

Geographically conserved rates of background mortality among common reef-building corals in Lhaviyani Atoll, Maldives, versus northern Great Barrier Reef, Australia

Chiara Pisapia^{1,2} · Michael Sweet³ · Hugh Sweatman⁴ · Morgan Stuart Pratchett¹

Received: 20 April 2015 / Accepted: 1 July 2015
© Springer-Verlag Berlin Heidelberg 2015

Abstract Even in the absence of major disturbances (e.g., cyclones and bleaching), corals are consistently subject to high levels of background mortality, which undermines individual fitness and resilience of coral colonies. Most studies of coral mortality however only focus on catastrophic mortality associated with major acute disturbance events, neglecting to consider background levels of chronic mortality that have a significant influence on population structure and turnover. If, for example, there are geographic differences in the prevalence of injuries and rates of background mortality, coral communities may vary in their susceptibility to acute large-scale disturbances and environmental change. This study quantified the prevalence and severity of partial mortality for four dominant and widespread coral taxa (massive *Porites*, encrusting *Montipora*, *Acropora hyacinthus*, and branching *Pocillopora*) at Lhaviyani Atoll, Maldives, and on the northern Great Barrier Reef, Australia. The prevalence and severity

of sublethal injuries varied greatly among taxa, but was generally similar between locations; on the Great Barrier Reef, 99.4 % *Porites* colonies, 66 % of *A. hyacinthus*, and 64 % of *Pocillopora* had conspicuous injuries, compared to 92.4 % of *Porites*, 47.5 % of *A. hyacinthus*, and 44 % of *Pocillopora* colonies in Lhaviyani Atoll. These results suggest that background rates of mortality and injury, and associated resilience of coral populations and communities to large-scale disturbances, are conserved at large geographic scales, though adjacent colonies can have markedly different injury regimes, likely to lead to strong intraspecific variation in colony fitness and resilience.

Introduction

Coral reef scientists and managers are increasingly focused on the effects of large-scale and often acute disturbances, including severe tropical storms, outbreaks of crown-of-thorns starfish, and climate-induced coral bleaching (Madin and Connolly 2006; Kayal et al. 2012), generally attributing widespread declines in coral cover on reefs to a combination of such disturbances (Bellwood et al. 2004; De'ath et al. 2012). However, reef-building corals are also subject to a wide range of chronic and/or small-scale disturbances (e.g., predation, disease, competition, and sedimentation) that can cause high rates of background coral mortality and injury (Stimson 1985; Hughes 1989; Connell 1997; Wakeford et al. 2008; Pratchett et al. 2013; Madin et al. 2014). These background rates of coral mortality and injury are critically important if we are to understand the structure and dynamics of coral populations and communities (Madin et al. 2014), and may significantly influence susceptibility of coral populations to increasing incidence and severity of large-scale, acute disturbances (Henry and Hart 2005; Bruckner and Hill 2009).

Communicated by L. Mydlarz.

Reviewed by S. Sandin and an undisclosed expert.

✉ Chiara Pisapia
chiara.pisapia@my.jcu.edu.au

¹ ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

² AIMS@JCU, Australian Institute of Marine Science, School of Marine Biology, James Cook University, Townsville, Australia

³ Molecular Health and Disease Laboratory, Department of Conservation, Biology and Ecosystems, University of Derby, Kedleston Road, Derby DE22 1GB, UK

⁴ Australian Institute of Marine Science, Townsville, QLD, Australia

To advance the understanding of the effects of large-scale and acute disturbances, it is important to compare resulting rates of coral mortality to normal background levels of coral mortality (Wakeford et al. 2008), rather than attributing all recent mortality to one or more specific disturbances (e.g., De'ath et al. 2012). Currently, however, there is very limited understanding of background rates of coral mortality. For example, it is not known how background levels of coral mortality and injury vary regionally, nor how background mortality rates ultimately influence the resulting levels of coral mortality following a major disturbance. Normal background rates of whole-colony mortality have been estimated to be as high as 19 % per year in some locations (Bak and Luckhurst 1980), but vary greatly within and among coral taxa (Bak and Luckhurst 1980; Harriot 1985; Bythell et al. 1993; Wakeford et al. 2008; Pratchett et al. 2013; Madin et al. 2014). Regardless of background rates of whole-colony mortality, it is clear that a large proportion of coral colonies (close to 100 % Pisapia and Pratchett 2014) are injured at any given point in time, and the associated energy required for tissue repair will detract from maintenance, growth, and/or reproduction (Meesters et al. 1994), further reducing overall colony fitness.

The individual fitness and fate of scleractinian corals is strongly size-dependent (Hughes and Jackson 1985). Large colonies generally have greater regenerative abilities (Hughes and Jackson 1985; Bythell et al. 1993) and greater energy reserves that may be allocated in increased growth (Hughes and Jackson 1980) or disproportionate reproductive output (Harrison and Wallace 1990; Hall and Hughes 1996). Given their capacity for regeneration, but also because of their increased size relative to the scale of contact injuries, rates of whole-colony mortality often decline with increasing colony size (Hughes and Jackson 1985; Henry and Hart 2005). Conversely, larger colonies may well have higher prevalence of sublethal injuries (Hughes and Jackson 1980, 1985), due to increased exposure to agents of partial mortality, as well as accumulation of injuries over time.

Aside from size, susceptibility to, and persistence of, partial mortality varies among corals according to their differing morphology (Woodley et al. 1981; Hughes 1989; Glynn 1990; Chadwick-Furman 1995). In the extreme, *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 (Pisapia and Pratchett 2014). 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, 1997; Hall 1997).

The extent of such chronic disturbances has been shown to vary spatially over millimeters, centimeters, and meters (e.g., predation and bioerosion) to hundreds and thousands of kilometers (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) varies both at the large scale (locations separated by 500 km along the GBR) and at the small scale (between adjacent colonies) (Pisapia and Pratchett 2014).

Despite this, the majority of comparative studies focusing on coral recovery and/or resilience typically assume there is no background mortality (e.g., Baird and Marshall 2002; Halford et al. 2004; Gilmour et al. 2013). 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 dominant and widespread coral taxa (*Acropora hyacinthus*, branching *Pocillopora*, massive *Porites* spp., and encrusting *Montipora*) comparing between two distinct geographical locations, the Maldives in the Indian Ocean and the northern Great Barrier Reef (GBR), Australia. More specifically, this study 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).

Materials and methods

Study sites

Sampling was conducted at a hierarchy of spatial scales. At the largest scale, sampling was conducted at each of two distinct geographic locations, the northern Great Barrier Reef (GBR), Australia, and Lhaviyani Atoll, in the Maldives, separated by >8000 km. Within each location, sampling was conducted at each of three 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 reefs, three randomly selected sites were sampled. At each site, three replicate (10 × 5 m) belt transects were laid lengthwise along the reef crest (3 m deep in Australia and 5 m deep in the Maldives), with a minimum of 3 m separating adjacent transects.

Locations were sampled opportunistically. However, the surveyed reefs are broadly reflective of the locations more generally. On the GBR, Pisapia and Pratchett (2014) 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.

Survey of partial mortality

To quantify spatial and taxonomic variation in the incidence of coral injuries, we 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 tissue loss (partial mortality) among replicate colonies of four different taxa. The study taxa (*A. hyacinthus*, branching *Pocillopora* spp., massive *Porites* spp., and encrusting *Montipora*) were selected for their prevalence at each location. Moreover, each of these taxa is very widespread, and represents highly contrasting morphologies and life history strategies (Darling et al. 2012).

To quantify the prevalence and severity of partial mortality, we surveyed all colonies of each of the four coral taxa along fixed area transects (total of 150 m² per site), such that the actual number of the colonies sampled varied according to the local abundance of each taxa. All colonies were inspected in situ due to difficulties in capturing the full extent of injuries (especially on the sides and base of

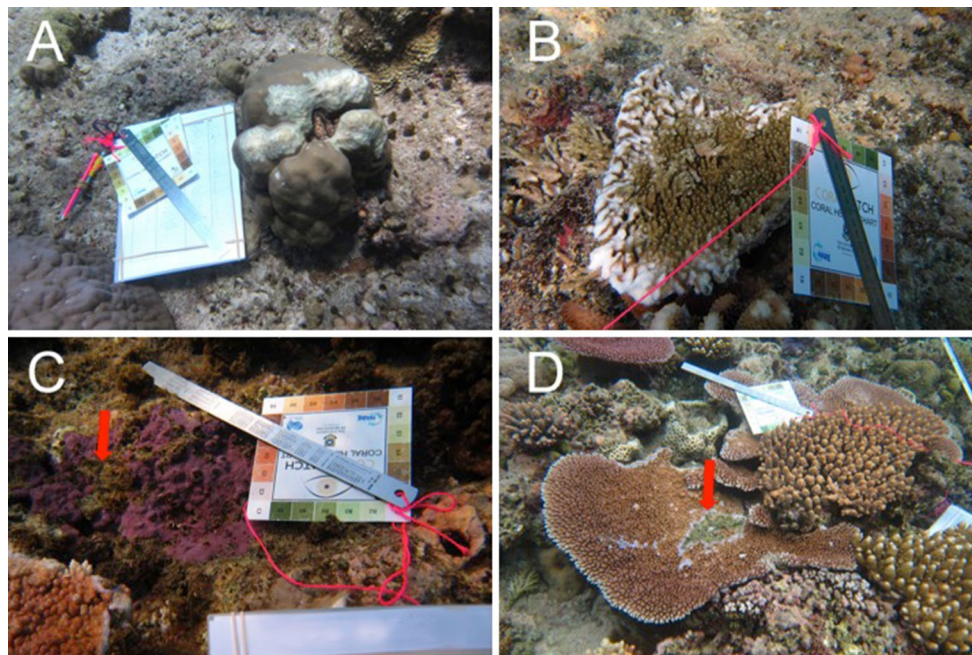


Fig. 1 Partial mortality in (a) *Porites* massive in the Maldives, (b) in *A. hyacinthus* in the Maldives, (c) in *Montipora* on the GBR, and (d) in *A. hyacinthus* on the GBR. In figures c and d, injuries are fully covered in algae (red arrows). Partial mortality was calculated as the proportion of dead to live tissue within the overall physical extent of

each coral colony. In *Porites* (a) percentage of tissue loss was 30 %, in *A. hyacinthus* (b) was 40 %, while in *Montipora* (c) and *A. hyacinthus* (d), partial mortality was estimated as 35 and 10 %, respectively. Photograph credits: Chiara Pisapia

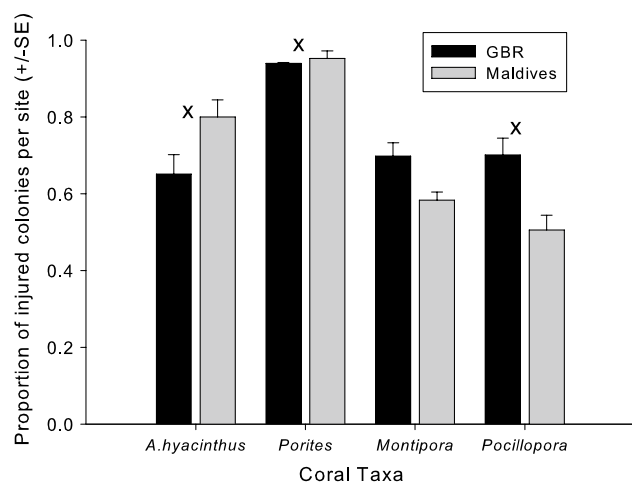


Fig. 2 Proportion of injured colonies per site in *A. hyacinthus*, massive *Porites*, encrusting *Montipora*, and branching *Pocillopora*, in the two geographic locations: Lhaviyani Atoll, Maldives, versus northern Great Barrier Reef, Australia. The “x” indicates the statistical significant comparisons

colonies) in a single photograph. Severity of tissue loss was calculated to the nearest 5 %, ranging from zero (no injury) to close to 100 %, and no measurements of each injured part of the colony were taken (Fig. 1). Each colony was visually inspected to record the presence/absence of various prominent “band” diseases at the time of sampling. Due

to difficulty in identifying most diseases, only prominent active “band” diseases were surveyed and were identified looking at the characteristic band that separates “healthy” coral tissue from exposed coral skeleton. Each colony was then photographed from the top with appropriate scale references to quantify colony size. Images were processed using the ImageJ software (<http://imagej.nih.gov/ij>) to estimate the planar areal extent for each colony, following Pisapia and Pratchett (2014).

Data analysis

Variation in the prevalence of partial mortality (the proportion of colonies on a given transect with injuries) was analyzed using a hierarchically nested general linear model (GLM), testing for differences among taxa (fixed factor, four levels: *A. hyacinthus*, branching *Pocillopora*, massive *Porites* spp., and encrusting *Montipora*), among locations (fixed factor, three levels: Lhaviyani Atoll and northern GBR), among reefs (random factor, 3 per location), and among sites (random factor, three per reef). 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 were calculated to assess whether variation in prevalence and/or severity increases with respect to scale.

Table 1 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	<i>Acropora hyacinthus</i>	Massive <i>Porites</i>	Encrusting <i>Montipora</i>	Branching <i>Pocillopora</i>
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

Table 2 Results of hierarchically nested ANOVAs to test for taxonomic and spatial variation in the prevalence of injury (proportion of injured colonies per site)

	SS	df	MS	F	p	Var (%)
Species	2.28	3	0.76	80.8	<0.001	55.8
Location	0.36	2	0.18	19.4	0.18	11
Reef	0.03	2	0.01	1.85	0.16	2.6
Species × location	0.08	2	0.04	4.26	0.02	
Species × reef	0.36	6	0.06	6.55	<0.001	
Location × reef	0.017	4	0	0.46	0.76	
Species × location × reef	0.23	4	0.05	6.31	<0.001	20.8
Error	0.4	43	0.009			9.9

Percentages in bold (var %) refer to variance partitioning for each variable individually

Taxonomic and spatial variation in the extent of coral injuries (estimated as the proportional area of individual colonies that were injured) was analyzed using a log-linear analyses, comparing the number of colonies that had ≤5, 20, 50, 80, >80 % of the colony extent actually injured, among taxa, between locations, among reefs, among sites, and among transects.

Results

Prevalence of coral tissue loss (partial mortality)

We surveyed a total of 1761 colonies across all four coral taxa and both locations, of which 1419 (81 %) had conspicuous evidence of recent or sustained tissue loss. The prevalence of partial mortality was very high across all taxa ranging from 62 % in *Pocillopora*, 66 % of *A. hyacinthus*, up to 96 % for massive *Porites*, and 98 % for encrusting *Montipora* (Fig. 2; Table 1). Prevalence of partial mortality was also significantly different among taxa (percent variation explained by taxa regardless of location: 55.8 % Table 2) with *Montipora* and *Porites* showing significantly higher prevalence of partial mortality than *Pocillopora* and *A. hyacinthus* in the Northern GBR (Table 2; Tukey's test < 0.05). While there was limited spatial variation in the prevalence of coral injuries between reefs (2.6 %), there was greater large-scale (between locations) variation (percent variation explained solely by location: 11 % Table 2), with higher prevalence of tissue loss recorded on the northern GBR (Tukey's test < 0.005, Table 2).

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, the various prominent "band" diseases were not recorded for any coral taxa in any

location at the time of sampling. However, even if band diseases were not active at the time of the study, it is highly likely that in some colonies the observed partial mortality was due to a disease that had already left the colony.

Severity of coral mortality

For the 1419 colonies that exhibited some level of tissue loss, the proportion of the total colony area that was affected ranged between 2 and 80 %, with an overall mean (\pm SE) of 6.83 ± 0.6 . Severity of partial mortality was remarkably consistent among locations in all coral taxa, and it did not vary significantly also at smaller spatial scales (reefs, sites, and transects). The number of colonies that had ≤5, 20, 50, 80, >80 % of the colony extent actually injured did not vary significantly between locations, among reefs, among sites, and among transects (maximum likelihood $X^2 = 87.6$, $df = 84$, $p = 0.37$; $X^2 = 84.7$, $df = 84$, $p = 0.45$). However, for *Porites*, frequency of colonies with high extent of injury (>80 %) was found to be higher in Lhaviyani Atoll (64 %) than those recorded in the northern GBR (5.8 %) (Fig. 3).

Severity of partial mortality varied significantly among coral taxa ($X^2 = 422.5$, $df = 49$, $p < 0.00001$). For *Porites* and *Montipora*, there were a higher frequency of partial mortality observed compared to that for *A. hyacinthus* and *Pocillopora* (Fig. 3). However, in general, frequency of partial mortality was consistently high for all coral taxa studied (Fig. 3). Massive *Porites* showed the highest frequency of partial mortality with 64 % of colonies suffering from injuries >80 % of colony area (Fig. 3).

Discussion

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, it is still poorly understood and likely

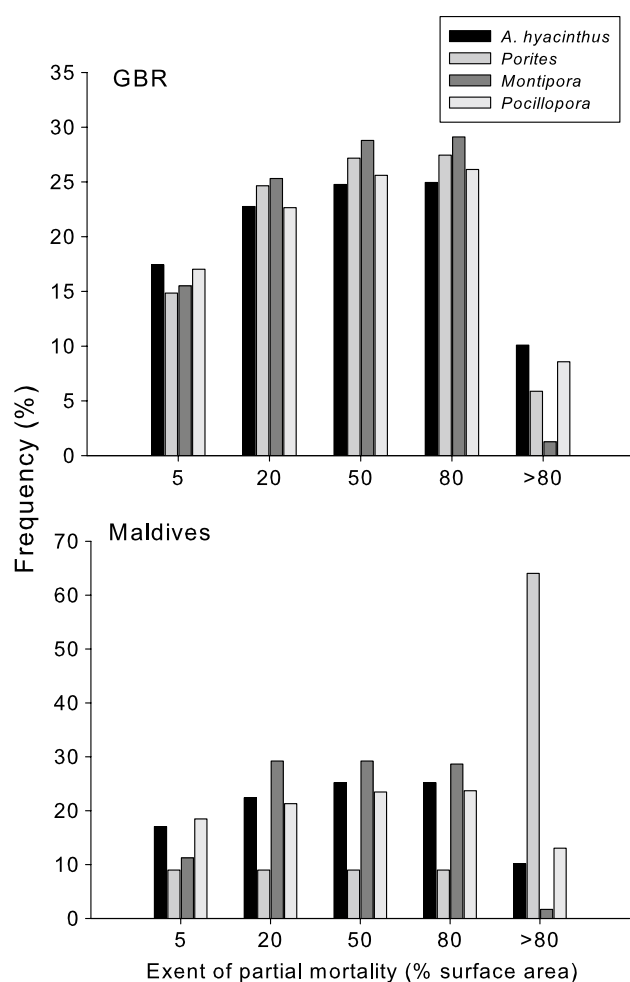


Fig. 3 Frequency distribution for the degrees of mortality (percent surface area loss) in the two geographic locations: Lhaviyani Atoll, Maldives, versus northern Great Barrier Reef, Australia, pooled among taxa. Individual colonies from all coral taxa were pooled together

to be important in better understanding spatial variation in recovery capacity. This is the first study to explicitly test for differences in severity and prevalence of coral injuries at a hierarchy of spatial scales, encompassing very large-scale (between distinct geographic locations) and small-scale (e.g., among adjacent coral colonies) comparisons. This study documented that prevalence and severity of sublethal injuries was generally similar between locations. 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 1999; Edwards et al. 2001), a result which may have potentially important consequences on coral regeneration rates, as corals have been shown to have greater regeneration in lower solar radiation and intermediate surface temperatures (Roberts et al. 1982; Titlyanov et al. 2005; Denis et al. 2011). Moreover, 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). However, fishery in the Maldives has not been historically based on reef fish but on tuna, which is used for consumption and export (Adams 2004). Anthropogenic pressures also differ between locations. While the reefs surveyed on the northern GBR are exposed to limited human pressures (e.g., two reefs surrounding unpopulated islands), the three reefs surveyed in Lhaviyani Atoll (and all Maldivian reefs) are exposed to varying degree of human pressure: 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 disease, bioerosion, scouring by sand and/or physical damage by the waves and currents (Brown and Howard 1985; Hutchings 1986; Meesters et al. 1996; Dikou and van Woesik 2006). For instance, predation rates greatly vary among different coral colonies of the same species (Cumming 1999; Cole and Pratchett 2011). The observed differences in severity of partial mortality between adjacent colonies suggested that disturbance history is likely to be highly variable among colonies at the same site, and it may be more variable than it is among disparate populations. Therefore, there is also likely to be a marked variation in susceptibility and subsequent recovery capacity to these acute disturbances at the local scale (Oliver 1985; Jokiel and Coles 1990; Cumming 2002; D’Croze and Mate 2004; Carilli et al. 2009).

This study documented taxonomic differences in prevalence and severity of partial mortality. *Porites* and *Montipora* showed higher prevalence compared to *A. hyacinthus* and *Pocillopora*, whereas previous studies have suggested that branching corals are disproportionately susceptible to many routine agents of coral injuries (e.g., breakage, Meesters et al. 1996; coral feeding, Cole and Pratchett 2011; competition, Lang 1973). Interestingly, the higher prevalence of partial mortality in massive and encrusting corals observed here does not relate to broad bleaching susceptibility patterns (Loya et al. 2001). *Acropora* and *Pocillopora* are generally more susceptible to bleaching than *Porites* massive and *Montipora* encrusting (Loya et al. 2001; Baird and Marshall 2002) but yet they showed lower prevalence of injury in the present study. The taxonomic differences in prevalence and severity of partial mortality observed here might be due to host differences in symbionts, tissue thickness, growth rates, and especially investment in repair (Meesters et al. 1992, 1996; Hall 1997; Meesters et al. 1997; Loya et al. 2001). Coral taxa have different amount and type of injuries (e.g., Meesters et al. 1996, 1997) as well as different regeneration abilities and rates (Meesters et al. 1992; Hall 1997). *Acropora* spp. generally show greater ability to heal (Meesters et al. 1996; Hall 1997) which can result in lower levels of tissue loss as observed here, while massive and encrusting taxa have limited capacity for lesion regeneration (Meesters et al. 1994, 1997; Denis et al. 2011), so injuries are more likely to be preserved for longer term (Meesters et al. 1996; Denis et al. 2011) resulting in higher prevalence and severity of injury. As such, it is likely that observed taxonomic differences in the prevalence of injuries are more a function of regeneration capacity than inherent differences in susceptibility to chronic disturbances.

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.

Acknowledgments This study was funded by the ARC Centre of Excellence of Coral Reef Studies and AIMS@JCU. The authors are indebted to M. Trapon, K. Anderson, J. Casey, D. Burn, and B. Taylor for assistance in the field and to the staff at Lizard Island Research Station, and Korallionlab for field and logistical support.

References

- Adams MS (2004) Review of the state of world marine capture fisheries management: Indian Ocean. Country review: Maldives. www.fao.org/docrep (Access Nov 2004)
- Ateweberhan M, McClanahan TR, Graham NAJ, Sheppard CRC (2011) Episodic heterogeneous decline and recovery of coral cover in the Indian Ocean. *Coral Reefs* 30:739–752
- Baird A, Marshall P (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Mar Ecol Prog Ser* 237:133–141
- Bak RPM, Luckhurst BE (1980) Constancy and change in coral reef habitats along depth gradients at Curaçao. *Oecologia* 47:145–155
- Bak RPM, Steward-Van Es Y (1980) Regeneration of superficial damage in the scleractinian corals *Agaricia agaricites* F. *Purpurea* and *Porites astreoides*. *Bull Mar Sci* 30:883–887
- Bak RPM, Brouns JJWM, Heys FML (1977) Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricites* and *Montastrea annularis*. In: Proceedings of 3rd international coral reef symposium Miami I. pp 143–148
- Bellwood DR, Hughes TP (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science* 292:1532–1535
- Bellwood D, Hughes T, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429:827–833
- Brown BE, Howard LS (1985) Assessing the effects of ‘stress’ on reef corals. *Adv Mar Biol* 22:1–63
- Bruckner AW, Hill RL (2009) Ten years of change to coral communities off Mona and Desecheo Islands, Puerto Rico, from disease and bleaching. *Dis Aquat Organ* 87:19–31
- Bythell JC, Gladfelter EH, Bythell M (1993) Chronic and catastrophic natural mortality of three common Caribbean reef corals. *Coral Reefs* 12:143–152
- Carilli JE, Norris RD, Black BA, Walsh SM, McField M (2009) Local stressors reduce coral resilience to bleaching. *PLoS One* 4:e6324
- Chadwick-Furman NE (1995) Effects of scuba diving on coral reef invertebrates: relative vulnerabilities and critical levels of diving activity. In: Proceedings of 6th international conference coelenterate biology, vol 1. pp 91–100
- Cole A, Pratchett M (2011) Inter-specific variation in susceptibility to grazing among common reef corals. *Mar Ecol Prog Ser* 422:155–164
- Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16:S101–S113
- Cumming R (1999) Predation on reef-building corals: multiscale variation in the density of three corallivorous gastropods, *Drupella* spp. *Coral Reefs* 18:147–157
- Cumming RL (2002) Tissue injury predicts colony decline in reef-building corals. *Mar Ecol Prog Ser* 242:131–141
- D’Croz L, Maté JL (2004) Experimental responses to elevated water temperature in genotypes of the reef coral *Pocillopora damicornis* from upwelling and non-upwelling environments in Panama. *Coral Reefs* 23:473–483
- Darling ES, Alvarez-Philip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. *Ecol Lett* 15:1378–1386
- Déath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc Natl Acad Sci* 109:17995–17999
- Denis V, Debreuil J, De Palmas S, Richard J, Guillaume MMM, Bruggemann JH (2011) Lesion regeneration capacities in populations of the massive coral *Porites lutea* at Réunion Island: environmental correlates. *Mar Ecol Prog Ser* 428:105–117
- Dikou A, van Woessik R (2006) Partial colony mortality reflects coral community dynamics: a fringing reef study near a small river in Okinawa, Japan. *Mar Pollut Bull* 52:269–280

- Done TJ (1988) Simulation of recovery of pre-disturbance size structure in populations of *Porites* spp. damaged by the crown of thorns starfish *Acanthaster planci*. *Mar Biol* 100:51–61
- Edwards AJ, Clark S, Zahir H, Rajasuriya A, Naseer A, Rubens J (2001) Coral bleaching and mortality on artificial and natural reefs in Maldives in 1998, sea surface temperature anomalies and initial recovery. *Mar Pollut Bull* 42:7–15
- Fisher EM, Fauth JE, Hallock-Muller P, Woodley CM (2007) Lesion regeneration rates in reef-building corals *Montastraea* spp. as indicators of colony condition. *Mar Ecol Prog Ser* 339:61–71
- Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an isolated coral reef system following severe disturbance. *Science* 340:69–71
- Glynn PW (1990) Coral mortality and disturbances to coral reefs in the tropical Eastern Pacific. In: Glynn PW (ed) Global ecological consequences of the 1982–83 El Niño-Southern Oscillation event on corals and coral reefs of the eastern Pacific. Elsevier Oceanogr Ser 52, Amsterdam, pp 55–126
- Halford A, Cheal A, Ryan D, Williams DM (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology* 85:1892–1905
- Hall VR (1997) Interspecific differences in the regeneration of artificial injuries on scleractinian corals. *J Exp Mar Biol Ecol* 212:9–23
- Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. *Ecology* 77:950–963
- Harriot VJ (1985) Mortality rates of scleractinian corals before and during a mass bleaching event. *Mar Ecol Prog Ser* 21:81–88
- Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) Ecosystems of the world: coral reefs. Elsevier, Amsterdam, pp 133–207
- Henry LA, Hart M (2005) Regeneration from injury and resource allocation in sponges and corals—a review. *Int Rev Hydrobiol* 90:125–158
- Hughes TP (1989) Community structure and diversity of coral reefs: the role of history. *Ecology* 70:275–279
- Hughes TP, Jackson JBC (1980) Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. *Science* 209:713–715
- Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. *Ecol Monogr* 55:141–166
- Hutchings PA (1986) Biological destruction of coral reefs. *Coral Reefs* 4:239–252
- Jokiel PL, Coles SL (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* 8:155–162
- Kayal M, Vercelloni J, Lison de Loma T, Bosserelle P, Chancerelle Y et al (2012) Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. *PLoS One* 7:e47363
- Lang J (1973) Coral reef project—papers in memory of Dr. Thomas F. Goreau. 11. Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. *Bull Mar Sci* 23:260–279
- Lough JM (1999) Sea surface temperatures on the Great Barrier Reef: a contribution to the study of coral bleaching. (Research publication 57) Great Barrier Reef Marine Park Authority. Australian Institute of Marine Science, Townsville
- Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, Van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecol Lett* 4:122–131
- Madin JS, Connolly SR (2006) Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature* 444:477–480
- Madin JS, Baird AH, Dornelas M, Connolly SR (2014) Mechanical vulnerability explains size-dependent mortality of reef corals. *Ecol Lett*. doi:10.1111/ele.12306
- McClanahan TR, Ateweberhan M, Darling ES, Graham NAJ, Muthiga NA (2014) Biogeography and change among regional coral communities across the Western Indian Ocean. *PLoS One* 9:e93385
- Meesters EH, Bos A, Gast GJ (1992) Effects of sedimentation and lesion position on coral tissue regeneration. In: Proceedings of 7th international Coral Reef, vol 2, pp 681–688
- Meesters EH, Noordeloos M, Bak RPM (1994) Damage and regeneration: links to growth in the reef-building coral *Montastraea annularis*. *Mar Ecol Prog Ser* 112:119–128
- Meesters EH, Wesseling I, Bak RPM (1996) Partial mortality in three species of reef-building corals and the relation with coral morphology. *Bull Mar Sci* 58:838–852
- Meesters EH, Wesseling I, Bak RPM (1997) Coral colony tissue damage in six species of reef-building corals: partial mortality in relation with depth and surface area. *J Sea Res* 37:131–144
- Oliver J (1985) Recurrent seasonal bleaching and mortality of corals on the Great Barrier Reef. In: Proceedings of 5th international coral reef congress, vol 4, pp 201–206
- Pisapia C, Pratchett MS (2014) Spatial variation in background mortality among dominant coral taxa on Australia's Great Barrier Reef. *PLoS One* 9:e100969
- Pratchett MS, Pisapia C, Sheppard C (2013) Background mortality rates for recovering populations of *Acropora cytherea* in the Chagos Archipelago, central Indian Ocean. *Mar Environ Res* 86:29–34
- Roberts HH, Rouse LJ, Walker ND, Hudson JH (1982) Cold-water stress in Florida Bay and northern Bahamas—a product of winter cold-air outbreaks. *J Sediment Petrol* 52:145–155
- Stimson J (1985) The effect of shading by the table coral *Acropora hyacinthus* on understory corals. *Ecology* 66:40–53
- Titlyanov EA, Titlyanova TV, Yakovleva IM, Nakano Y, Bhagooli R (2005) Regeneration of artificial injuries on scleractinian corals and coral/algal competition for newly formed substrate. *J Exp Mar Biol Ecol* 323:27–42
- Veron JEN (1986) Corals of Australia and the Indo-Pacific. Angus and Robertson Publishers, London
- Wakeford M, Done TJ, Johnson CR (2008) Decadal trends in a coral community and evidence of changed disturbance regime. *Coral Reefs* 27:1–13
- Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC et al (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749–755
- Yap H, Alino PM, Gomez ED (1992) Trends in growth and mortality of three coral species (Anthozoa: Scleractinia) including effects of transplantation. *Mar Ecol Prog Ser* 83:91–101