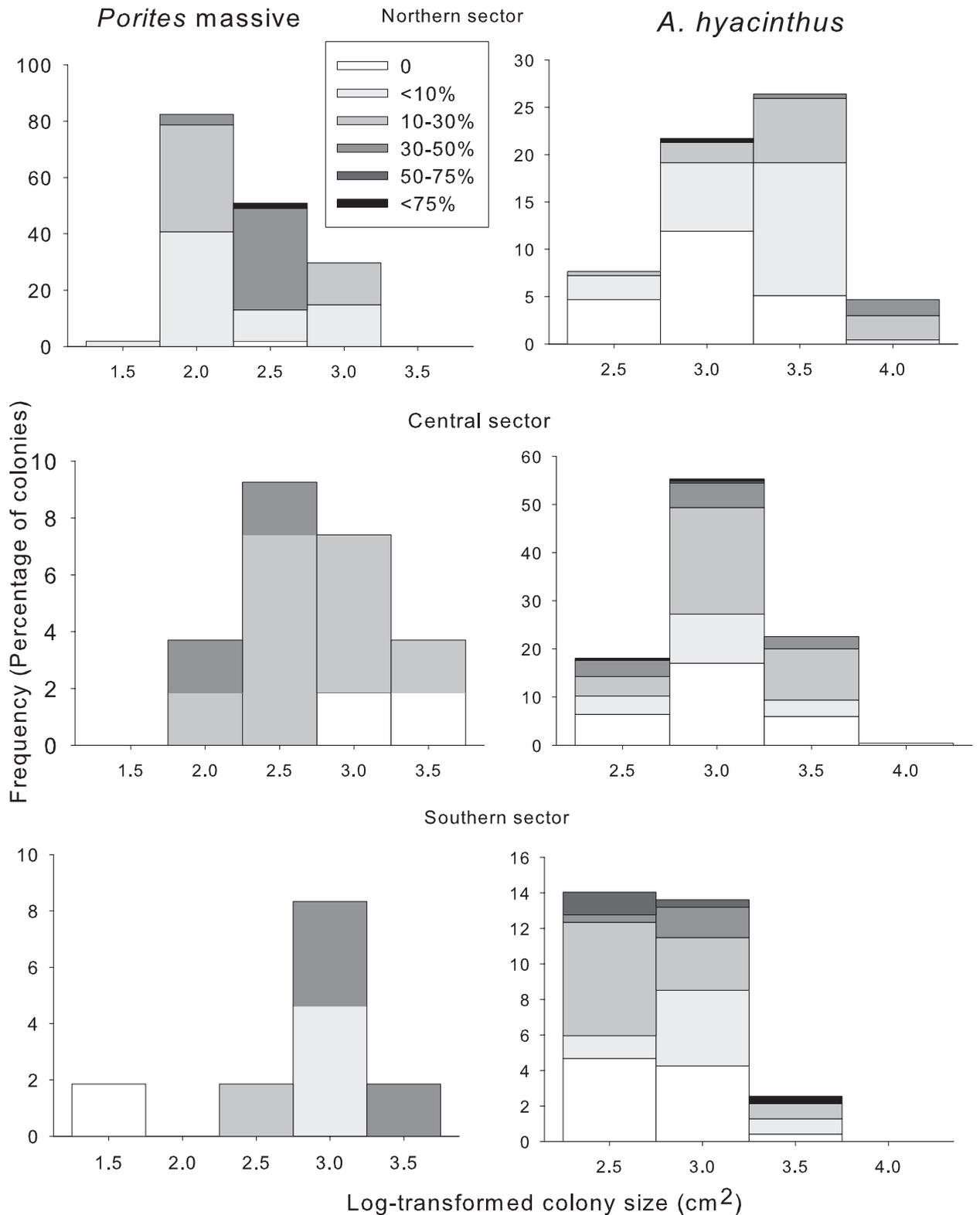
Figure 2.2 Size-frequency distributions (percentage of colonies) and percentage partial mortality for each size class in each latitudinal sector for *Porites* massive, and *Acropora hyacinthus*. Size classes were log10 transformed estimates of colony surface area.
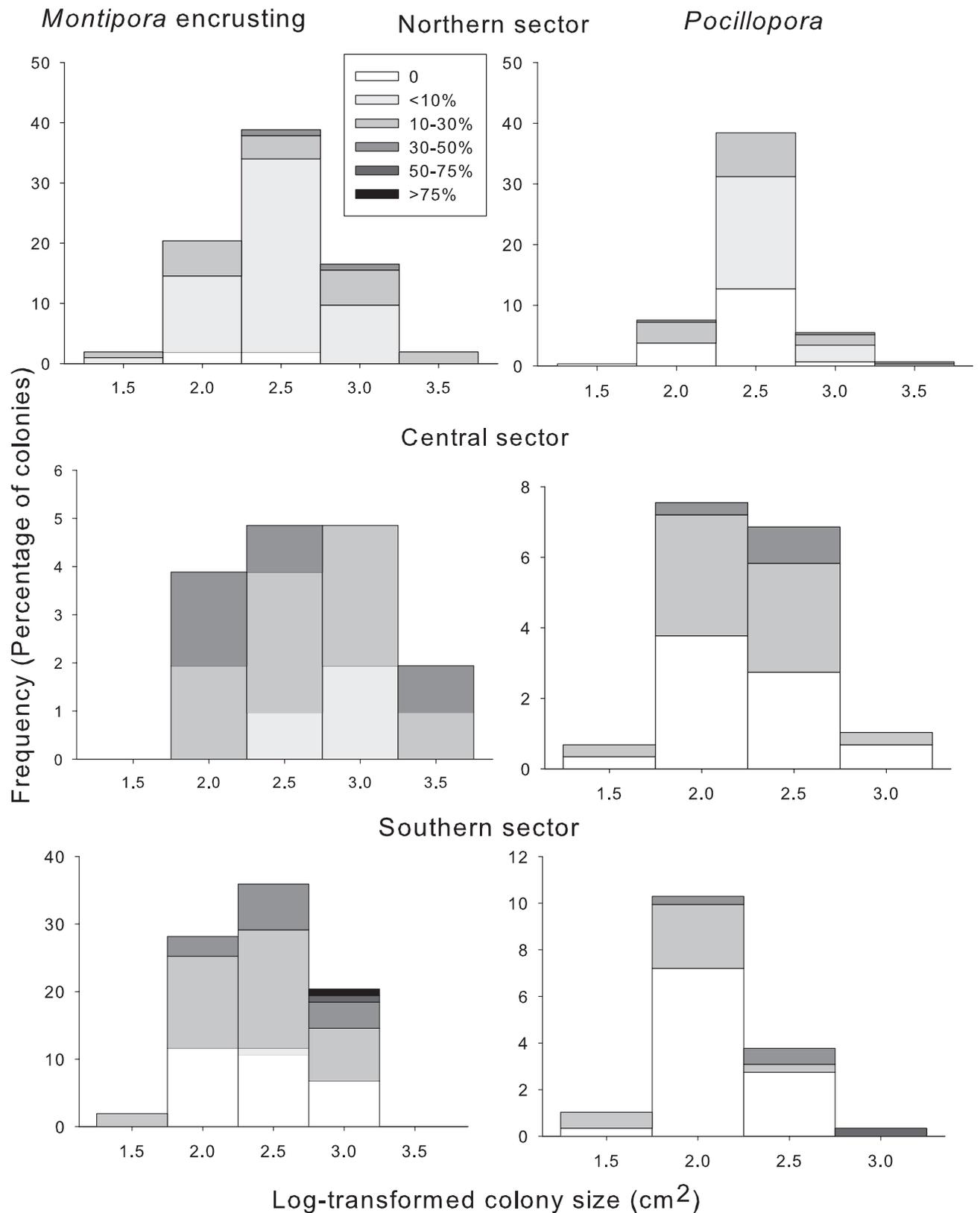
Figure 2.3 Size-frequency distributions (percentage of colonies) and percentage partial mortality for each size class in each latitudinal sector for encrusting *Montipora,* and *Pocillopora*. Size classes were log10 transformed estimates of colony surface area.

Table 2.2 Linear regression outcomes to investigate the effect of colony size on the severity (extent of injury) and on the prevalence (proportion of injured colonies) of partial mortality in each coral taxa.

Severity of partial mortality	R^2	df	F	p
A. hyacinthus	0.007	1/468	3.7	0.05
Porites spp	0.05	1/109	3.25	0.59
Montipora encrusting	0.01	1/203	3.81	0.53
Pocillopora	0.31	1/292	9.56	0.002
Prevalence of partial mortality	R^2	df	F	p
A. hyacinthus	0.49	1/22	1.14	0.29
Porites spp	0.01	1/17	0.01	0.89
Montipora encrusting	0.01	1/25	0.04	0.82
Pocillopora	0.09	1/22	0.2	0.65

Prevalence of partial mortality (proportion of injured colonies) varied significantly both among reefs and among sectors for *Montipora* encrusting (Table 2.3), with the greatest variation at sector level (54.1%). For all other coral taxa variation was most apparent at the smallest scales (within reefs), and there was no significant variation among reefs or among sectors. As for prevalence, the severity of partial mortality (the extent of injuries on individual colonies) varied most (>80%) at smallest scales, and in this case among colonies within the same transect (Table 2.4). There was however, significant variation in the severity of partial mortality at the largest scale (among sectors) for *A. hyacinthus* and encrusting *Montipora*. For encrusting *Montipora,* mean severity of partial mortality was highest (21%) in the central sector, while mean severity of partial mortality was lowest (5%) for *A. hyacinthus* in the northern sector (Figure 2.4).

In *Pocillopora* and *Montipora* spp the majority of the colonies were smaller than 1000 cm^2, while in *A. hyacinthus* colony surface area ranged from 90 cm^2 up to 37.240 cm^2, and in *Porites* ranged from 75 cm^2 to 2410 cm^2.

Table 2.3 Results of hierarchically-nested ANOVAs to test for spatial variation in prevalence of injury (proportion of injured colonies per site) for each coral taxa.

	SS	df	MS	F	p	var (%)
A. hyacinthus						
Sector	0.07	2/16	0.03	0.89	0.42	0
Reef (Sector)	0.38	6/15	0.06	1.6	0.2	16.1
Error	0.6	16	0.04			83.9
Porites spp						
Sector	0.08	2/11	0.04	0.79	0.47	1.8
Reef (Sector)	0.34	5/11	0.06	1.31	0.32	1.2
Error	0.58	11	0.05			97
Montipora encrusting						
Sector	0.84	18/2	0.42	19.2	<0.001	54.1
Reef (Sector)	0.35	6/18	0.05	2.6	0.05	16.5
Error	0.39	18	0.02			29.4
Pocillopora						
Sector	0.06	2/15	0.03	0.51	0.6	0
Reef (Sector)	0.38	6/15	0.06	0.9	0.47	1.6
Error	0.1	15	0.7			98.4

Table 2.4 Results of hierarchically-nested ANOVAs to test for spatial variation in severity of partial mortality (specifically, the proportional extent of dead versus living components of each colony) for each coral taxa at all spatial scale.

	SS	df	MS	F	p	var (%)
A. hyacinthus						
Sector	1.15	2/450	0.57	13.15	>0.001	4.2
Reef (Sector)	0.58	4/450	0.14	3.32	0.01	14.2
Site (Sector*Reef)	0.5	4/450	0.12	2.87	0.02	0.4
Transect (Sector*Reef*Site)	0.13	4/450	0.03	0.76	0.54	0.2
Error	20.6	450	0.04			81
Porites spp						
Sector	0.03	2/94	0.01	0.67	0.51	8.3
Reef (Sector)	0.2	4/94	0.06	2.75	0.03	0
Site (Sector*Reef)	0.09	4/94	0.02	0.96	0.43	0
Transect (Sector*Reef*Site)	0.05	4/94	0.01	0.57	0.67	0.3
Error	2.27	94	0.02			91.4
Montipora encrusting						
Sector	0.38	2/185	0.19	4.8	>0.001	6.4
Reef (Sector)	0.27	4/185	0.06	1.7	0.1	4.2
Site (Sector*Reef)	0.07	4/185	0.01	0.45	0.7	4.9
Transect (Sector*Reef*Site)	0.06	4/185	0.01	0.38	0.8	1.1
Error	7.4	185	0.04			83.4
Pocillopora						
Sector	0.14	2/283	0.07	1.8	0.16	0.4
Reef (Sector)	0.14	4/283	0.03	0.93	0.44	1.4
Site (Sector*Reef)	0.25	4/283	0.06	1.61	0.17	1.4
Transect (Sector*Reef*Site)	0.2	4/283	0.05	1.29	0.27	5
Error	11.3	283	0.04			91.9
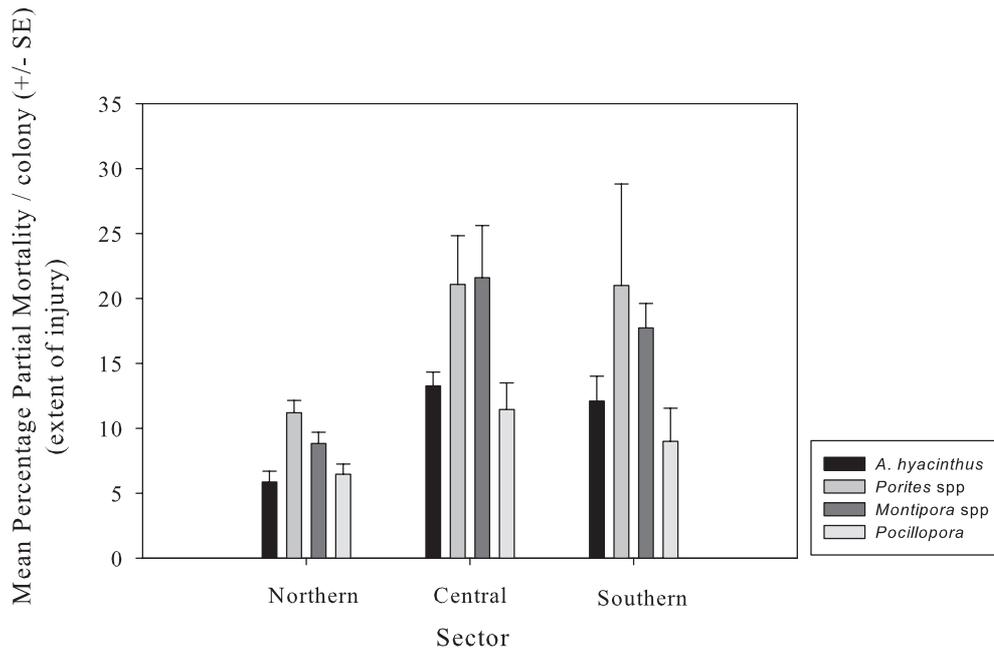
Figure 2.4 Mean (± SE) percentage partial mortality per colony (severity of partial mortality) in *Acropora hyacintus*, *Porites* massive, *Montipora* encrusting and *Pocillopora*, in the three latitudinal sectors: the northern, the central and the southern sector. Partial mortality was calculated as the proportion of dead to live tissue within the overall physical extent of each coral colony.

2.4 Discussion

Prevalence of injuries was consistently high (>80%) across all taxa and all locations, showing that background mortality is likely to occur even in the absence of any major disturbances. Accordingly, Wakeford et al. (2008) found that annual background mortality at Lizard Island on the GBR, was ca 22% for *P. damicornis,* ca 18% for *A. hyacinthus* and ca 10% for *Porites* massive. This is much lower than recorded in this study, but Wakeford et al. (2008) did not account for partial mortality. Even higher rates of annual background partial mortality were recorded in the Caribbean compared to the GBR. In Curacao in 2005 corals exhibited between 14 and 48% of tissue loss mainly due to disease (Bruckner and Bruckner 2006), while in Bonairie in 2011 extent of injury ranged between 0 and 99% for *Montastrea* complex and was around 8% for other scleractinians (Bruckner 2012a). Similarly, in Florida Keys, prevalence of recent partial mortality during periods of background, low-stress environmental conditions was still <5% for the 11 most abundant species (Lirman et al. 2013). Differences among species, studies and regions may be due to taxonomic differences in regeneration rates and abilities (Hall 1997). They may also be due to the fact that some studies considered both recent and old injury, while other studies focused mainly on recent injury (e.g., dead tissue not covered by algae) (Lirman et al. 2013; Pratchett et al. 2013). Even though recent partial mortality can be an early indicator of stressful condition (Lirman et al. 2013), old partial mortality greatly determines coral capacity to regenerate and ultimately to survive because it can limit the energy available for recent injuries (Hughes and Jackson 1985).

High rates of background partial mortality within a population may lead to a decline in population densities through time because they can result in reduced colony growth (Bak 1983; Meesters et al. 1994), reproductive output (Rinkevich and Loya 1989; Manfred 1994), and reduced colony size (Henry and Hart 2005) of individuals. Cumming (2002) showed that

the recent regime of injuries can predict colony fate even more than colony size. However, even though partial mortality can negatively affect coral community dynamics (Dikou and van Woesik 2006), it is also true that it may partially enable reef recovery by providing substrate for corals to settle, thus maintaining coral dominated reefs (Bruckner 2012a; Toh and Chou 2013).

The mean severity of background mortality varied among taxa suggesting that some species may be more resistant to routine agents and/or have better recovery potential. Massive *Porites* is a long-lived, slow growing coral, with generally low regenerative capabilities (Meesters et al. 1996, 1997a; Wesseling et al. 2001; Denis et al. 2011) so old injuries are likely to accumulate through time. Conversely, branching corals, such as *Acropora* have high regeneration capacities, rapid linear growth, and short generation time (less than 30 years) (Yap et al. 1992; Adjeroud et al. 2007). The observed taxonomic differences in prevalence of injury recorded during this study broadly correspond with differences in growth rates and relative investment in repair (Hughes 1989; Yap et al. 1992; Meesters et al. 1992, 1996, 1997a). It is possible therefore, that *Acropora* have equal or higher incidence of injuries compared to massive *Porites*, but higher rates of whole colony mortality and/ or more rapid regenerative capacity, leading to lower levels of instantaneous partial mortality.

Branching corals, such as *Acropora* spp would intuitively appear much more vulnerable to breakage and injuries than massive corals (Meesters et al. 1996). However, the agents of partial mortality are likely to vary greatly among taxa. For example, fish predation is often not visible on branching corals, while it is conspicuous on massive *Porites*, which shows the highest rates of grazing scars compared to other coral species (Bonaldo and Bellwood 2011). It appears however, that taxonomic differences in the severity of injury are most likely due to differences in persistence of injuries, or the rate of repair.

Previously published data documented marked latitudinal differences in population replenishment (highest in the northern GBR) despite similar adult abundance (measured as number of adult colonies per transect), suggesting that there are marked differences in the underlying dynamics of coral populations along the GBR (Hughes et al. 1999). More specifically, since high population replenishment did not correspond with high number of adult colonies, high rates of mortality (and/or reduced growth rates) may be responsible for differences between recruitment and adult populations. Based on these findings, it was expected background rates of partial mortality would be highest in the northern GBR and lowest in southern GBR. Conversely, background levels of partial mortality were found to be lower in the northern GBR and higher in the central and southern, with greatest variability apparent within sites or reefs, rather than among than sectors. Latitudinal gradients in key environmental variables (e.g., temperature and light) may in part influence rates of background mortality, modifying susceptibility or causing marked differences in recovery capacity. Temperature and light may affect background colony mortality by reducing or increasing regenerative abilities in colonies (Roberts et al. 1982; Titlyanov et al. 2005; Denis et al. 2011). For instance reduced temperatures have been shown to cause polyp mortality (Roberts et al. 1982) and declines in regeneration rates (Denis et al. 2011) and it may explain the higher rates of severity of partial mortality measured here in the southern GBR. Similarly, reduced light levels may cause a drop in regeneration rate due to reduced supply of photosynthetic products from zooxanthellae (Meesters et al. 1996; Titlyanov et al. 2005; Denis et al. 2011). However, in the present study, latitude seemed to play a minor role in driving severity of background partial mortality, with only two of the four coral taxa showing latitudinal variation in the extent of injury.

Spatial variation in background partial mortality can greatly affect the response (e.g., capacity for recovery) of coral populations subject to increasing acute and anthropogenic

disturbances. The drivers of the observed spatial variation are still unclear as the source of mortality was often hard to determine. Many *A. hyacinthus* and branching *Pocillopora* colonies had injuries at the edge of the colony suggesting that partial mortality was likely due to agents that were restricted to the bottom such as competition, polychaetes, or gravity causing scouring sand and moving coral fragments (Meesters et al. 1996). The reef-to-reef and site-to-site variability within sectors observed in *Porites* and *A. hyacinthus*, were likely the result of physical and biological routine agents such as fishes, echinoids, asteroids, molluscs, polychaetes and microorganisms (Brown and Howard 1985; Hutchings 1986), acting at spatial scales smaller, equal to or larger than individual reefs. These findings suggest that both disturbance regimes, and the responses of each species to routine agents are irregular, and may vary according to small differences in environmental conditions. The observed spatial variation in tissue loss supports results from other studies (Jackson 1979; Done 1988; Done et al. 1991; Bythell et al. 1993; Hughes 1994; Bythell et al. 2000; Wakeford et al. 2008) showing how coral populations are subject to a wide range of different levels of disturbances and trajectories of recovery.

The most notable result from this study, is that variation in the prevalence and severity of partial mortality is most apparent at small (e.g., within reef) rather than larger, latitudinal scales. This shows that the disturbance history is likely to be more variable among colonies at the same site, than it is among disparate populations, suggesting that there is also likely to be marked variation in resilience to acute disturbances at this local scale (Oliver 1985; Jokiel and Coles 1990; D'Croz and Mate 2004). Colonies with high prevalence or severity of injuries are likely to have a generally lower capacity to withstand, and recover from, environmental changes or acute disturbances, leading to intraspecific differences in susceptibility to future acute disturbances. Accordingly, Chapter 5 showed that adjacent colonies may vary greatly in their physiological condition due to localized differences in

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chronic disturbance regimes, though it is yet to be shown that this then leads to localized selectivity in the effects of major disturbances.

Mortality regimes of corals are expected to be strongly size-dependent, whereby the prevalence of partial mortality is expected to increase with colony size, while the probability of whole-colony mortality decreases with colony size (Highsmith et al. 1980; Hughes 1984; Hughes and Jackson 1985; Babcock 1991; Ginsburg et al. 2001; Henry and Hart 2005) because at least some portion of the colony is likely to persist in increasingly large colonies. In this study however, neither prevalence or severity of partial mortality showed a strong relationship with colony size; for branching *Pocillopora* there was a weak, though significant relationship between severity of injuries and colony size, but no such relationship existed for any other coral taxa. A lack of any relationship between size and severity of partial mortality was also observed in the Caribbean (Bruckner 2012a) where it was attributed to high variability in the extent of injury across all size classes. Moreover, differences in the repair and regenerative capacities of colonies of different sizes, may obscure such a relationship, whereby larger colonies may experience higher incidence of injury, but also have greater capacity for tissue repair (Loya 1976; Hughes and Jackson 1985; Nugues and Roberts 2003). An injury of a given size is also going to require greater proportional investment in repair for smaller colonies (Connell 1973; Henry and Hart 2005). Therefore, repeated measurements through time of observable injuries on the same colonies are needed to better investigate recovery rates and capacity of these taxa.

Background levels of partial mortality are likely to have a fundamental effect on the fitness of individual colonies and the capacity of populations to withstand, and recover from, major acute disturbances (Dikou and van Woesik 2006; Lirman et al. 2013). This is the first large-scale study of background levels of partial mortality, testing for large (latitudinal) and small (site) scale differences in the prevalence and severity of injuries across four dominant

taxa of scleractinian corals. The findings from this study provide an insight in rates of mortality along the GBR, which can be used as a guideline for global comparisons and for evaluating environmental impacts on reefs or establishing monitoring projects. Instantaneous measures of observable injuries in adult coral colonies allow quantifying mortality events that are visible, and have lasting effects on coral colonies, as well as provide baseline estimates of coral mortality (Bak and Steward-van Es 1980; Dikou and van Woesik 2006). However, since coral lesions regenerate at different rates, regeneration can stop before the injuries are fully healed or it can continue for over a year with lesions that do not initially regenerate healing later (Fisher et al. 2007). Future studies should combine instantaneous measures of observable injuries with repeated measurements over time to provide explicit estimates of the rate of injury. This research also needs to be combined with experimental studies to assess the effects of chronic injuries on colony physiological condition and on the capacity of colonies to withstand major acute disturbances.

Chapter 3. Background rates of coral mortality along Australia's Great Barrier Reef[1]

Abstract

Until now, most studies of coral mortality have focused on catastrophic mortality associated with acute disturbances (e.g., coral bleaching and outbreaks of crown-of-thorns starfish), but background rates of mortality have a critical influence on population dynamics and resilience of coral populations. This study quantified prevalence (proportion of colonies with injuries) and severity (areal extent of injuries on individual colonies) of partial mortality for four common coral taxa (massive *Porites*, encrusting *Montipora, Acropora hyacinthus* and branching *Pocillopora*) on the Great Barrier Reef, Australia. Sampling was conducted over three consecutive years during which no major acute disturbances occurred. A total of 2,276 adult colonies were surveyed each year across three latitudinal sectors, nine reefs and 27 sites along the Great Barrier Reef. The prevalence of injuries was very high (>83%) and differed significantly between taxa. *Porites* (91%) and *Montipora* (85%) showed significantly higher proportion of injured colonies compared to *Pocillopora* and *A. hyacinthus*. For *Montipora* and *Pocillopora* there was also significant temporal and spatial variation in prevalence of partial mortality. Severity of partial mortality on injured colonies ranged from 5% for *A. hyacinthus* up to 21% for *Montipora*, but this varied among years and among sites. Importantly, prevalence and severity had no bearing on the realised growth of colonies in any coral taxa, which confirm that the energy allocated to regeneration tends to be detracted from reproduction rather than growth. Understanding background levels of injury on common

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corals is important for predicting susceptibility to, and capacity to recover from, acute disturbances, which are increasing in incidence on coral reefs globally.

3.1 Introduction

Disturbances have a pervasive influence on the structure and dynamics of natural populations, communities and ecosystems (White and Pickett 1985), but the specific effects vary depending on the frequency, severity and extent of the disturbance. Disturbance ecology is largely focused on the effects on infrequent and unpredictable, but often severe and large-scale, disturbances, such as fires, floods and outbreaks of pest species (Scatena and Lugo 1995; Lugo and Scatena 1996). These acute disturbances tend to cause high levels of instantaneous mortality, especially among key habitat-forming organisms, but can also have important indirect or secondary impacts (Connell 1997), and may have strong selective pressures on community structure and ecosystem function (White and Pickett 1985). It is important to realize however, that these acute disturbances operate against a backdrop of more persistent or chronic disturbances, which can exert significant influence on demographic rates and outcomes of biological interactions (Connell et al. 1997; Death et al. 2009), thereby affecting susceptibility to, and recovery from, acute disturbances (Andres and Witman 1995).

Acute disturbances (e.g., severe storms) are increasing in frequency and intensity (Mendelsohn et al. 2012; van Hooidonk et al. 2013; Emanuel 2013), partly due to increasing effects of global climate change. Climate change is however, also having more chronic effects on organisms and environments (Hoegh-Guldberg et al. 2007; Mendelsohn et al. 2012; IPCC 2013). In temperate forests, for example, background mortality rates for many species of trees have increased in recent decades due to regional warming and reduced rainfall (van Mantgem et al. 2009). Similarly, on coral reefs, changes in water pH are

reducing growth rates of massive corals (De'ath et al. 2009), while on Jamaican reefs, chronic declines in rate of survival, recruitment and population growth had a strong bearing on persistence of coral populations following cyclone Allen (Hughes and Tanner 2000).

Coral reefs are renowned for being highly dynamic ecosystems, strongly structured by acute disturbances (Connell 1997). On Australia's Great Barrier Reef, for example, sustained declines in live coral cover over the last 27 years have been largely attributed to severe storm events and episodic outbreaks of crown-of-thorns starfish (De'ath et al. 2012). It is possible that background rates of coral mortality and injury have also increased over this period, owing to increased intensity of chronic disturbances and sustained environmental change (Wakeford et al. 2008), but this is hard to assess given the general lack of baseline information on background mortality rates.

For colonial organisms, such as reef-building corals, mortality can occur at the level of the polyps, resulting in partial mortality or injury (Hughes and Connell 1987) at the level of the colony (e.g., Madin et al. 2014). Previous studies have tended to focus exclusively on rates of whole colony mortality (Wakeford et al. 2008; Sweatman et al. 2011; Death et al. 2012). However, injuries can reduce fitness of colonies and hence affect susceptibility and resilience of corals to recover from major disturbances. Injured colonies also often allocate energy towards repairing and regenerating damaged tissues and skeleton, diverting energy from other metabolic processes and principally reproduction (Hall 1998). While background mortality rates (both partial and whole colony mortality) of reef-building corals have been shown to be significant (e.g., Done 1988; Bythell et al. 1993; Madin et al. 2014; Chapter 2), the extent to which these background mortality rates vary spatially, temporally, or taxonomically is poorly understood. Most previous studies of background mortality tend to focus only on instantaneous measures of partial mortality or injury, which may be confounded by differences in the time taken for injured colonies to regenerate (Hall 1997;

Lirman et al. 2013) or die.

The purpose of this study was to resample individual coral colonies over a 3-year period to provide explicit estimates of the rate of injuries and the fate of injured colonies. Sampling was intentionally spread across distinct latitudinal sectors, testing for large-scale variation in the prevalence and severity of injuries among common coral taxa. Marked spatial variation in the prevalence and severity of background injuries is likely to have an overarching influence on underlying life-history dynamics of scleractinian corals, potentially accounting for apparent discrepancies in the ratio of population replenishment to adult abundance (e.g., Hughes et al. 1999). Hughes et al. (1999) showed that abundance of adult corals was relatively homogeneous along the length of Australia's Great Barrier Reef, despite low levels of coral recruitment at high latitudes. If this discrepancy is attributable to latitudinal differences in the incidence of chronic disturbances, we expected to find consistently higher incidence of partial mortality at lower latitudes across all coral taxa. This is the first study to explicitly test for spatial, temporal and taxonomic differences in background rates of coral injury.

3.2 Materials and Methods

3.2.1 *Study sites*

The prevalence (the proportion of colonies with injuries) and severity (the relative extent of injuries on individual colonies) of partial mortality on adult coral colonies were measured at a hierarchy of spatial scales on Australia's Great Barrier Reef. At the largest scale, three distinct latitudinal locations (14°S, 18°S and 23°S) were considered: the northern sector in the vicinity of Lizard Island (14° 41'S, 145°129 28'E), the central sector, in vicinity of Trunk Reef (18 25'S, 146 °47'E), and the southern sector, in the vicinity of Heron Island (23° 27'S. 155° 55'E) (Figure 3.1). At each location, three reefs were sampled, and within

each reef three sites along the exposed reef crest were sampled. To avoid any effect of cross shelf variation, the study was conducted exclusively on mid-shelf reefs. At each site, three replicate 10 x 5m belt transects orientated parallel to, and positioned within 5-10m of, the reef crest were marked using stainless steel stakes. Each transect was re-surveyed every 12 months from 2011 to 2014, to capture and compare annual mortality and injury regimes within and among common coral taxa.
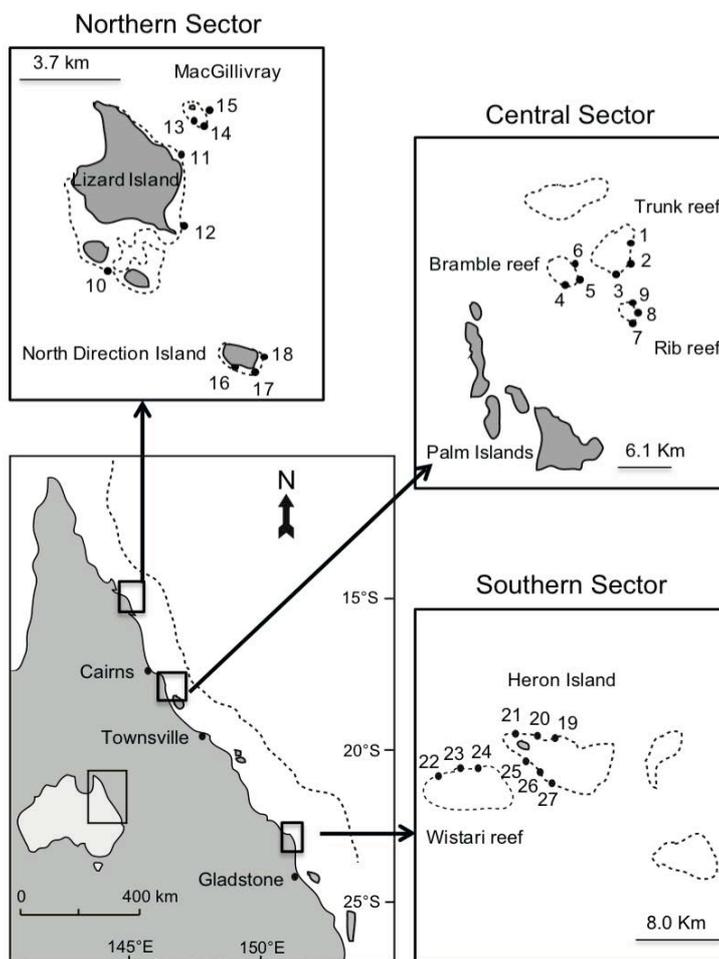
Figure 3.1 Map of the three study sectors (northern, central and southern) along the Great Barrier Reef, Australia. Within each latitudinal sector, three mid-shelf reefs, each with three sites on the exposed reef crest, were sampled once per year from 2011 to 2014. Figure adapted from Trapon et al. 2013.

3.2.2 *Partial mortality*

This study focused on four distinct coral taxa; *Acropora hyacinthus*, branching *Pocillopora*, massive *Porites* spp and encrusting *Montipora* spp., which were selected based on their contrasting morphologies and life-history strategies (Darling et al. 2012) and their high abundance at the study sites (Veron and Wallace 1984; Trapon et al. 2013). To quantify incidence and severity of partial mortality, all living adult colonies (>10cm) of each of the four study taxa within each transect (n = 200-300 per sector) were surveyed every year. Each year, every colony was photographed from the top with appropriate scale reference. Photographs were then processed using the software Image J, to precisely estimate the areal extent of each colony. The prevalence and severity of injuries were however, recorded *in situ* due to difficulties in capturing the full extent of injuries (especially on the periphery and base of colonies) based on a single photograph. The extent of injuries recorded for individual colonies ranged from zero (no apparent injuries) through to 100% (whole colony mortality). To ensure partial mortality was recorded for the exact same individuals each year, position of colonies along transects was recorded using transect coordinates. However, it is possible that for colonies that can lose fragments (e.g., branching and plating *Pocillopora* and *A. hyacinthus*), partial mortality was under-estimated.

During the study period there were no major acute disturbances such as cyclones, mass bleaching events, disease and/or crown-of-thorns starfish outbreaks (AIMS Long Term Monitoring program, Madin et al. 2014). Thus, the present study documented background mortality rates in common corals.

3.2.3 *Data analyses*

Temporal, spatial and taxonomic variation in prevalence of partial mortality (specifically, the proportion of injured colonies per transect) was analysed using a

Generalized Linear Model (GLM) with a binomial link-function, comparing among taxa, years, colony size, sectors and reefs nested within sectors. Similarly, temporal and spatial variation in severity of partial mortality (areal extent of injuries across individual colonies) was analyzed using a GLM with a binomial link-function, using a hierarchically-nested design, with transects (3 per site) nested within site, sites (3 per reef) nested within reef, and reefs (3 per sector) nested within sectors (3 sectors). Colony size and taxa were also treated as an independent variable to investigate whether partial mortality was interactively affected by coral taxa and colony size. More specifically, the fixed factors were sector (3 levels: latitudinal sectors), taxa (four coral species), colony size and years (three years), while reef (3 per sector), site (3 per reef), and transect (3 per site), were random factors. To establish the spatial scale that captured most variation in partial mortality, models with different nested structures were compared using AIC.

To investigate taxonomic differences in severity of partial mortality, variation in the extent of partial mortality was compared among coral taxa using a Chi-square test, comparing the number of colonies with different degree of partial mortality in all coral species. The categories used were extent of partial mortality (percent surface area loss) $\leq 5\%$, 5-20%, 21-50%, 51-80%, >80% during the three years. Spatial difference between transects, sites, reefs and sectors were not considered for any coral species.

To test whether partial mortality impacted on the growth rates of individual colonies, changes in the areal extent of individual colonies over the course of the study (size at year 3 – size at year 1) was related to both the prevalence (colonies with injury) and severity of partial mortality recorded in each year of the study. The significance of these relationships was tested using a regression for each taxa, with data aggregated over the full duration of the study.

3.3 Results

3.3.1 *Taxonomic differences in background partial mortality*

A total of 2,276 colonies were surveyed along the GBR to assess background rates of injury and mortality, including 862 colonies of *A. hyacinthus*, 301 colonies of massive *Porites*, 505 colonies of branching *Pocillopora* and 608 colonies of encrusitng *Montipora*. Rates of whole colony mortality, ranged from 1-8% depending on taxa, and generally reflected mortality rates reported previously (e.g., Wakeford et al. 2008; Madin et al. 2014). More specifically, 52 (out of 862) *A. hyacinthus*, 17 (out of 608) *Montipora* encrusting, 38 (out of 505) branching *Pocillopora* and 2 (out of 301) *Porites* spp experienced whole colony mortality.

Prevalence of partial mortality (the proportion of colonies with conspicuous recent or lasting injuries) were very high across all taxa, averaging 71% for *Acropora*, 59% for branching *Pocillopora*, 85% for encrusting *Montipora* and 92% for *Porites* across all sectors, reefs and sites (Figure 3.2).
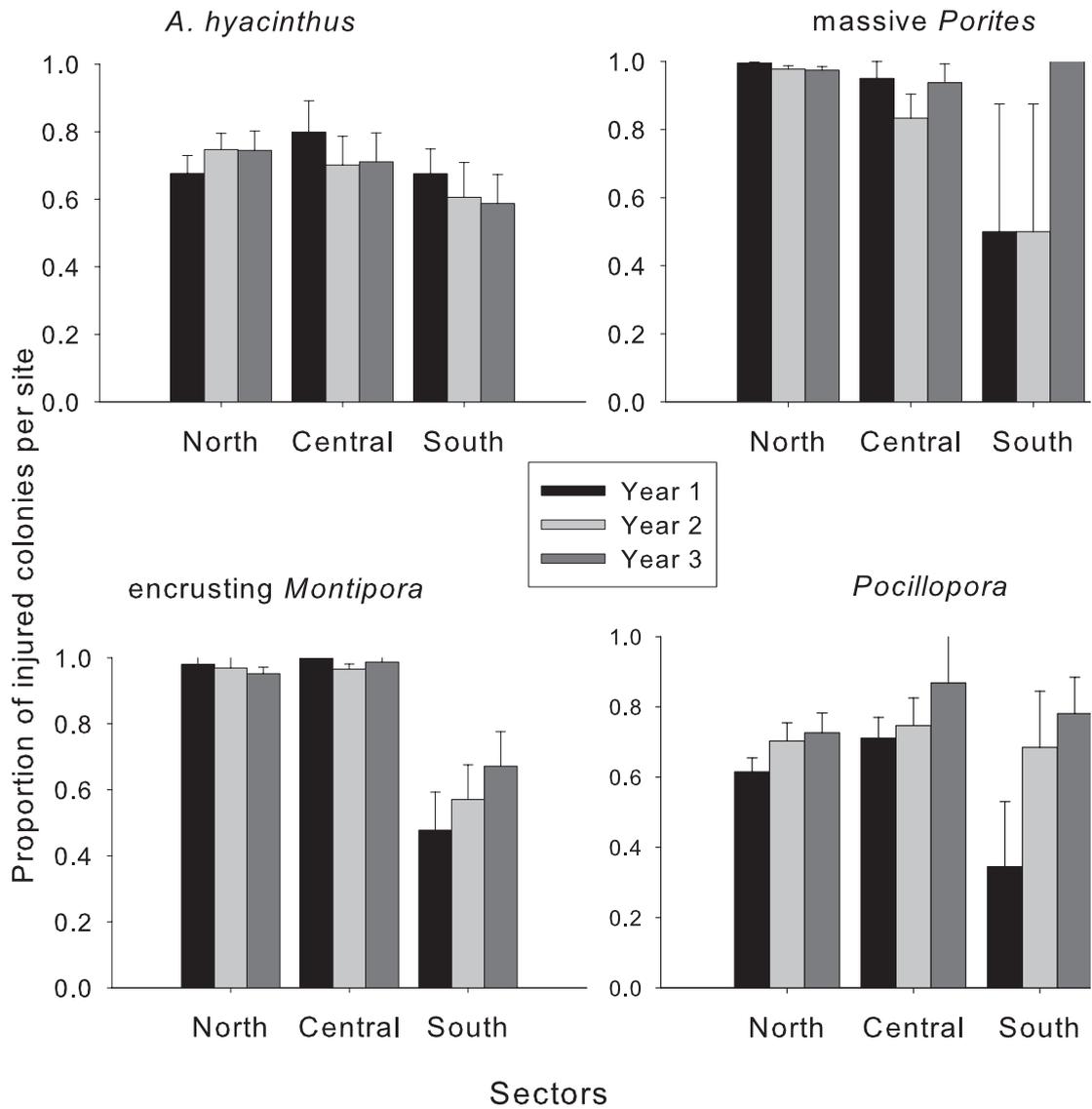
Figure 3.2 Prevalence of mortality (proportion of injured colonies) per site during the three survey years in the three latitudinal sectors: the northern, the central and the southern sector in the four coral taxa *Acropora hyacintus*, *Porites* massive, *Montipora* encrusting and *Pocillopora*.

Coral taxa showed significant differences in the distribution of degrees of partial mortality (X^2 = 69.5, df = 12, p=< 0.00001). *Porites* and *Montipora* had slightly higher proportion of colonies with partial mortality >50% of the colony area compared to *A. hyacinthus* and *Pocillopora* (Figure 3.3). However, frequency of partial mortality was high in all coral taxa (>25% of colonies showed degrees of partial mortality ranging between 50 and 80% of surface area (Figure 3.3)). When proportion of colonies with partial mortality >50% of the colony area was analysed in each taxa separately, it was high and slightly varied between latitudinal sectors during the three years (Figure 3.4), being higher in the southern than in the central and northern GBR for all coral taxa (Figure 3.4).

All the injuries were covered in algae, with some injuries being relatively old with corallite structures gone or covered by algae and/or other organisms. White exposed skeleton indicating recent injury (occurred few days prior survey) were only noticed in some massive *Porites* due to grazing marks. During the three years some injuries showed reduced areal extent indicating signs of regeneration, while the size of most injuries did not vary with time. Interestingly, diseases were only recorded for a few *A. hyacinthus* colonies in the Central GBR in the first year and three affected colonies died during the study period.
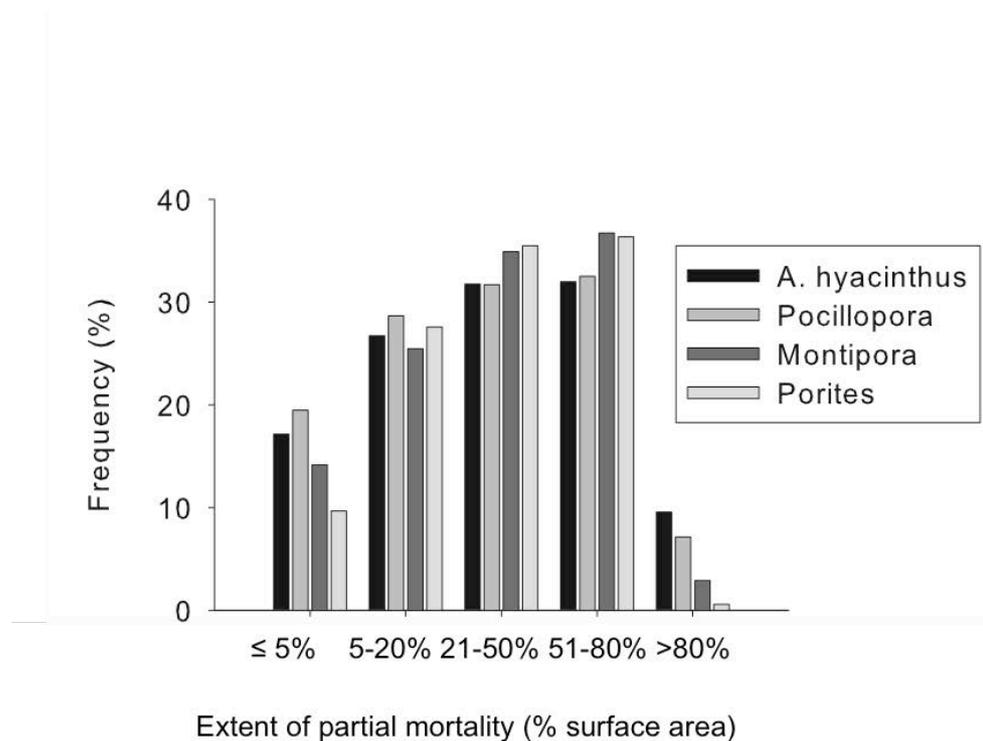
Figure 3.3 Frequency distribution for the degrees of mortality (percent surface area loss) during the three years pooled among taxa.

3.3.2 *Spatial and temporal variation in prevalence and severity of partial mortality*

Prevalence of partial mortality was consistently high across all years, with no significant variation among years, except for *Pocillopora* spp, which showed a slight increase in proportion of new colonies that were injured in the third year, and only in the southern sector (Figure 3.4). The prevalence of injury was also very consistent among sectors and reefs, while most of the variation occurred within reefs rather than between sectors and reefs (Table 3.1). Prevalence of partial mortality was significantly affected by taxa (10% Table 3.1), with *Montipor*a and *Porites* showing significantly higher prevalence of partial mortality than *Pocillopora* and *A. hyacinthus* (Table 3.1; Figure 3.4). Conversely, colony size did not have an effect on the proportion of injured colonies (Table 3.1).

Table 3.1 Results of Generalised Linear Model (GLM) with a binomial link-function to test for temporal and spatial variation in prevalence of injury (proportion of injured colonies per site) from 2011 to 2014. Percentage of variation in prevalence of injury with time associated with particular spatial scales is also included. Model building results: lowest AIC= 939.7, L ratio Chi ^{2} = 1023.1, p=0.000.

	df	Wald stat	p	var (%)
Sector	1	0.38	0.53	8.8
Reef (Sector)	1	0.09	0.92	21
Year	2	0.03	0.98	1
Taxa	2	0.02	0.05	10
Size	1	0.04	0.88	
Error				59.2

Severity of partial mortality varied mainly among reefs (Table 3.2), however the greatest variation was observed within transects (96.6% Table 3.2). Colony size did not have any effect on severity of injury, while coral taxa affected the extent of partial mortality (Table3.2). However, the variation explained by coral taxa was still very low (3.4% Table3.2). For encrusting *Montipora,* severity of injury was significantly lower (9.0%) in the northern sector compared to the other two sectors (24% and 16%) and rising up to 20% during the three years (Figure 3.4). Severity of partial mortality varied through time only in *Pocillopora* (Figure 3.4), however *Porites* showed an increase in severity of injury from 5.4% to 20% from the second year to the third year in the southern sector (Figure 3.4).

Table 3.2 Results of a GLM with a binomial link-function to test for temporal and spatial variation in severity of injury (specifically, the proportional extent of dead versus living components of each colony) for each coral taxa from 2011 to 2014 at all spatial scales. Model building results: lowest AIC= 235.0, L ratio Chi ^{2}=598, p=0.000.

	df	Wald stat	p	var (%)
Sector	1	0.18	0.14	
Reef (Sector)	1	9.49	<0.001	
Site (Reef)	1	7.56	0.06	
Transect (Site)	2	5.31	0.14	
Year	3	8.31	0.05	
Taxa	2	29.1	<0.001	3.4
Size	2	9.54	0.22	
Error				96.6
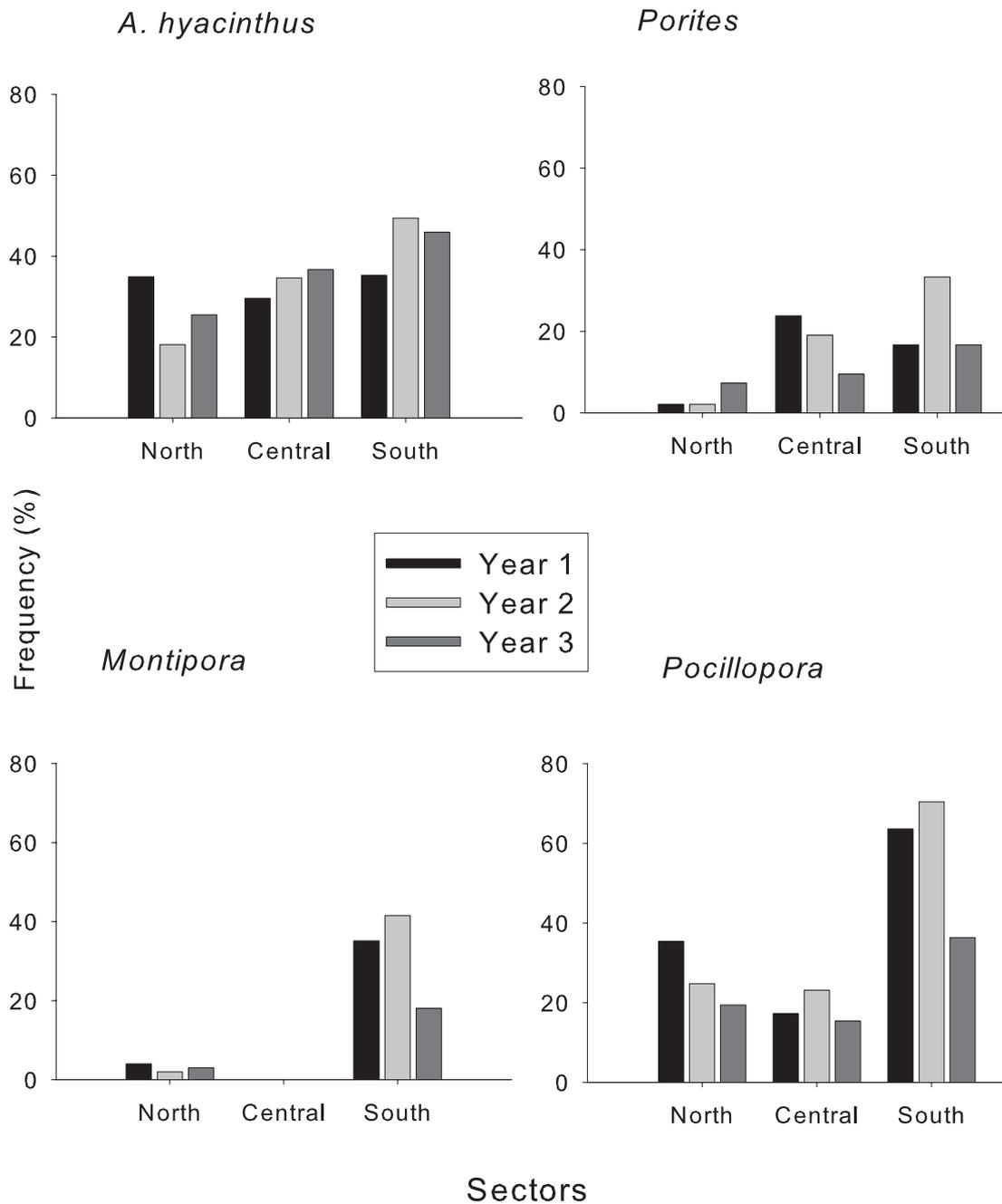
Figure 3.4 Frequency distribution for the degrees of mortality (colonies with partial mortality >50% of the colony area) in *Acropora hyacintus*, *Porites* massive, *Montipora* encrusting and *Pocillopora* branching, in the three latitudinal sectors: the northern, the central and the southern sector from 2011 to 2014.

3.3.3 *Effect of prevalence and severity of partial mortality on colony growth*

Colony growth (expressed as changes in colony surface area) during the three years averaged 47.9 cm^2 ($\pm$ 1.5) in *A. hyacinthus*, 3.36 cm^2 ($\pm$ 45.6), 13.7 cm^2 ($\pm$ 2.0) and 0.5 cm^2 ($\pm$4.0) in *Montipora*, *Pocillopora* and *Porites* respectively. Proportion of injured colonies per site (prevalence of injury) was not a good predictor of colony growth (measured as the difference in size between the last and the first year) in any coral taxa, *A. hyacinthus* was the only taxa showing an increase in size through time.

Similarly, severity of partial mortality did not have an effect on colony growth in any coral taxa, the r^2 was extremely low and never significant suggesting that high severity of injury did not constrain the change in size of individual colonies (*A. hyacinthus* r^2=0.01, n= 392 p=0.5; *Montipora* r^2=0.01, n=172 p=0.8; *Pocillopora* r^2=0.01, n=254 p=0.5; *Porites* r^2=0.01, n=215 p=0.5).

3.4 Discussion

This study documented high prevalence and extent of partial mortality across four dominant coral taxa on Australia's Great Barrier Reef. While rates of whole colony mortality ranged between 1 and 8% per annum, the majority of colonies had the appearance of recent, and sometimes very severe injuries. The prevalence of injuries varied by genera, but was particularly high for *Porites* and *Montipora* (91% and 85%, respectively). The prevalence of injuries recorded during this study is very high compared to other reported values. For example, in the Indian Ocean prevalence of partial mortality for *Acropora cytherea* was 27.5% (Pratchett et al. 2013), while in the Florida Keys among the most abundant corals (e.g., *Agaricia* spp, *Diploria strigosa*, *Montastrea cavernosa*) prevalence of injuries was reported to be generally <5% (Lirman et al. 2013). This study documented higher proportion of injured colonies compared to other published studies likely because both recent and old

injuries were considered, while other studies focused mainly on recent injuries (e.g., dead tissue not covered by algae) (Lirman et al. 2013; Pratchett et al. 2013). Even though recent partial mortality may be a useful indicator of changing conditions (e.g., Lirman et al. 2013), our aggregated estimates of partial mortality provide a much more ecological relevant measure of injury regimes (Hughes and Jackson 1985), affecting the fitness and potentially the fate of colonies.

Consistently high background levels of coral injury have the capacity to significantly affect fitness of individual colonies and hence reduce recovery capacity of populations between major acute disturbances (Johnson and Preece 1992; Langmead and Sheppard 2004; Habeeb et al. 2007; Wakeford et al. 2008; Bruckner and Hill 2009; Fung et al. 2011). Recovery rates following bleaching are likely to be lower in injured colonies compared to uninjured ones (Meesters and Bak 1994 Baird and Marshall 2002; Fine et al. 2002). However, recovery rates largely depend upon current level of lipid reserves (Anthony et al. 2009). High amount of lipids in coral tissues is vital for survival (Bachok et al. 2006), because corals tend to consume their lipid reserves when maintenance costs exceed carbon acquisition such as during a bleaching event (Anthony et al. 2009).

The few studies that have documented natural rates of injuries (Hughes and Jackson 1985; Hall 1998; Cumming 2002; Bruckner 2012a; Lirman et al. 2013; Pisapia and Pratchett 2014 – Chapter 2), are based on static measures involving a single assessment, often at small spatial scales. Chapter 2 did investigate partial mortality over a large spatial scale, but is still based on a single set of instantaneous measures of injury. The current study is differentiated from Chapter 2 and most previous studies in that it specifically tests for temporal variation in the extent of injuries, by monitoring the same coral colonies through time (over 3 years). Even though it is critical to investigate the natural occurrence of tissue loss, the key parameter that has not been investigated yet, and will ultimately determine recovery capacity

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of corals, is the change in rates of tissue loss.

Importantly, this study documented taxonomic differences in prevalence of partial mortality. Massive and encrusting corals showed higher prevalence (>80%) and frequency of partial mortality compared to plate and branching corals. The taxonomic differences in rates of partial mortality broadly correspond with differences in growth rates and investment in repair (but may also be due to observational bias). Branching corals, such as *Acropora* and *Pocillopora* have high regeneration capacities, rapid linear growth, high rates of recruitment, high rate of mortality and short generation time (less than 30 years), all resulting in highly dynamic populations with rapid turnover (Yap et al. 1992; Adjeroud et al. 2007). Conversely, massive *Porites* invest less energy in regeneration, which is generally slow (Denis et al. 2011), show slow growth rates, large colony size, low whole colony mortality, low rates of recruitment, and long life duration, all resulting in slow population turnover (Bak and Engel 1979; Adjeroud et al. 2007).

Coral species differ in their vulnerability to different routine agents (e.g., branching species are more vulnerable to breakage, while massive and encrusting species are more prone to overgrowth by algae (Hughes 1989)) and consequently have different amounts and types of injuries (e.g. Meesters et al. 1996, 1997a) as well as different regeneration abilities and rates (Meesters et al. 1992; Hall 1997). *Acropora* spp are more vulnerable to breakage and injuries than massive corals and consequently often show the greatest severity of partial mortality, much higher than massive species (Meesters et al. 1996). For instance, *Acropora cervicornis* suffers chronic tissue loss from damselfish grazing in the Caribbean. However, branching corals also show greater ability to heal (Meesters et al. 1996; Hall 1997), which can result in lower levels of observable tissue loss. Conversely, massive corals have limited capacity for lesion regeneration (Meesters et al. 1994, 1997a; Denis et al. 2011), so injuries are more likely to be preserved for longer term (Meesters et al. 1996; Denis et al. 2011).

Massive corals with high prevalence of partial mortality may be in a chronic state of regeneration from past injuries, and because regeneration requires energy usually allocated to other vital processes such as growth and reproduction, and can reduce resilience and recovery rates, background mortality is likely to play a bigger role in the population dynamics of massive corals compared to branching corals.

Previously published data documented marked latitudinal differences in population replenishment (highest in the northern GBR) despite similarities of adult abundance (Hughes et al. 1999), suggesting that there must be marked differences in the underlying dynamics of coral populations along the GBR. If so, it would be expected that background rates of mortality would be highest in the northern GBR and lowest in southern GBR. However, this study documented consistency in prevalence and severity of partial mortality between sectors in all coral taxa. Large-scale trends were only observed in *Montipora* with lower prevalence of partial mortality in the southern sector. However, in all taxa the large-scale (sector) trends were obscured by noise at the smallest scales, suggesting that there was greater variation in the severity of injuries among adjacent colonies within the same reef habitat than among colonies in different latitudinal sectors. The lack of conformity between recruitment and adult abundance highlighted by Hughes et al. (1999) may likely be due to differences in growth and mortality of newly settled corals or latitudinal variation in adult growth rather than differences in rates of tissue loss.

Specific drivers of the observed small-scale (reef, site and transect) differences in the prevalence and severity of coral injuries remain unclear, as the source of mortality was rarely apparent. Even though it is critical to identify the direct links between the stress and response, this is almost impossible in complex ecosystems like coral reefs (Lirman et al. 2013). In corals, partial mortality is a general stress response and to attribute the cause of injury to a specific agent, the sampling frequency and intensity needs to be very high and would need to

be integrated with controlled laboratory studies and/or the disturbances event must be clearly identifiable such a grazing parrotfish bites. However, some colonies especially *A. hyacinthus* and massive *Porites,* also showed injuries completely surrounded by living tissue. This sort of tissue damage is harder to pin down, but may be due to senescence (Rinkevich and Loya 1989), fish bites, past incidences of disease, sedimentation, and/or direct damage, such as that caused by divers or anchors (Meesters et al. 1996).

High prevalence and severity of partial mortality can constrain the change in size of individual colonies. Following injury, limited resources within a colony are often re-directed into regeneration, and this change in energy allocation may limit resources available for other demographic processes such as growth (Meesters et al. 1997a). The patterns of this resource allocation will depend upon the degree of physiological integration (Bazzaz et al. 1987). Growth is often reduced in regenerating corals (Bak 1983; Liddle and Kay 1987; Guzman et al. 1994; Meesters et al. 1994; Lirman 2000). However, sometimes growth rates may be faster in injured colonies compared to the uninjured ones (Loya 1976). In the present study prevalence and severity of partial mortality had no bearing on the realised growth of colonies in any coral taxa. This is an important finding and largely confirms that the energy allocated to regeneration tends to be detracted from reproduction rather than growth (Hall 1998). Hall (1998) documented a marked effect of partial mortality on reproduction but not on colony survival and growth inferring a clear trade-off between reproduction and regeneration. Following injury, growth is more likely to be maintained but at the cost of future reproduction.

This study documented high prevalence and severity of partial mortality in four dominant coral taxa on the GBR. Prevalence and severity of background mortality have significant ramifications for coral capacity to cope with increasing acute disturbances, such as climate-induced coral bleaching. Colonies with low partial mortality and hence in high

physiological condition may have a better potential to withstand and recover from environmental changes (i.e. are more resilient) than conspecifics with high partial mortality and hence in poor condition, and will therefore have a disproportionate role in population recovery. Background mortality rates have rapidly increased in temperate forests (van Mantgem et al. 2009), and if this is also happening on coral reefs, the capacity for recovery of these ecosystems will likely be dramatically reduced.

Chapter 4. Prevalence and severity of coral injuries in Lhaviyani Atoll, Maldives versus northern Great Barrier Reef, Australia[2]

Abstract

Corals are subject to a range of chronic, often small-scale disturbances that can cause high rates of background mortality even in the absence of (or in between) major acute disturbances. While small-scale (e.g., between adjacent colonies) variation in the prevalence of partial mortality has been explored at several locations, large-scale variation (e.g., between geographically disparate locations) has never been tested. This study compared the prevalence and severity of partial mortality for four widespread and dominant coral taxa (massive Porites, encrusting *Montipora*, *Acropora hyacinthus* and branching *Pocillopora*) among multiple reefs and sites at Lhaviyani Atoll, Maldives and on the northern Great Barrier Reef, Australia. Prevalence of coral partial mortality was consistently higher in Lhaviyani Atoll (95% in *Porites*, 80% in *Acropora hyacinthus*) than on the Great Barrier Reef (93% of colonies in *Porites*, 65% in *Acropora hyacinthus*). The severity of partial mortality was higher for *Montipora* and *Porites* (13.3% and 12.2%, respectively) at Lhaviyani Atoll than on the Great Barrier Reef (10.7% in *Montipora* and 9.6% in *Porites*). However, marked differences in severity of partial mortality were apparent at the very smallest spatial scale (e.g., among colonies located on the same transect, or within the same habitat). Spatial variation in prevalence and severity of partial mortality has ramifications for coral resilience because colonies with high prevalence and severity of partial mortality may be in poor physiological condition and have a limited capacity to withstand and recover from

increasing acute disturbances, such as climate-induced bleaching. Such information is important for understanding coral responses to background chronic stressors, and in particular for predicting their capacity to recover between subsequent major disturbances.

4.1 Introduction

While coral reef scientists are heavily focused on the effects of distinct disturbance events on coral cover and composition (e.g., cyclones, outbreaks of crown-of-thorns starfish, and climate-induced bleaching; De'ath et al. 2012), background mortality rates are relatively less well studied. However, these background rates are critically important if we are to understand the structure and dynamics of coral populations and communities (Madin et al. 2014). Corals are subject to a range of chronic, often small-scale disturbances (e.g., predation, disease, competition, and sedimentation) that can cause high rates of partial and/or whole colony mortality (Stimson 1985; Hughes 1989; Connell 1997; Wakeford et al. 2008; Pratchett et al. 2013; Madin et al. 2014). These disturbances often have an overriding influence on coral cover and composition, as well as affecting the individual, population and community resilience (Wakeford et al. 2008). Normal background rates of whole colony mortality have in some geographical areas been estimated to be as high as 19% per year (Bak and Luckhurst 1980). Yet they have also been shown to vary greatly within and among specific coral species (Bak and Luckhurst 1980; Harriot 1985; Bythell et al. 1993; Wakeford et al. 2008; Pratchett et al. 2013; Madin et al. 2014). Even for those colonies that do not experience whole colony mortality, a very large proportion of colonies (close to 100% in some instances Chapter 2) exhibit evidence of tissue loss in the form of partial mortality. The associated energy required in terms of tissue repair, will undoubtedly detract energy away from other important functions such as general maintenance, growth, and/or reproduction (Bak 1983; Meesters et al. 1994). This would therefore, overall reduce colony fitness.

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Furthermore, colony fitness is often considered to be strongly size-dependent in scleractinian corals. Even though Chapter 3 showed that larger colonies do not necessarily have more partial mortality, generally large colonies have greater regenerative abilities (Hughes and Jackson 1985; Bythell et al. 1993), faster growth (Hughes and Jackson 1980) and higher fecundity (Harrison and Wallace 1990; Hall and Hughes 1996). Therefore ultimately, larger colonies should be less likely to experience whole colony mortality (Hughes and Jackson 1985; Henry and Hart 2005). However, interestingly, larger colonies appear to have higher incidences of partial mortality (Hughes and Jackson 1980, 1985), this is thought to be attributable to increasing exposure to agents of mortality, as well as accumulation of injuries over time.

Aside from size, variation in susceptibility to, and persistence of, partial mortality varies among corals with differing morphology (Woodley et al. 1981; Hughes 1989; Glynn 1990; Chadwick-Furman 1995). For instance, *Acropora* corals tend to be much more susceptible to injuries compared to massive *Porites*, but also have higher regenerative capacity, leading to lower prevalence of partial mortality (Chapter 2). Furthermore, different coral species differ greatly in their allocation of resources between regeneration and other demographic processes (Bak et al. 1977; Bak and Steward-Van Es 1980; Meesters et al. 1994). Prevalence of partial mortality may therefore, depend more on relative investment in repair rather than overall susceptibility to aspects of partial mortality (Hughes 1989; Meesters et al. 1992; Yap et al. 1992; Meesters et al. 1996; Meesters et al 1997a; Hall 1997).

The extent of such chronic disturbances has been shown to vary spatially over millimetres, centimetres and metres (e.g., predation and bioerosion) to hundreds and thousands of kilometres (e.g., sedimentation and disease). Therefore, the prevalence of partial mortality (measured based on instantaneous estimates of the proportion of colonies that have conspicuous tissue loss), vary both at the large scales (locations separated by 500km along

the GBR) and small scale (between adjacent colonies) (Chapter 2). Despite this, the majority of comparative studies focusing on coral recovery and/or resilience, typically assume there is no background mortality. Even those that do take this into account (Done 1988; Wakeford et al. 2008), assume equal levels of background mortality within and among all reefs. This may have strong repercussions on data analysis of such studies and future predictions of the state of reef health in changing climates.

The purpose of this study was to quantify prevalence and severity of background mortality for four widespread and dominant coral taxa (*Acropora hyacinthus*, branching *Pocillopora*, massive *Porites* spp and encrusting *Montipora*) over two wide geographical locations (the Maldives in the Indian Ocean and the northern Great Barrier Reef (GBR), Australia). More specifically, we tested whether geographic differences in prevalence and severity of partial mortality (tissue loss) are greater than variation recorded among nearby reefs or among nearby colonies.

The recent disturbance history of Maldivian reefs is very different to that of the northern GBR, though there is considerable overlap in the coral fauna (Veron 1986; Bellwood and Hughes 2001). Notably, Maldivian reefs were severely impacted by the 1998 mass-bleaching event (Ateweberhan et al. 2011), and there has been slow recovery (McClanahan et al. 2014), potentially attributable to high rates of background mortality. Conversely, reefs in the northern GBR have been relatively unaffected by recent bleaching events (De'ath et al. 2012), and coral cover tends to recover quickly in the aftermath of disturbances, which are mostly associated with outbreaks of crown-of-thorns starfish (Wakeford et al. 2008). We hence, hypothesized that there would be significant differences between geographic locations with higher background partial mortality in the Maldives.

4.2 Material and Methods

4.2.1 *Study sites*

This study was conducted over two distinct geographic locations: the northern Great Barrier Reef (GBR), Australia, and Lhaviyani Atoll, in the Maldives. The recent disturbance history of Maldivian reefs is very different to that of the northern GBR, though the coral fauna overlaps substantially (Veron 1986; Bellwood and Hughes 2001). Within each location, sampling was conducted at three individual reefs separated by at least 1.5 km; Lizard Island 14°40'S, 145°27'E, Mac Gillivray Reef 14°39' S, 145°29'E and North Direction 14°44'S, 145°30'E, on the GBR and at Vavvaru 5°25'N, 73°21'E, Komandoo 5°29'N, 73°25'E and Veyvha 5°25'N, 73°21'E, islands in Lhaviyani Atoll. Within each reef, three randomly selected sites were sampled. For each site, three replicate (10 x 5m) belt transects, parallel to depth contours, were laid on the reef crest (1-2m depth on the GBR and 3-5m depth in Lhaviyani Atoll), with a minimum of 3 m separating consecutive transects. Surveys were carried out in March 2014 on the northern GBR and in April 2014 in Maldives.

Locations were sampled opportunistically. However, the surveyed reefs are broadly reflective of the locations more generally. On the GBR, Chapter 2 documented very limited large-scale variation in prevalence and severity of partial mortality along the length of the GBR spatial, suggesting that background mortality in the northern latitudinal sector is well representative of the whole GBR.

4.2.2 *Survey of partial mortality*

This study investigated tissue loss (partial mortality) and assessed both the prevalence (proportion of colonies with conspicuous evidence of tissue loss) and severity (the proportional area of tissue loss recorded for any given colony) of observable tissue loss (partial mortality) for four distinct coral taxa: *Acropora hyacinthus*, branching *Pocillopora*

spp., massive *Porites* spp and encrusting *Montipora*. These coral taxa are not only among the most common in each of the two study locations (Veron and Wallace 1984), but are very widespread, and represent highly contrasting morphologies and life-history strategies (Darling et al. 2012).

To quantify the prevalence and severity of partial mortality, each of the four coral taxa were surveyed along fixed area transects (total of 150m^2 per site), such that variation in the actual number of the colonies sampled corresponded with their local abundance. All relevant colonies within the sample area were visually inspected in situ to determine the severity of tissue loss (ranging from 0 to <100%, and estimated to the nearest 5%). These were then photographed to later quantify colony size. Each colony was photographed from the top with appropriate scale references, and all images were processed using the software Image J (http://imagej.nih.gov/ij). This allowed quantification of the planar areal extent as a measure of colony size, following Chapter 2.

4.2.3 *Data analysis*

Variation in the severity of partial mortality (the proportional extent of dead versus living surface area of each colony) was analysed using a hierarchically nested Generalised Linear Model (GLM). The GLM tested for differences with location (fixed factor, 2 levels: Lhaviyani Atoll and northern GBR), reef (random factor, 3 per location), site (random factor, 3 per reef) and transect (random factor, 3 per site). To avoid inherent interspecific biases in prevalence of coral injuries (discussed previously), separate analyses were run for each of the four coral taxa (*A. hyacinthus*, *Pocillopora* spp., massive *Porites* spp and encrusting *Montipora*). Similarly, spatial variation in prevalence of coral injuries (estimated as the proportion of colonies per transect that exhibited >0% tissue loss) was analyzed using a hierarchically nested GLM, comparing locations, reef and site. All data were arcsine-square root transformed prior to analysis. Due to the unbalanced design, the F-statistic and p values

resulting from the Type III sum of square have been reported. Tukey's HSD post hoc tests were used to establish key differences among group means, and variance components calculated to assess whether variation in prevalence and/or severity increases with respect to scale. Since mortality is size specific, the effect of colony size (measured as colony surface area from photos in Image J) on prevalence and severity of partial mortality was investigated with two logical regressions for each species. This was conducted using colony size as the predictor variable and response a 0 or 1 depending on if the colony was injured or not. For severity of partial mortality, the response was the area injured while the predictor was total colony size.

All tests were performed with STATISTICA 7.0 (StatSoft) software.

4.3 Results

4.3.1 *Prevalence of coral tissue loss (partial mortality)*

A total of 1,761 colonies from the four coral taxa were surveyed in the northern GBR and in Lhaviyani Atoll, of which 1,419 (81%) had conspicuous evidence of tissue loss. The prevalence of partial mortality varied among coral taxa, ranging from 62% in *Pocillopora* up to 96% for massive *Porites* and 98% for encrusting *Montipora* (Figure 4.1, Table 4.1).

Within taxa, there was significant spatial variation in the prevalence of coral injuries for all but encrusting *Montipora* (Table 4.2), with much higher prevalence of tissue loss recorded on the northern GBR (Tukey test <0.005, Table 4.2). *A. hyacinthus*, *Pocillopora* and *Porites* showed a significantly higher (Tukey test <0.005) proportion of injured colonies (between 21 and 53%, Table 4.2) on the northern GBR compared to Lhaviyani Atoll. Interestingly only one of the four coral taxa, *A. hyacinthus*, exhibited a significant variation in the prevalence of partial mortality among reefs within locations (Tukey test <0.005, Table 4.2).

Table 4.1 The number of injured colonies as a fraction of the total number of colonies surveyed at each site, within each reef and geographic location for four coral taxa.

Region	Reef	Site	*Acropora hyacinthus*	massive *Porites*	encrusting *Montipora*	branching *Pocillopora*
GBR	Lizard Island	1	9/16	16/16	56/56	10/13
GBR	Lizard Island	2	44/68	15/15	13/13	15/23
GBR	Lizard Island	3	0/0	41/43	14/14	12/24
GBR	Mac	1	9/14	28/28	6/6	21/38
GBR	Mac	2	34/50	12/12	9/9	3/4
GBR	Mac	3	30/60	17/17	37/37	20/34
GBR	North Direction	1	13/20	19/19	26/26	34/44
GBR	North Direction	2	16/19	32/32	40/42	35/62
GBR	North Direction	3	39/51	28/28	7/8	59/87
Tot GBR			**194/298**	**208/210**	**208/211**	**209/329**
Maldives	Veyvah	1	0/0	28/33	20/20	7/11
Maldives	Veyvah	2	0/0	21/22	17/17	8/9
Maldives	Veyvah	3	0/5	23/23	6/6	7/15
Maldives	Vavvaru	1	0/0	35/39	12/15	6/17
Maldives	Vavvaru	2	0/0	36/36	4/4	22/28
Maldives	Vavvaru	3	22/24	19/20	6/6	15/22
Maldives	Komandoo	1	35/45	44/44	6/6	11/17
Maldives	Komandoo	2	51/62	20/22	12/12	3/12
Maldives	Komandoo		26/29	44/45	22/22	12/22
Tot Maldives			**134/168**	**270/284**	**105/108**	**91/153**
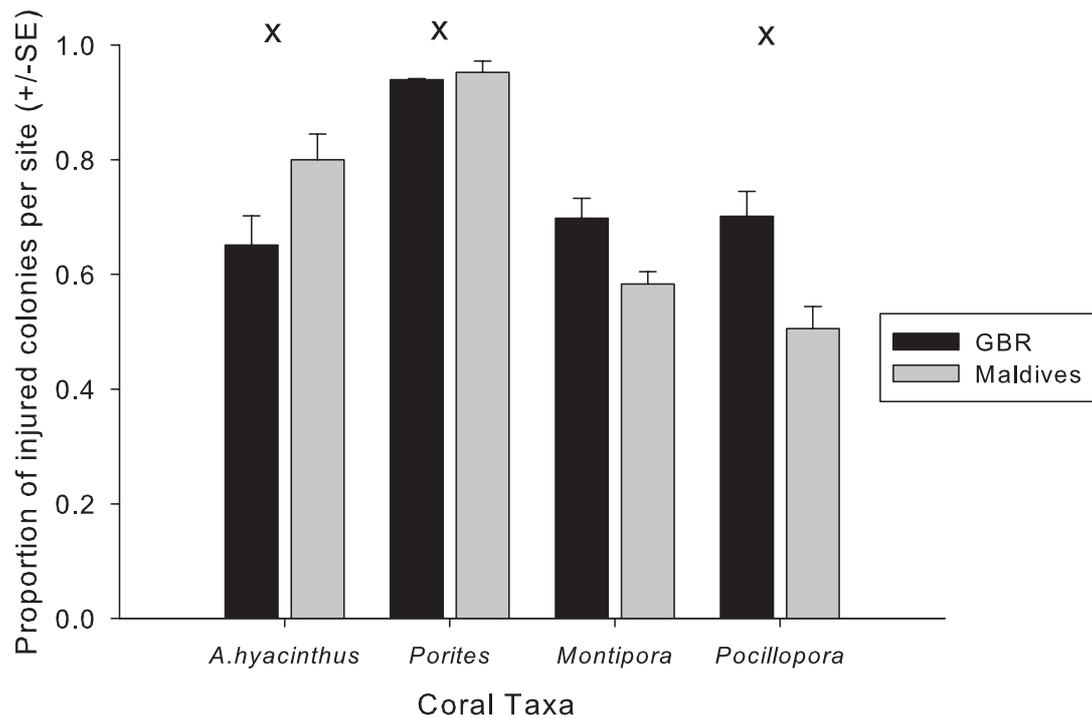
Figure 4.1 Proportion of injured colonies per site in *Acropora hyacinthus*, massive *Porites*, encrusting *Montipor*a and branching *Pocillopora*, in the two geographic locations: Lhaviyani Atoll, Maldives versus northern Great Barrier Reef, Australia.

The "x" indicates the statistical significant comparisons.

In both the northern GBR and Lhaviyani Atoll, all areas with dead tissue were covered in algae and/or other colonizing organisms, and the corallite structure was partly eroded, indicating that partial mortality was more than several days to months old. The main exception to this pattern was in the Maldives where all the colonies of massive *Porites* showed clear white grazing marks, likely caused by parrotfish grazing. Interestingly, diseases were not recorded for any coral taxa in any location at the time of sampling.

Table 4.2 Results of hierarchically-nested ANOVAs to test for spatial variation in prevalence of injury (proportion of injured colonies per site) for each coral taxa.

	SS	df	MS	F	p	var (%)
A. hyacinthus						
Location	0	1	0	99.9	<0.001	52.5
Reef (Location)	0	2	0	74.6	<0.001	44.9
Error	0	7	0			2.2
Porites spp						
Location	0	1	0	10.4	0.007	53.2
Reef (Location)	0	2	0	0.15	0.86	0.8
Error	0	12	0			46
Montipora encrusting						
Location	0	1	0	0	0.95	0.0
Reef (Location)	0	2	0	0.14	0.87	5.9
Error	0	12	0	1.19		94.1
Pocillopora spp						
Location	0	1	0	8.94	0.01	30.5
Reef (Location)	0	2	0	2.29	0.14	25.4
Error	0	12	0			44.1

4.3.2 *Severity of coral mortality*

For the 1,419 colonies that exhibited some level of tissue loss, the proportion of the total colony area that was affected ranged between 2 to 80%, with an overall mean ($\pm$SE) of 6.83 $\pm$ 0.6. Within taxa, mean severity of partial mortality varied at both larger (location) and smaller (site, transect) spatial scales (Table 4.3). Massive *Porites* showed between region differences in extent of injury with higher severity in Lhaviyani Atoll (12.2%) compared to the northern GBR (9.6%) (Tukey <0.05) (Figure 4.2). However, for *Porites* extent of injury varied more within location than between locations (Table 4.3). Together with *A. hyacinthus*, and *Pocillopora, Porites* showed the greatest spatial variation at the smallest scale (among adjacent colonies) (<69.7%) (Table 4.3). Conversely, in encrusting *Montipora* even though extent of tissue loss varied significantly among sites, most of the variation was explained by the interaction between geographic locations, reefs, sites and transects (46%) (Table 4.3).

Table 4.3 Results of hierarchically-nested ANOVAs to test for spatial variation in severity of partial mortality (specifically, the proportional extent of dead versus living components of each colony) in each coral taxon across spatial scales.

	SS	df	MS	F	p	var (%)
A. hyacinthus						
Location	0.02	1	0.02	0.47	0.48	0.3
Reef (Location)	0.31	4	0.07	1.8	0.12	3.3
Site (Location *Reef)	0.22	7	0.03	0.74	0.63	
Transect (Location *Reef*Site)	1.04	23	0.04	1.03	0.42	22
Error	8.9	204	0.04			71.7
Porites spp						
Location	0.19	1	0.19	6.39	0.01	5.4
Reef (Location)	0.07	4	0.01	0.65	0.62	2.6
Site (Location *Reef)	0.36	12	0.03	1.02	0.42	1.3
Transect (Location *Reef*Site)	1.23	34	0.03	1.21	0.21	21
Error	7.32	245	0.02			69.7
Montipora encrusting						
Location	0	1	0	0.01	0.91	
Reef (Location)	0.23	4	0.05	2.26	0.06	
Site (Location *Reef)	1.49	12	0.12	4.82	<0.001	4.4
Transect (Location *Reef*Site)	0.59	29	0.02	0.79	0.75	35.4
Error	2.6	101	0.02			29.1
Pocillopora						
Location	0.15	1	0.15	3.47	0.06	
Reef (Location)	0.72	4	0.18	3.91	0.004	
Site (Location *Reef)	0.68	12	0.05	1.23	0.26	1.5
Transect (Location *Reef*Site)	1.39	35	0.03	0.86	0.68	1.7
Error	11.68	254	0.04			61.6
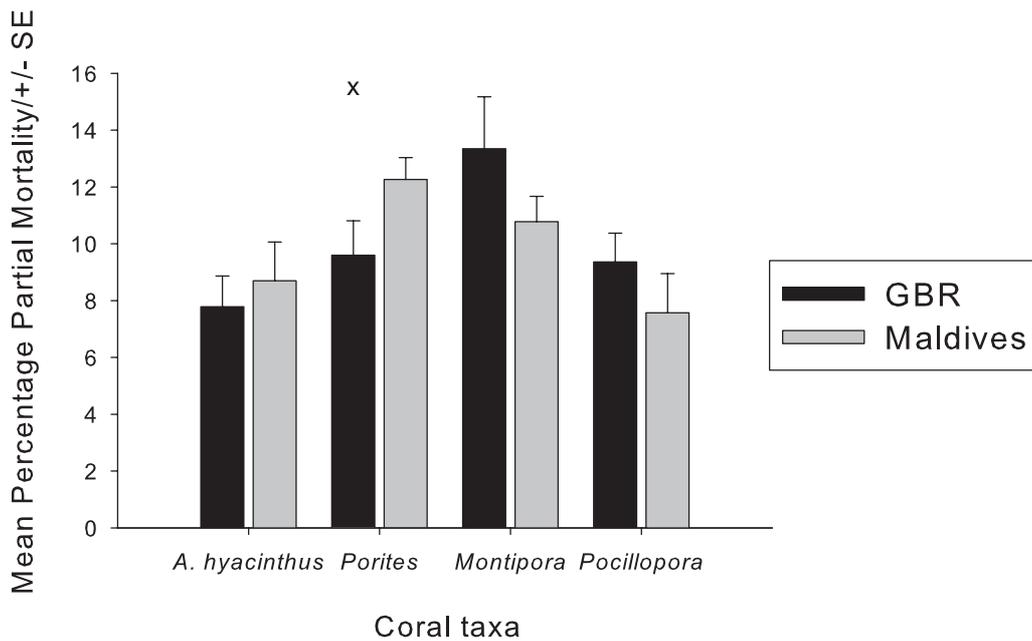
Figure 4.2 Mean (± SE) percentage partial mortality per colony (severity of partial mortality) in *Acropora hyacinthus*, massive *Porites*, encrusting *Montipor*a and branching *Pocillopora*, in the two geographic locations: Lhaviyani Atoll, Maldives versus northern Great Barrier Reef, Australia.

Partial mortality was calculated as the proportion of dead to live tissue within the overall physical extent of each coral colony.

The "x" indicates the statistical significant comparisons.

4.3.3 *Size-dependence in prevalence and severity of partial mortality*

Prevalence of injuries was found to be independent of colony size (except for *A. hyacinthus* and *Pocillopora)* (Table 4.4) whereby 72% of the corals <1000cm^2 exhibited tissue loss compared to 83% of colonies >1000cm^2 and <9323cm^2. Similarly, severity of partial mortality was not related to colony size in *A. hyacinthus* (Table 4.4), while it was significant, but only weakly related to colony size for massive *Porites*, encrusting *Montipora*

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and *Pocillopora*. However, the r^2 values only explained a very small proportion (between 4 and 9%) of the total variation observed (Table 4.4).

Table 4.4 Results of logistic regression of the effect of colony size on the severity (extent of injury) and on the prevalence (proportion of injured colonies) of partial mortality in each coral taxon.

Severity of partial mortality	R^2	df	F	p
A. hyacinthus	0.09	10/242	0.77	0.76
Porites spp	0.01	45/245	1.84	<0.001
Montipora encrusting	0.09	16/137	3.03	0.006
Pocillopora	0.09	183/251	106	<0.001
Prevalence of partial mortality	R^2	df	F	p
A. hyacinthus	0.11	1/240	32.8	<0.001
Porites spp	0.16	1/289	2.06	0.15
Montipora encrusting	0.05	1/152	1.16	0.20
Pocillopora	0.08	1/1012	7.35	0.00

4.4 Discussion

This study revealed significant differences in the prevalence and severity of partial mortality between geographically separated locations (Lhaviyani Atoll, Maldives and the northern Great Barrier Reef, Australia). However, the patterns of variation observed were not consistent among the different coral taxa studied, and there was often more variation within, rather than between locations. This is the first study to explicitly test for differences in severity and prevalence of tissue loss at both large (geographic location) and small (site

specific) spatial scales.

Given broad regional differences in environmental conditions and management structures, it was expected that there would be marked differences in the prevalence and severity of partial mortality between the northern GBR and Lhaviyani Atoll, Maldives. Most notably, reefs in the northern GBR have a shallower reef crest (between 1 and 3 m) directly exposed to breaking waves, while in the Maldives the crest was well below the depth of breaking waves (3–5 m), but subject to strong currents at the edge of the atoll. Light and temperature also differ between the two locations (higher in the Maldives, Lough 1998; Edwards et al. 2001), which may have potentially important consequences for tissue regeneration following sever injuries (Roberts et al. 1982; Titlyanov et al. 2005; Denis et al. 2011). Also, limited fishing is permitted in each of the reefs sampled on the GBR, whereas there are currently no restrictions on fishing in the Maldives (Adams 2004). That said, fisheries in the Maldives are largely focused on tuna (rather than reef fishes), which is used for consumption and export (Adams 2004). Even so, direct anthropogenic pressures do differ between these locations. Most notably, the reefs surveyed on the northern GBR are all situated 10-15km offshore and >300km from the major urban centers, whereas three reefs surveyed in Lhaviyani Atoll (and all Maldivian reefs) vary greatly in their proximity, and exposure, to human populations: one reef surrounding a resort island, one reef surrounding a populated island, and one reef surrounding an island with very limited human use, and these are well representative of human pressure in all the Maldivian atoll. Despite these geographic-scale differences, much of the variation observed in prevalence and extent of coral injuries was at the smallest spatial scales (e.g., between colonies occurring on the same transect within the same general habitat and environment). Moreover, there was more variation in the prevalence of injuries among taxa, than between locations separated by >8000 km, and taxonomic differences in the incidence of injuries were highly conserved between

locations.

Aside from large-scale, ocean-wide, differences in background rates of partial mortality, marked differences in severity of tissue loss were apparent at the very smallest spatial scales (e.g., among colonies located on the same transect, or within the very same habitat). This suggests that many of the processes that injure these dominant coral taxa are very localized, ranging from damage caused by fishes and other microorganisms to bioerosion, scouring by sand and/or physical damage by the waves and currents (Brown and Howard 1985; Hutchings 1986; Meesteers et al. 1996; Dikou and van Woesik 2006). The observed differences in severity of partial mortality between adjacent colonies showed that the causes of such injuries are extremely patchy at relatively fine spatial scales, such that is more likely to observe differences in the prevalence and severity of injuries among closely positioned coral colonies (within a site or on the same transect), than among disparate populations.. Therefore, there is also likely to be a marked variation in susceptibility to, and subsequent recovery capacity from, acute disturbances at the local scale (Oliver 1985; Jokiel and Coles 1990; Cumming 2002; D'Croz and Mate 2004; Carilli 2009).

Size-based differences in the susceptibility of corals to tissue loss are widely documented, and there are strong theoretical grounds for expecting that the incidence of partial mortality will increase with colony size (Jackson 1979; Hughes and Jackson 1985; Babcock 1991). However, such differences in prevalence and severity of background rates of partial mortality were not observed in this study. In support of this, Bak and Meesters (1998) also found no consistent trend in the incidence of partial mortality with colony size. If larger colonies do not have proportionally higher severity of partial mortality compared to smaller ones, then it is possible that age rather than size may play a larger role and should be taken into account when assessing reef health status.

In conclusion, this study showed that prevalence and severity of background mortality is

conserved at large geographic scales. Importantly, findings from this study provided direct evidence that background partial mortality is consistently high in both locations and should be taken into account when assessing recovery capacity of corals. However, it must be noted that instantaneous measures of observable tissue loss in adult coral colonies (as was undertaken in this study) only allow quantification of recent mortality events (Hall 1997; Fisher et al. 2007; Denis et al. 2011). Therefore, it is highly likely there will be significant temporal variation in prevalence and severity of partial mortality, which should be accounted for in future studies.

Chapter 5. Intraspecific variation in physiological condition of reef-building corals associated with differential levels of chronic disturbance[3]

Abstract

Even in the absence of major disturbances (e.g., cyclones, bleaching), corals are subject to high levels of partial or whole-colony mortality, often caused by chronic and small-scale disturbances. Depending on levels of background mortality, these chronic disturbances may undermine individual fitness and have significant consequences on the ability of colonies to withstand subsequent acute disturbances or environmental change. This study quantified intraspecific variations in physiological condition (measured based on total lipid content and zooxanthellae density) through time in adult colonies of two common and widespread coral species (*Acropora spathulata* and *Pocillopora damicornis*), subject to different levels of biological and physical disturbances along the most disturbed reef habitat, the crest. Marked intraspecific variation in the physiological condition of *A. spathulata* was clearly linked to differences in local disturbance regimes and habitat. Specifically, zooxanthellae density decreased (r^2=26, df=5,42, p<0.02, B= -121255, p=0.03) and total lipid content increased (r^2=14, df=5,42, p=0.01, B=0.9, p=0.01) with increasing distance from exposed crests. Moreover, zooxanthellae density was strongly and negatively correlated with the individual level of partial mortality (r^2 =26, df=5,42, p<0.02, B= -7386077, p=0.01). Conversely, *P. damicornis* exhibited very limited intraspecific variation in physiological condition, despite marked differences in levels of partial mortality. This is the first study to relate intraspecific

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variation in the condition of corals to localized differences in chronic disturbance regimes. The next step is to ascertain whether these differences have further ramifications for susceptibility to periodic acute disturbances, such as climate-induced coral bleaching.

5.1 Introduction

Coral reefs are very dynamic ecosystems, impacted by a variety of natural and anthropogenic processes, which may vary in scale, frequency, and intensity (Karlson and Hurd 1993). Even in the absence of major disturbances (e.g., cyclones, bleaching or outbreaks of crown-of-thorns starfish), corals are still subject to a range of chronic, often small-scale disturbances that cause relatively high rates of background mortality (annual background mortality rates can generally vary from 1 to 30%: Stimson 1985; Connell 1997; Wakeford et al. 2008; Pratchett et al. 2013). These background mortality agents (such as predation, competition and disease) are a normal part of the natural dynamics and turnover in coral populations and communities (Hughes and Jackson 1985; Knowlton et al. 1990; Bythell et al. 1993). However, increases in prevalence and impact of chronic disturbances undermine the resilience of coral colonies and populations (Bak and Luckhurst 1980; Harriott 1985; Bythell et al. 1993; Wakeford et al. 2008; Pratchett el al. 2013), which are subject to ever-increasing threats from climate change and other more direct anthropogenic disturbances (Hughes et al. 2003; De'ath et al. 2012).

Background mortality agents can trigger complex responses in corals that may affect colony physiological condition, alter demographic performance, especially growth (Cox 1986; Tanner 1997; Henry and Hart 2005) and reproduction (Hall and Hughes 1996; Strauss and Agrawal 1999; Henry and Hart 2005) and they can therefore have significant consequences on the ability of colonies to withstand and survive periodic acute disturbances and environmental changes (Rotjan et al. 2006). Intraspecific competition, for example, can

substantially reduce fitness and growth rates of colonies engaged in competitive interactions (Tanner 1997). Tanner (1997) documented a reduction in growth rates from 120 to 35% in *Acropora hyacinthus* when engaged in competitive interactions, and a decrease in growth from 45 to -16% in *Pocillopora damicornis*. Similarly, chronic predation can inflict a significant energetic cost to prey corals and may accelerate rates of coral decline following a disturbance (Cole et al. 2011). Coral grazing fishes are a potentially important source of background coral mortality (Cole et al. 2011), even when they do not leave any visible signs of damage on coral colonies (Hourigan et al. 1988). Rates of tissue removal from individual coral colonies can be considerable (16.75 ± 0.30 bites per 20 min, Cole et al. 2011) and this chronic removal of live tissue can have potentially important consequences for colony fitness. Similarly, sedimentation can affect coral physiological condition by exerting significant energetic costs due to the removal of particles from colonies and limit energy availability due to reduced light and photosynthetic activity (Guzman et al. 1994; Henry and Hart 2005). *Siderastrea siderea* reduced linear extension rates from 3.5 mm to 3 mm three years following an oil spill, which caused increased sedimentation levels (Guzman et al. 1994).

The physiological condition of a colony is largely determined by the energy available and by the partitioning of energy reserves among maintenance, growth, and reproduction (Anthony et al. 2009). Energy within a colony is a limited resource and it is distributed among costly life history processes. If a coral invests heavily in repairing tissues damaged by chronic predation or sedimentation, or is investing heavily in interspecific competition, then this will reduce resources available for growth and reproduction. Evidences of energy trade-offs have been widely documented in corals, with injury often causing a decline in growth (Bak 1983; Meesters et al. 1994) or fecundity (Kojis and Quinn 1985). Moreover, diversion of essential energy reserves may undermine the capacity of corals to withstand periodic acute disturbances, such as anomalous temperatures that cause widespread bleaching (Anthony et

al. 2009). When injured, corals often divert energy towards regeneration of lost tissue, and species with high regenerative capacity (such as *Acropora* spp) being able to fully heal the injury in less than 80 days (Bak 1983). However, environmental stresses, large lesions and competition may impair regeneration and hence compromise survival (Bak 1983; Meesters et al. 1992). The bare skeleton resulting from tissue loss can be colonized by algae, pathogens or bioeroders, which may undermine the integrity of the colony (Bak et al. 1997; Titlyanov et al. 2005). These organisms may later compete with the coral for food and space, or cause structural damage to the coral skeleton (Bak et al. 1997; Titlyanov et al. 2005).

The capacity of corals to withstand ongoing disturbances is strongly size-dependent, with small colonies being often more vulnerable to whole-colony mortality than larger ones (Hughes and Jackson 1985, but see Madin et al. 2014). Corals as modular organisms are made up of repeated units (polyps), each of which can function and survive as physiologically independent entities. However, partial mortality and the consequent decline in the total number of polyps that make up a colony can greatly reduce individual fitness and resilience (Hughes and Jackson 1985; Hall and Hughes 1996; Bruckner and Hill 2009). A reduction in size results in fewer polyps available to support colony vital processes and will generally reduce survivorship (Hughes and Jackson 1985; Babcock 1991), growth (Bak 1983; Meesters et al. 1994), reproduction and regeneration (Henry and Hart 2005). Large colonies have greater regenerative abilities (Hughes and Jackson 1985; Bythell et al. 1993), growth (Hughes and Jackson 1980), are more fecund (Hall and Hughes 1996) and have lower rates of total mortality compared to smaller colonies (Hughes and Jackson 1985; Hall and Hughes 1996). Likelihood of survival in larger colonies is greater than smaller ones because there is a higher probability that part of the colony may remain unaffected (Jackson 1979). Particularly, following a disturbance, big colonies can make a disproportionate contribution to population as they produce more eggs per unit area (Hall and Hughes 1996).

Intra-specific variation of corals in responses to stresses is largely due to genotypic and phenotypic variation among both corals and their zooxanthellae (Black et al. 1995; Baker and Rohan 1997; D'Croz and Maté 2004), however the disturbance history and current physiological condition of individual colonies may also play a critical role. The exhaustion of energy available to maintain vital processes represents a physiologically critical threshold for survival (Gurney et al. 1996). During a bleaching event for instance, a key determinant for survival and recovery of a coral is its amount of lipid reserves (Anthony et al. 2009). When bleaching occurs the energy acquisition by the zooxanthellae stops, hence the coral must use its energy reserves accumulated in the form of lipids in order to survive (Szmant and Gassman 1990; Fitt et al. 2000; Grottoli et al. 2004; Rodrigues and Grottoli 2007). So colonies in good physiological conditions, with a great magnitude of lipid reserves, are more likely to survive and recover from a bleaching event, than colonies with lower level of lipid reserves (Grottoli et al. 2006; Anthony et al. 2009). Also colonies, which survived a previous disturbance and are potentially in good physiological condition, can substantially contribute to community recovery through their growth and through their reproductive output (Hall and Hughes 1996; Connell et al. 2004; Halford et al. 2004).

The purpose of this study is to quantify intra-specific variation in physiological condition (specifically, total lipid content and zooxanthellae density) through time in adult colonies exposed to several biological and environmental factors. Colony condition was assessed based on symbiont density and total lipid content, which are good proxies of coral health and have been shown to vary with changes in environmental conditions (Rowan et al. 1997; Jones 1997; Fagoone et al. 1999; Anthony et al. 2009). Variation in colony condition among individuals may account for differences in susceptibility to disturbances. Many studies have documented significant variation in the capacity of corals to withstand and recover from major disturbances (Bythell et al. 1993; Baird and Marshall 2002; Wakeford et al. 2008;

Darling et al. 2012), but the underlying basis of this variation is still poorly understood. Most of these studies have focused on among-species variability for stress resistance. Hoegh-Guldberg (1999) suggested that in the aftermath of climate change some coral species are more likely to adapt and survive better than others. But still little is known on intraspecific variability to environmental changes.

5.2 Material and Methods

5.2.1 *Chronic disturbances*

This study was conducted at Lizard Island (14°40'S, 145°27'E) in the northern Great Barrier Reef, Australia. 24 colonies, ranging in size from 9 cm up to 35 cm diameter, of *Pocillopora damicornis* and *Acropora spathulata* were individually tagged and sampled in May and October 2012 to test for intraspecific differences in physiological condition. At the same time, detailed observations were undertaken to quantify intra-specific differences in background disturbance regimes (NB. There were no major bleaching events or other acute disturbances during the conduct of this study). Colonies at the same depth were selected from the reef crest in two different sites, one sheltered and one in the windward side of the island. For each coral colony we measured the distance from the reef crest (presumed to reflect colony physical position in respect of local hydrodynamic regime), proportional tissue loss attributable to coral competition and/ or coral disease, and also rates of predation by corallivorous fishes. Variation in the level of predation among individual coral colonies was documented using GoPro cameras, deployed to record the total number of bites taken by all corallivorous fishes within replicate one-hour periods. The fish species and size were also recorded. Partial mortality was measured by quantifying the exact proportion of dead versus living tissue within the overall physical extent of each coral colony, using the software Image J. Growth rates were also calculated using areal photos taken from the top of the colony and

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comparing colony surface area from pictures in May and in October for each individual colony.

5.2.2 *Colony Physiological Condition*

Colony condition was assessed based on total lipid content and zooxanthellae density. The size of lipid reserves is a good measure of colony condition because it represents an alternative source of fixed carbon, which can be allocated to vital processes such as growth or reproduction. Lipid reserves can also allow the host to meet its daily metabolic energy needs in absence of endosymbionts, such as during a bleaching event (Grottoli et al. 2006). Similarly, the symbiotic relationship between the coral colonies and the symbionts makes zooxanthellae density a good proxy of coral condition (Sheppard et al. 2009). Zooxanthellae density has been shown to decrease in response to chronic stresses such as exposure to both low and high temperature (Baker et al. 2008), sedimentation (Peters and Pilson 1985), disease (Cervino et al. 2001), and water quality (Cooper and Ulstrup 2009; Cooper et al. 2009), and has been widely measured to assess coral condition in response to stimulants, as well as natural variation in environmental factors (Fagoonee et al. 1999; Ferrier-Page's et al. 2001; Cooper and Ulstrup 2009; Cooper et al. 2009). To measure both total lipid content and zooxanthellae density, one branch was collected from each of the tagged colony in May and October. To minimize within-branch variability in lipids, only central inner branches were collected (Stimson 1987).

Branches were fixed in 10% formalin seawater and decalcified in 5 % formic acid for 1 day followed by 10% formic acid for 5 days and then stored in 70% ethanol. To extract total lipids, coral branches were dried in the oven at 55°C for 24 h, weighed and placed in a solution of chloroform: methanol (2:1, v:v) to dissolve the lipids (Barnes and Blackstock 1973). The tissues were redried at 55°C overnight and reweighed. The difference in weight

was due to lipids loss, with total lipid content then expressed as percentage of dry weight. Total lipid content was analysed instead of lipid classes because the total lipids, triacylglycerol and wax esters, are the main storage lipids in corals, and can account for 40–73% of total lipids (Patton et al. 1977; Harland et al. 1993; Oku et al. 2003).

Zooxanthellae density (per unit surface area (cells/cm^2)) was quantified for each coral based on samples (5mm x 5mm) from the collected branch (4 replicates per branch). Each sample was homogenized and the ground solution was examined on a glass slide under a microscope and counts were normalized to coral surface area, following McCowan et al. 2011.

5.2.3 *Data analyses*

To test whether there were significant differences in partial mortality, in total lipid content, in zooxanthellae density, in competition and in the number of fish bites, between May and October, a series of paired t-tests were carried out for each variable. Proportional mortality of individual coral colonies was Arcsin transformed prior to analyses. A One-Way ANOVA was carried out to further investigate whether colonies exposed to predation had lower lipid content than colonies that did not receive any bite. To test whether physiological condition of coral colonies relates to biological and physical disturbance regimes, we used a stepwise Multiple Regression model, testing the extent to which 1) partial mortality, 2) mean number of fish bites, 3) extent of coral competition, 4) colony size, 5) distance from crest, and 6) Site, explained intraspecific variation in either total lipid content or zooxanthelae density for each coral species. Separate analyses were carried out for total lipid content and zooxanthellae density. Bivariate correlations were also used to test for any relationship between zooxanthellae density and total lipid content in each coral species.

5.3 Results

5.3.1 *Chronic disturbances*

Competitive interactions and partial mortality were constant between May and October in both coral species (Figure 5.1). Only the number of fish bites differed significantly with time, being 23 times higher in October than in May for *P. damicornis* (paired t-test, $p < 0.05$). Some colonies received few bites in May (from 0 to 4 bites per hour) while they were exposed to high predation pressure in October (163 and 392 bites per hour). In *A. spathulata*, overall predation pressure was two times lower in October, but given marked intra-specific variation this was not statistically significant (Figure 5.1). Bite rate varied among colonies in *P. damicornis*, ranging from 0 to >100 bites per hour among colonies. In both coral species, the colonies that received most bites in May were not the same ones that received most bites in October, while some colonies did not receive any bite in either May or October.

In *P. damicornis* the majority of the colonies were smaller than 1.000 cm^2, with colony surface area ranging from 161 cm^2 to 679 cm^2, while in *A. spathulata* colony surface area ranged from 160 cm^2 up to 1.830 cm^2. Colony growth (expressed as changes in colony surface area) from May to October in *A. spathulata* was 118.3 cm^2, while *P. damicornis* showed a negative growth rate (-10.3 cm^2) due to partial mortality.

5.3.2 *Intraspecific variation in colony condition*

All the sampled corals survived the entire study period. Colony condition was found to vary between May and October in both coral species (Figure 5.2). Specifically, a significant decline in total lipid content was observed in October compared to May (Table 5.1, 5.2; Figure 5.2). In *A. spathulata* energy reserves in October were almost half compared to May (declined from 13.7 (± 7.5) % to 7.8 (±1.8) %), while in *P. damicornis* the decline was two-fold during the same time (Figure 5.2). Zooxanthellae density on the other hand,

remained constant and did not change significantly between sampling periods in either coral species (Figure 5.2). For *P. damicornis*, intra-specific variation in total lipid content was strongly correlated with zooxanthellae density (r = 99, df = 5,42, p<0.001), but no such relationship was found for *A. spathulata*.
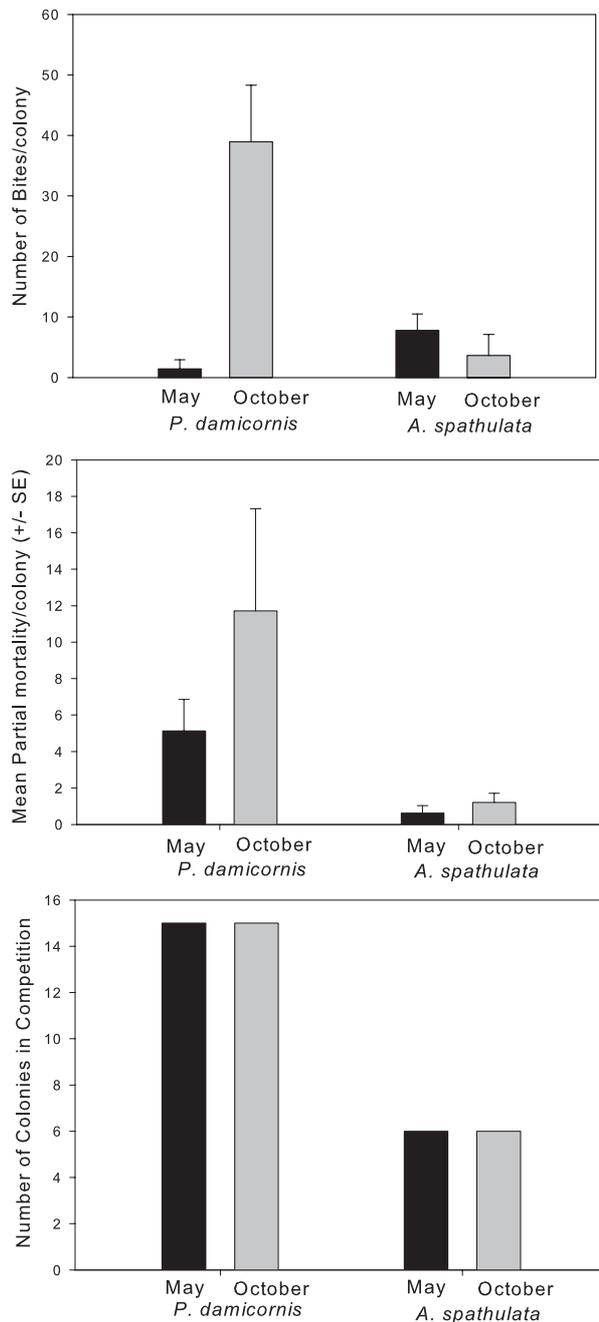
Figure 5.1 Chronic disturbance regimes in May and October in the two reef-building corals *P. damicornis* and *A. spathulata.* A) Predation - mean no. of bites taken per colony in

replicate three-minute observations, B) Partial mortality - proportion of dead versus living tissue within the overall physical extent of each coral colony, C) – number of colonies engaged in competitive interactions.
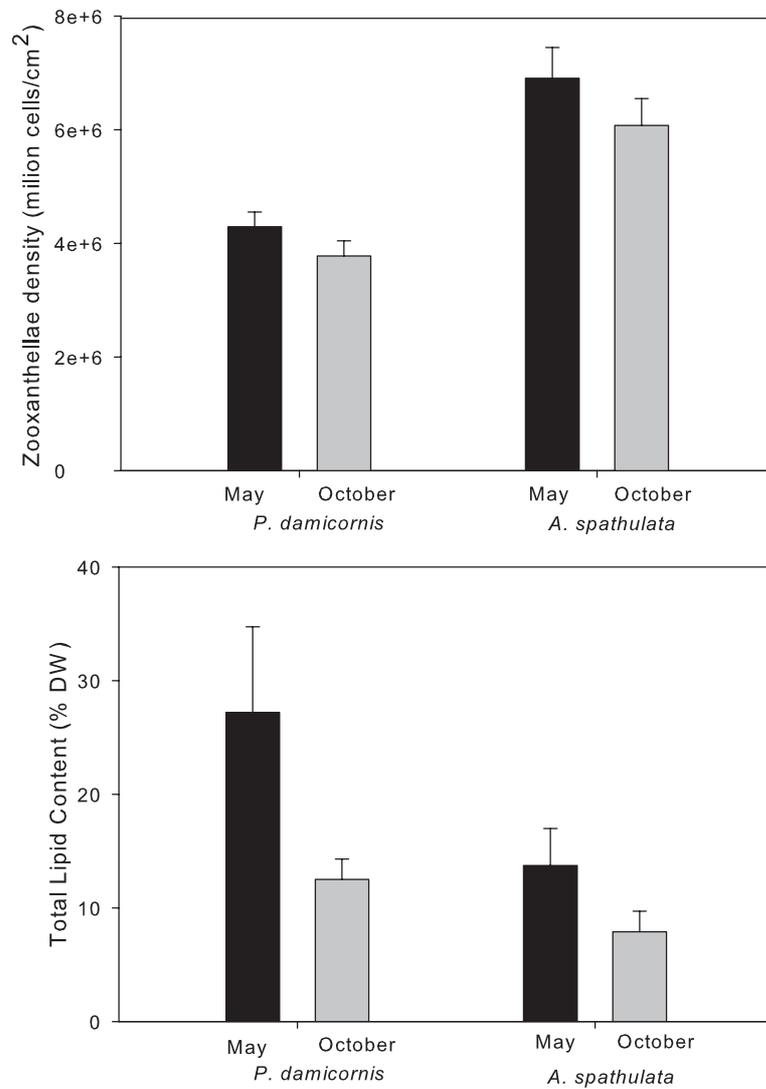
Figure 5.2 Physiological condition, specifically A) total lipid content and B) zooxanthellae density, in May and October in the two reef-building corals *P. damicornis* and *A. spathulata.*

Table 5.1 Multiple Regression for zooxanthellae density and total lipid content in *P. damicornis*. B are the unstandardized coefficients and are in the original units of the variables.

Zooxanthellae	B	StdErr of B	t(42)	p
Intercept				
Partial Mortality	-14	834221	-1.7	0.08
Competition	-44	312617	-1.4	0.1
Number of bites	1632	2745	0.5	0.5
Size	174	1044	0.16	0.8
Site	2338	374570	0.06	0.9
Distance from crest	68	61603	1.1	0.2
Lipid content	B	StdErr of B	t(42)	p
Intercept				
Partial Mortality	-23	13.7	-1.7	0.09
Competition	-3.6	5.1	-0.7	0.4
Number of bites	0.008	0.04	0.1	0.8
Size	0.003	0.01	-1.7	0.8
Site	3.96	6.14	0.64	0.5
Distance from crest	-1.6	1.01	-1.5	0.1

Pocillopora damicornis showed a high variation within colonies in partial mortality (between 0 and 20%), number of fish bites (between 0 and 392 bites per hour) and total lipid content (between 1.5 and 80% dw). By comparison, intraspecific variation in partial mortality and disturbance rates for *A. spathulata* were much smaller (Figure 5.1).

In *P damicornis*, partial mortality, number of fish bites, competition, distance from crest and size were poor predictors of both lipid content (Multiple Regression total lipid content r^2=11, df=5,42, p=0.27; Table 5.1); and zooxanthellae density (r^2=25, df=5, 42, p=0.3; Table 5.1): the regressions explained only a very small proportion of the total variation (<12%). Conversely in *A. spathulata*, partial mortality and distance from crest were found to have a significant effect on both total lipid content and zooxanthellae density (Multiple Regression

total lipid content *A. spathulata* r^2=14, df= 5,42, p =0.021; zooxanthellae density r^2 =26, df = 5,42, p =0.021; Table 5.2). In particular, total lipid content increased with distance from crest, while zooxanthellae density declined with increasing partial mortality and distance from crest (Table 5.2).

Table 5.2 Multiple Regression for zooxanthellae density and total lipid content in *A. spathulata*. B are the unstandardized coefficients and are in the original units of the variables.

Zooxanthellae	B	StdErr of B	t(18)	p
Intercept				
Partial Mortality	-7386077	2909017	-2.5	0.01
Competition	-543263	551519	-0.98	0.3
Number of bites	22837	19454	1.17	0.24
Size	-487	643	-0.75628	0.4
Site	-510264	500279	-1.019	0.3
Distance from crest	-121255	55915	-2.16854	0.03
Lipid content	B	StdErr of B	t(42)	p
Intercept				
Partial Mortality	-2.1	18.5127	-0.11	0.9
Competition	0.7522	3.5098	0.21	0.8
Number of bites	-0.04	0.1238	0.33	0.7
Size	0	0.004	-0.05	0.9
Site	-1.87	3.2105	-0.58	0.5
Distance from crest	0.9	0.3558	2.57	0.01

5.4 Discussion

This is the first study that attempts to relate intraspecific variation in physiological condition of scleractinian corals to small-scale differences in chronic disturbances, such as fish predation. It is well known that coral colonies living in close proximity may exhibit vastly different demographic rates (Hughes and Jackson 1985; Bythell et al. 1993; Hughes 1994; Baird and Marshall 2002), possibly reflective of differences in their disturbance history and subsequent energy allocation (Bak et al. 1977; Hall 1997). The difficulty in making this

link is that very subtle differences in disturbance regimes, operating at any time in the lifetime of each coral, may lead to marked differences in contemporary condition and fitness of individual coral colonies. We acknowledge that the current study provides very limited insights on lifetime differences among closely positioned colonies, mainly due to the limited observational periods, and the range of factors that may be impacting on individual coral colonies. However, it is interesting that we saw no significant temporal shifts in rates of partial mortality, competition and predation between the two observational periods. The high degree of constancy in background mortality may be evidence that there is a high stability in terms of routine mortality.

Under low levels of background mortality, demographic models of scleractinian corals predict constant growth and fecundity of individual colonies, enabling rapid recovery following major acute disturbance (Done 1988; Gurney et al. 1996; Wakeford et al. 2008). However, in the present study, even within relatively constant rates of biological and physical disturbances, the incidence of injuries still varied among colonies. For instance, some coral colonies did not receive any fish bites in either May or October. Similarly, some colonies of *P. damicornis* that were not injured in May showed partial mortality in October, while some colonies never showed partial mortality. In the long term, these differences among colonies may likely be responsible for important inter-colony differences in condition and fitness. Importantly, variation in the disturbance history of individual colonies may have important ramifications for their long-term fate, especially during major disturbances (e.g., climate-induced coral bleaching).

Not unexpectedly, this study revealed marked intraspecific variation in the physiological condition of both *A. spathulata* and *P. damicornis*. However, these differences were only partially explained by inter-colony differences in rates of partial mortality, competition, predation, colony size or the position of the colony relative to the reef crest.

Comparing to other studies, which documented a lipid level of 35% in tissue of *P. damicornis* (Stimson 1987; Ward 1995), this study found a lower lipid content (27% dw). Conversely, zooxanthellae density was found to be higher (3.0 cells/cm^2 in May) than what reported in the literature (1.0 cells/cm^2, (Stimson 1997)). Also differences in colony condition, specifically in total lipid content, were greater among adjacent colonies of *P. damicornis* than when compared to colonies of *A. spathulata,* revealing intraspecific differences in physiological condition and in susceptibility to chronic disturbances. These differences (in *A. spathulata)* suggest that coral physiological condition can be more variable than predicted with the outcome depending, in part, on flow, partial mortality, and position of the colony.

Predation rates on coral colonies were higher in October than in May in both coral species, especially in *P. damicornis*. Similarly, coral grazing parrotfishes have been shown to exhibit higher feeding rates in October compared to April on the GBR (Bonaldo et al. 2012). For parrotfishes, temporal differences in feeding rates have been previously attributed to differences the nutritional quality of colonies associated with gametogenesis (Rotjan and Lewis 2009). For butterflyfishes, which tend to take very shallow bites (Motta 1988), it is unlikely that gametogenesis of the corals would influence feeding behavior, but changes in the nutritional content may still occur within and among coral colonies. For instance mucus production can drive feeding preferences in butterflyfishes (Cole et al. 2009; Pisapia et al. 2012). In October, colonies may have released more mucous as a stress response to environmental changes (Reigl and Branch 1995) and this discharge may have increased their desirability as food source. The observed differences in bite rates could also be due to seasonal differences in the metabolic rate of food demands of the fishes themselves.

Chronic disturbances were found to affect physiological condition only in. *A. spathulata*, which exhibited strong intraspecific variation that was explained to a large extent by inter-colony differences in biological disturbances and physical position, however these

differences were not observed in *P. damicornis*. Even though both study species (*A. spathulata* and *P. damicornis*) are shallow, fast-growing, branching corals, they have slightly different life-histories strategies, which can explain observed differences. *P. damicornis* is a brooding, opportunistic coral which colonizes very disturbed habitats and it is one of the most resilient corals (Darling et al. 2012). These characters may explain why *P. damicornis* was more resilient to chronic background disturbances than *A. spathulata*, which instead seems to dominate communities in relatively stable environments (Darling et al. 2012). *A. spathulata* showed higher lipid reserves with increasing distance from the crest and lower symbiont density with increasing partial mortality and distance from crest. The observed increase in total lipid content with distance from crest may be due to the higher energetic cost of this reef habitat.

The reef crest is a shallow wave-exposed habitat, where water flow strongly influences organisms mechanically and physiologically with important consequences on community structure (Madin et al. 2013). To avoid hydrodynamic dislodgment, colonies on the crest may need to invest more resources in growth to reach the dislodgment threshold (Madin et al. 2013), but since energy is limited within a colony, if more resources are allocated to increase colony size, less energy will be available to store. The findings from this study suggest that colonies in the intermediate position between reef crest and reef flat have better performance than conspecifics on the crest. However, even though the reef crest is an energetic costly habitat, the high flow can positively affect colonies as they can benefit from it for feeding and excretion (Mass et al. 2011). Together with light, flow is a critical abiotic factor affecting colony condition (Mass et al. 2011). Colonies exposed to high flow generally have higher skeletal density, higher protein concentration, zooxanthellae density, chlorophyll content, and higher number and size of oocytes compared to colonies exposed to lower flow conditions (Mass et al. 2011). Flow enhances zooxanthellae density and photosynthesis due

to the enhanced nutrient supply (Muscatine et al. 1989) (and likely also enhance lipid content), and can explain the decreasing zooxanthellae density with distance from crest found in this study.

The symbiotic relationship between the zooxanthellae and the host may be affected by a variety of internal and external factors and processes, the composition of which still has not been fully investigated (Fagoonee et al. 1999; Strickland 2010). Findings from this study suggest that increasing partial mortality and distance from crest may lead to a decline in density of *Symbiodinium*. Not many studies have shown differences in zooxanthellae density among reef habitats regardless of depth. For instance Strickland (2010) did not find any difference in zooxanthellae density with increasing distance from the reef crest or location along the reef. Conversely, zooxanthellae within the same reef habitat have been shown to vary with environmental fluctuations and season cycles (Rowan et al. 1997; Jones 1997; Fagoonee et al. 1999).

Despite consistency in levels of routine or background mortality, the lipid content within coral tissues consistently declined across all coral colonies between May and October in both *P. damicornis* and *A. spathulata*. The decline in total lipid content observed in October in both coral species may partly be explained by sustained and ongoing rates of background mortality, though the declines may also reflect limited productivity during winter months, due to both reduced temperature and reduced day length (Cooper et al. 2011). Zooxanthellae supply corals with an excess of lipids and a limitation in their activity can results in a decline in lipid reserves (Crossland et al. 1980; Stimson 1987). Stimson (1987) documented a decrease in total lipid content following about one month in *P. damicornis* due to light limitation. Corals tend to consume their lipid reserves when maintenance costs of a colony exceed carbon acquisition (Anthony et al. 2009), during environmental unfavourable conditions such as limited light (Hughes and Jackson 1985; Harland et al. 1993;

Hoogenboom et al. 2010), during reproductive events (Richmond 1987; Pernet et al. 2002; Leuzinger et al. 2003) or whenever an increase in energy demand occurs such as the development of a tumor in coral tissue (Yamashiro et al. 2001).

Larger colonies generally have greater regenerative abilities (Hughes and Jackson 1985; Bythell et al. 1993), greater growth (Hughes and Jackson 1980), are more fecund (Hall and Hughes 1996) and have lower rates of total mortality compared to smaller colonies (Hughes and Jackson 1985; Henry and Hart 2005). Consequently we were expecting larger colonies to be more resilient to chronic background disturbances than smaller ones. Conversely, in the present study chronic disturbances had a similar effect on physiological condition of colonies regardless of the size, suggesting that larger colonies are not necessarily more resilient than smaller colonies. Similar incidence of chronic disturbances on coral colonies regardless of the size also suggests a lack of size-specific susceptibility to agents of coral mortality (Bak and Meesters 1998). Other studies documented a lack of differences in resilience between small and large colonies (Nugues and Roberts 2003). For instance *Siderastrea siderea* exposed to partial mortality continued to dedicate resources to reproduction even after the colony had shrunk below their size of maturation while larger colonies reduced their fecundity (Graham and van Woesik 2013). Often recent injuries play a bigger role than size in predicting colony fate (Cumming 2002). Large colonies with higher partial mortality may die before small colonies with no injuries (Cumming 2002).

Extensive research effort has focused on understanding the ability of reef corals to withstand and absorb disturbances, thereby contributing to the persistence and resilience of coral colonies, populations and species (Karlson and Hurd 1993; Connell 1997; Marshall and Baird 2000; Grottoli et al. 2006; Baker et al. 2008; Linares et al. 2011; De'ath et al. 2012). Quantifying the effects of essentially routine and ongoing disturbances on colony condition and assessing intraspecific differences in colony condition added to this understanding and it

is critical because background mortality influences recovery capacity, time and vulnerability to future disturbances.

This study documented significant effects of partial mortality and distance from crest on zooxanthellae density in *A. spathulata* with important ecological consequences for recovery capacity in the aftermath of climate change. A reduction in performances arising from these sub-lethal stressors, is likely to reduce colony resilience and hence increase chances of whole-colony mortality so that colonies suffering from partial mortality may not survive a subsequent acute disturbance. The approach used here, investigating drivers of colony-condition and their energetic consequences for colony resilience, provides a strong framework for predicting resistance, recovery capacity and resilience of reef-building corals. If colonies in poor physiological conditions (e.g. less resilient) are more susceptible to bleaching, disease and other stressors, colonies capable of maintaining a higher physiological condition may have a distinct ecological advantage (Bachok et al. 2006; Anthony et al. 2009). Consequently, colonies of *A. spathulata*, with high partial mortality rates and located on the reef crest, may have a lower potential to withstand and recover from environmental changes compared to conspecific with lower rates of partial mortality and located in intermediate habitats. The observed differences in physiological conditions could have a strong bearing on the selectivity of major disturbances and the capacity of corals to withstand major disturbances, and thereby adapt to changing conditions.

This study is the first to document significant intra-specific variation in background mortality and colony condition, the next step is to investigate whether this variation impacts individual vulnerability of corals. If so, this will provide strong incentive to reduce background levels of stresses (e.g. control all the factors that routinely injure colonies such as predation or anchoring) as a sure way to increase resilience of corals subject to inevitable increases in acute disturbances in association with global climate change.

Chapter 6.   General Discussion

6.1. Partial mortality

Global declines in the abundance of scleractinian corals and associated degradation of coral reef ecosystems is generally attributed to elevated rates of coral mortality, as corals succumb to increasing incidence, severity and diversity of large-scale acute disturbances (De'ath et al. 2012). Accordingly, coral biologists are increasingly focussed on measuring the vulnerability of coral populations and species to different disturbances, mostly by comparing rates of whole-colony mortality (e.g., McClanahan et al. 2007). Rates of whole-colony mortality are arguably a key component of the population dynamics of scleractinian corals (Werner and Gillian 1984; Hughes and Jackson 1980, 1985; Bak and Meesters 1999; Madin et al. 2014), but variation in the severity and prevalence of injuries (or partial mortality) also have a major bearing on the fitness and fate of scleractinian corals (Bak 1983; Hughes and Connell 1987; Rinkevich and Loya, 1989; Meesters et al. 1994).

Injuries can adversely affect corals at the individual, population and community level. Injuries reduce fitness of individual colonies (Chapter 5) both through reductions in colony size (Hall and Hughes 1996) and the necessary diversion of limited energy towards tissue repair (Henry and Hart 2005). At the population level, high rates of injury may ultimately constrain reproductive potential, as resources are reallocated from reproduction to regeneration (Hall and Hughes 1996). However, energy investment strategies vary among coral species (Jackson 1979; Hall 1998), such that differential injury regimes may favour particular assemblage structure (Henry and Hart 2005; Dikou and van Woesik 2006). Spatial, temporal and taxonomic differences in injury regimes are therefore, important for understanding vulnerability and resilience of scleractinian corals to acute disturbances and environmental change.

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Previous studies on coral injuries have revealed marked inter-specific differences in the capacity of corals to repair experimentally induced injuries (e.g., Hall 1997). However, few studies have quantified natural rates of injuries (Bythell et al. 1993; Ginsburg et al. 2001; Dikou and Van Woesik 2006; Bruckner 2012a; Lirman et al. 2013; Pratchett et al. 2013), and until now, there has been no explicit consideration of spatial variation in rates of coral injury. The proportion of colonies with conspicuous injuries, even in the absence of acute disturbances, is very high (Bythell et al. 1993; Bruckner 2012b; Lirman et al. 2013; Pratchett et al. 2013), ranging from 29.5% to 99%. Although, these previous studies focused on one species or one coral morphology, making hard to investigate taxonomic differences in injury rates and regeneration. And interestingly, there were spatial differences in injury regimes when comparing among studies. At Chagos, in the Indian Ocean prevalence of partial mortality was 27.5% (Pratchett et al. 2013), while in the Florida Keys it was <5% (Lirman et al. 2013). Conversely, severity of injury was more variable, ranging from 0 to 99% in all geographic locations (Bythell et al. 1993; Bruckner 2012; Pratchett et al. 2013).

6.2. Spatial variation in rates of coral injury

Significant and consistent spatial variation in the prevalence and severity of background injuries is likely to have an overarching influence on underlying life-history dynamics of scleractinian corals, potentially accounting for apparent discrepancies in the ratio of population replenishment to adult abundance (e.g., Hughes et al. 1999). Hughes et al. (1999) documented that abundance of adult corals was relatively homogeneous along the length of Australia's Great Barrier Reef despite significant declines in rates of coral recruitment at higher latitudes. This suggests that high levels of population replenishment at higher latitudes are offset by higher rates of mortality and/ or injury. Contrary to expectations, my research has revealed limited evidence of large-scale latitudinal gradients in

rates of coral mortality or injury. Rather, there was greater variation in the severity of injuries among adjacent colonies within the same reef habitat than among colonies in different latitudinal sectors (Chapters 2 and 3). The lack of conformity between recruitment and adult abundance highlighted by Hughes et al. (1999) may likely be due to differences in growth and mortality of newly settled corals or latitudinal variation in adult growth rather than differences in rates of tissue loss.

This thesis presents the first empirical data on large-scale variation in the prevalence and severity of coral injuries. However, contrary to expectations, we failed to detect strong or consistent differences in prevalence or severity of coral injuries either along the length of Australia's Great Barrier Reef (Chapter 2 and 3) or when directly comparing between two geographically distinct locations (Chapter 4). Rather, it is possible that there is no large-scale variation or large-scale differences may be obscured by extreme variability at the smallest spatial scales, probably due to inherent stochasticity in the predominant causes of coral injuries, for instance, chronic predation greatly varies among coral colonies of the same species and can cause declines in tissue biomass (Cumming 1999; Cole and Pratchett 2011).

The specific causes of observed injuries are generally not discernable, consequently it was hard to make any concrete conclusions about what is driving fine-scale differences in the severity and prevalence of coral injuries. Partial mortality is a general response to stress (Lirman et al. 2013), and it can be difficult to identify the specific cause of tissue mortality unless repeated sampling occurs very frequently or the causative agent is clearly distinguishable, such as grazing bites by parrotfishes. Common drivers of partial mortality generally range from damage caused by fishes and other organisms (Cumming 2002; Williams and Miller 2012) to bioerosion and sedimentation (Guzman et al. 1994; Nugues and Roberts 2003).

6.3. Taxonomic differences in injury regimes

This thesis documented marked taxonomic differences in prevalence of partial mortality (Chapter 3), suggesting that some species are inherently much more resistant to routine agents of injury and/or have better recovery potential. Massive and encrusting corals showed higher prevalence and extent of partial mortality compared to plate and branching corals (Chapter 3). The observed taxonomic differences in prevalence and extent of partial mortality recorded in this thesis broadly correspond with differences in growth rates and relative investment in regeneration (Hughes 1989; Yap et al. 1992; Meesters et al. 1992, 1996, 1997a). For example, massive *Porite*s is a long-lived, slow growing coral, with generally low regenerative capabilities (Meesters et al. 1996, 1997a, Wesseling et al. 2001; Denis et al. 2011). Consequently, the high prevalence of injuries on massive *Porites* may reflect higher vulnerability to disturbances (e.g., Bonaldo and Bellwood 2012) and/ or accumulation and persistence of injuries over time. Conversely branching corals, such as *Acropora* have high growth rates and regeneration capacities (Yap et al. 1992; Adjeroud et al. 2007), such that, even if they were much more vulnerable to some or all agents of injury, instantaneous measures of injury prevalence and severity might suggest that they have low vulnerability.

Coral species are likely to vary much more in the types of disturbances to which they are vulnerable, rather than being consistently more vulnerable to all types of disturbances, reflective of inherent trade-offs associated with their growth form and life-history characteristics (Jackson 1979). Importantly, corals with limited vertical growth (e.g., some massive and encrusting species) will be more prone to overgrowth by competitors, while erect branching species are likely to be vulnerable to breakage (Hughes 1989; Madin and Connolly 2006).

In a scenario of increasing frequency and intensity of climatic disturbances (Webster

et al. 2005), the long-term persistence of different taxa will greatly depend upon their capacity for recovery between disturbances (Hughes et al. 2003). Massive colonies with low turnover rates, lower regeneration capacity and high rates of old injuries may have a limited potential to withstand and recover from environmental changes (i.e. are less resilient) than *Acropora* spp colonies with high turnover rates, and will therefore have less chances to survive and persist (Done and DeVantier 1990).

6.4. Size-based differences in prevalence and severity of injury

Mortality, growth and reproductive regimes of corals are strongly size-dependent (Harrison and Wallace 1990). For example, fecundity of colonies increases with colony size, both because large colonies have more polyps, but also large colonies produce more eggs per unit area and make a disproportionate contribution to population (Hall and Hughes 1996). Size-specific differences in polyp-level fecundity is generally explained based on size-based differences in energy allocations, whereby small colonies allocate proportionally more resources towards growth and maintenance (Szmant-Froelich 1985) to reduce the time that they are at small sizes, and more exposed to agents of whole colony mortality. It is widely accepted that the probability of whole-colony mortality decreases with increasing size in colonial organisms (but see Madin et al. 2014). While larger colonies will have lower probability of dying, they will also have generally higher exposure to agents of partial mortality (Hughes and Jackson 1985; Bythell et al. 1993; Madin et al. 2014). It is possible therefore, that larger colonies will have to invest disproportionately in tissue repair, further compounding size-based relationships between size and injury. Data from this thesis suggests that there is no relationship between colony size and incidence of injury; rather, there was relatively high incidence of partial mortality across the entire size range considered. A lack of any relationship between size and severity of partial mortality was also observed in the

Caribbean (Bruckner 2012b) where it was attributed to high variability in the extent of injury across all size classes. Importantly, differences in the repair and regenerative capacities of colonies of different sizes may obscure such a relationship, whereby larger colonies may experience higher prevalence of injury, but also have greater capacity for tissue repair (Loya 1976; Hughes and Jackson 1985; Nugues and Roberts 2003). An injury of a given size is also going to require greater proportional investment in repair than for smaller colonies (Connel 1973; Henry and Hart 2005).

Empirical data from this thesis also revealed that prevalence and severity of partial mortality had no bearing on the realised growth of colonies in any of the major coral taxa (Chapter 3). This may suggest that energy allocated to regeneration tends to be detracted from reproduction rather than growth (Hall 1998), though no measurements of fecundity or reproductive allocation were made during this study. If so, growth is more likely to be maintained following injury but at the cost of future reproduction (Rinkevich and Loya 1989; Hall 1998). Hall (1998) documented a marked effect of partial mortality on reproduction but not on colony survival and growth inferring a clear trade-off between reproduction and regeneration.

6.5. The role of disturbance on colony condition

Chronic stressors can trigger complex responses in corals that may affect colony physiological condition, alter demographic performance, especially growth (Cox 1986; Tanner 1997; Henry and Hart 2005) and reproduction (Hall and Hughes 1996; Strauss and Agrawal 1999; Henry and Hart 2005) and they can therefore have significant consequences on the ability of colonies to withstand and survive acute disturbances and environmental changes (Rotjan et al. 2006). Chronic predation for example, greatly varies among coral colonies of the same species (Cole and Pratchett 2011), and can inflict a significant energetic

cost to the colonies accelerating rates of coral decline following a disturbance (Cole et al. 2011). Similarly, intraspecific competition can substantially reduce fitness and growth rates of colonies engaged in competitive interactions (Tanner 1997).

The disturbance regime to which a coral has been exposed is important in determining its physiological condition and consequently its capacity to regenerate recent injuries, because past injuries limit the resources available for regeneration from more recent injuries (Cumming 2002; Henry and Hart 2005). Chapter 5 directly tested the influence of both observable and non-observable injury (such as feeding by butterfly-fish) on colony condition. Importantly, disturbances that do not leave any signs (non-observable injuries) likely impair regeneration and affect physiological condition. Chapter 5 documented that marked intraspecific variation in the physiological condition of *A. spathulata* was clearly linked to differences in local disturbance regimes and habitat. Conversely, *P. damicornis* exhibited very limited intraspecific variation in physiological condition, despite marked differences in levels of partial mortality.

6.6. Conclusions

This thesis shows that the prevalence of coral injuries is consistently high at all locations and latitudes, though the severity of injuries is highly variable among individual colonies. Such differences in severity of injuries among adjacent colonies may have important ramifications for individual susceptibility to acute disturbances and environmental change. Many studies have documented significant variation in the capacity of corals to withstand and recover from major disturbances, but the underlying basis of this variation was poorly understood. Some colonies are more affected and/or recover faster than other individuals from the same species and to better understand these intraspecific differences, it was critical to investigate why some corals are more influenced by biotic and abiotic

processes than others and why they respond in certain ways. The approach used in this thesis, investigating drivers of colony-condition provides a baseline, with which to test for changes in injury regimes, and the extent to which this might further increase susceptibility to and prevent recovery from, acute disturbances. Colonies with low partial mortality and hence in high condition may have better potential to withstand and recover from environmental changes (i.e. are more resilient) than conspecifics with high partial mortality and hence in poor condition, and will therefore have a disproportionate role in population recovery.

This study emphasises that partial mortality is highly prevalent among scleractinian corals and may be an important predictor of colony fate and resilience. In a scenario of increasing intensity and frequency of disturbances, the future management approach should be urgently addressed to reduce all anthropogenic causes and rates of chronic background mortality (i.e. a large range of mechanical damages to colonies, such as anchoring, abrasion or diving), which can reduce colony condition and recovery between major acute disturbances.

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Appendix

Other papers published or in preparation during my candidature

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