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Biennium horribile: very high mortality in the reef coral *Acropora millepora* on the Great Barrier Reef in 2009 and 2010

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ABSTRACT: Coral cover has declined markedly in the recent past in many regions of the world, including the Great Barrier Reef (GBR), Australia. The major causes of this decline are generally considered to be mortality associated with large-scale severe disturbances (i.e. catastrophic mortality), such as *Acanthaster planci* outbreaks, cyclones and bleaching. However, background rates of mortality (i.e. not associated with catastrophic disturbance), are rarely quantified, but without these it is difficult to assess the relative importance of these 2 types of mortality (catastrophic and background). We quantified spatial and temporal variation in catastrophic and background whole-colony mortality of the common reef coral *Acropora millepora* over 24 mo at 2 sites in 3 regions separated by 700 km along the GBR. The study period included 2 cyclones and a flood. Overall mortality rates were exceptionally high. Of 180 colonies tagged in April 2009, only 36 (20%) were alive in April 2011, and 68% of this mortality occurred in intervals following the 3 large disturbances. Background mortality rates were also high in the Palm Islands, where they approached 40% yr^{-1} compared to <5% in the Whitsunday and Keppel Islands. These results support the hypothesis that catastrophic mortality has been the major cause of coral loss in recent years on the GBR and also suggest that background rates of mortality are increasing at some locations. Projected increases in the agents of catastrophic mortality, such as cyclones and bleaching, as a result of global warming are likely to threaten the persistence of many coral species.

KEY WORDS: Coral reefs · Catastrophe · Cyclone · Disturbance · Flood

INTRODUCTION

Coral assemblages are highly dynamic (Hughes & Jackson 1985, Hughes & Connell 1999, Edmunds 2002). Despite the fact that catastrophic events on coral reefs occur quite frequently, until recently, background mortality from predation, competition and sedimentation has typically exceeded mortality caused by catastrophic disturbances (Connell 1973, Hughes & Jackson 1985, Bythell et al. 1993). However, these historical differences in the relative contribution of catastrophic and background mortality to population dynamics are changing in response to increasing anthropogenic sources of disturbance, in particular climate change and declining water quality, which are combining with natural disturbance to accelerate reef degradation on a global scale (Hughes et al. 2003, 2017a, Pandolfi et al. 2003, Richmond et al. 2007). The Great Barrier Reef (GBR) is no exception, with coral cover at historically low levels throughout most of the region (Bellwood et al. 2004, Hughes et al. 2011, 2017b, 2018a). The main drivers of this coral loss, at least on mid-shelf reefs, have been identified as catastrophic events, in particular cyclones, crown of thorns starfish (COTS) *Acanthaster planci* and bleaching (De'ath et al. 2012), suggesting that the historical

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dominance of background mortality is changing (Done et al. 2010, Hughes et al. 2018b).

Inshore reefs have experienced some of the greatest declines in coral cover seen on the GBR (Osborne et al. 2011, Sweatman et al. 2011). However, they differ from mid- and outer-shelf reefs in terms of the likely sources of mortality. Inshore reefs are not often damaged directly by cyclones, particularly on the sheltered side of high islands near the coast, and COTS outbreaks are rare (Pratchett et al. 2014). The main threats to inshore reefs are related to declines in water quality associated with agriculture and coastal development (Fabricius & De'ath 2004, Brodie et al. 2012, Kroon et al. 2012, Clark et al. 2017); water clarity is typically one-third of that found on mid-shelf reefs, and chlorophyll levels (a proxy for nutrient loads) are twice that of those found on mid-shelf reefs (De'ath & Fabricius 2010). In addition, inshore reefs are much more likely to be affected by floods (Brodie et al. 2012). The different nature of the disturbance regime is likely to affect the relative contribution of catastrophic versus background mortality to population dynamics.

Mortality rates in corals are generally size-specific (Hughes & Jackson 1980, 1985, Babcock 1991, Bythell et al. 1993) but also depend on colony shape (Madin & Connolly 2006). For example, the probability of whole-colony mortality increases for some morphologies, such as tabular species above a certain size, producing bath-tub shaped mortality curves (Madin et al. 2014). Similarly, mass transfer theory (Nakamura & van Woesik 2001) and empirical results suggest that small colonies, at least of some species (Alvarez-Noriega et al. 2018), are more resistant to bleaching mortality.

The aim of this study was to document spatial and temporal variation in whole-colony mortality among coral populations on inshore reefs in 3 regions separated by 700 km along the GBR. Individually tagged coral colonies were followed in order to (1) compare the contribution of mortality associated with catastrophic disturbance to that of background mortality and (2) to assess the patterns of mortality as a function of colony size. Environmental variables indicative of potential stressors were collated in order to explore relationships between these variables and colony mortality at the regional scale.

MATERIALS AND METHODS

Study sites and species

This study was conducted on the fringing reefs at 2 sites in each of 3 regions separated by approximately 5° of latitude along the GBR: Orpheus Island (18.62° S, 146.48° E) and Pelorus Island (18.55° S, 146.48° E) in the Palm Island region; Hook Island (20.17° S, 148.90° E) and Mid-Molle Island (20.23° S, 148.82° E) in the Whitsunday Island region; and Miall Island (23.15° S, 150.90° E) and Halfway Island (23.18° S, 150.97° E) in the Keppel Island region (Fig. 1). All sites were less than 20 km from the mainland and located on the western or leeward side of the islands at depths of between 1 and 3 m.

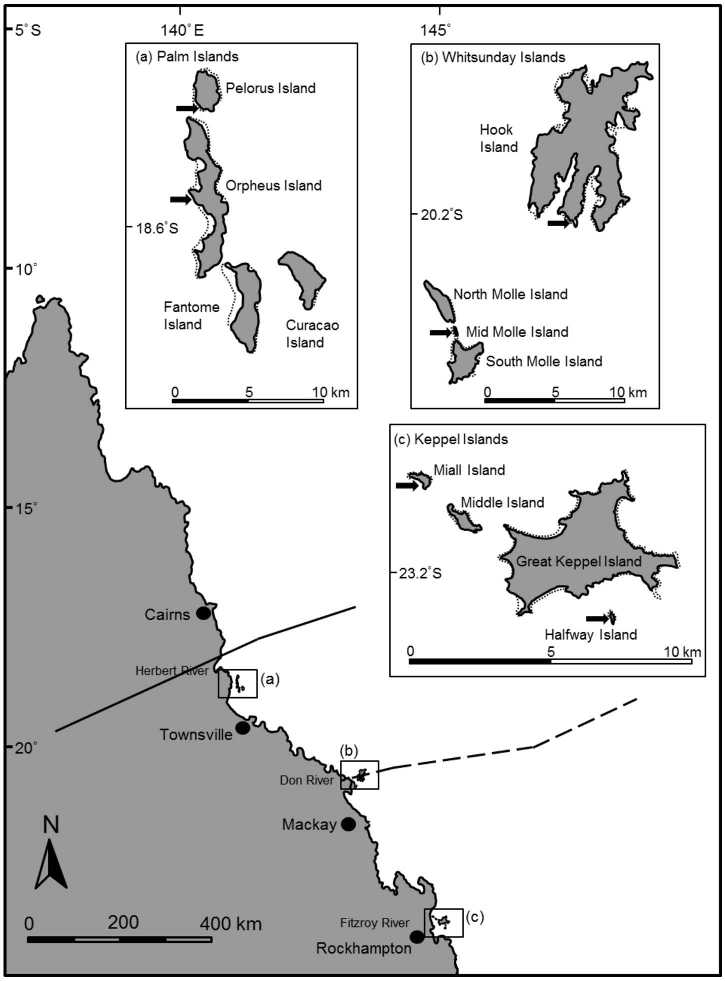

Fig. 1. Three sampling regions on the Great Barrier Reef. Insets show (a) Palm Islands (18° S), (b) Whitsunday Islands (20° S) and (c) Keppel Islands (23° S). Arrows indicate the exact position of sites within regions. Solid and dashed lines represent the tracks of Cyclones Yasi and Ului, respectively (Australian Bureau of Meteorology, www.bom.gov.au/cyclone/history/index.shtml)

Acropora millepora is a corymbose species, common in shallow water on most inshore reefs and in protected areas on mid- and outer-shelf reefs along most of the length of the GBR (Veron & Wallace 1984). The coral assemblages at all of the study sites were similar to one another and characteristic of assemblages on the western or leeward side of high islands on the GBR.

Sampling method

At each site, 30 *A. millepora* colonies were tagged in April or May 2009 and then revisited on another 4 trips over the next 2 yr, with the final trip in April 2011 (Table 1). Only colonies likely to be reproductively mature (maximum diameter >16 cm; Hall & Hughes 1996) and with no tissue damage were tagged. The track swum on the first sampling trip was logged using a GPS towed on a flotation device, and the position of each colony was recorded on this track. Laminated photographs of the position of all colonies with respect to the surrounding substratum were also prepared to assist in the location and identification of individuals on subsequent sampling trips.

Mortality estimates

Colonies were classified as dead when there was no live tissue remaining. Colonies that could not be relocated on 2 consecutive sampling trips were presumed to have been dislodged and were also classified as dead. Catastrophic mortality was defined as whole-colony mortality that occurred in sampling intervals affected by major disturbances that included 2 major cyclones and a large flood of the Fitzroy River. Following the cyclones, dead colonies were either overturned or could not be found, suggesting they had been dislodged by waves. Following the Fitzroy River flood, colonies remained attached but with 100% tissue loss. Background mortality was defined as whole-colony mortality that could not be attributed to catastrophic events.

Colony size and mortality

On each sampling occasion, all tagged colonies were photographed using a Canon Powershot G11 from approximately 1.5 m above and perpendicular to the surface of the colony to quantify horizontal planar surface area. A pre-calibrated 10 × 10 cm white Perspex scale bar was placed on the surface of each colony when photographed. Photographs were corrected for barrel distortion, and then horizontal planar surface area was quantified for each coral colony using the software package ImageJ (http://rsbweb.nih.gov/ij/).

Potential sources of mortality during the study

Three large-scale disturbance events occurred during the course of the study: 2 tropical cyclones and a major flood. Cyclone Ului formed on 9 March 2010 in the Coral Sea and made landfall on 21 March 2010, near Airlie Beach (20.27° S, 148.71° E) as a category 3 system (Australian Bureau of Meteorology, www.bom.gov.au/cyclone/history/ului.shtml).The closest wave-monitoring buoy at Hay Point (21.27° S, 149.31° E) recorded the highest single wave of 6.3 m at 04:30 h on 21 March 2010 (Queensland Government 2015a). Based on the track of Cyclone Ului (Fig. 1) it would have been expected to affect sites in the Whitsunday Islands. Cyclone Yasi developed on 29 January 2011 and made landfall at Mission Beach (18.13° S, 146.02° E), approximately 50 km north of the Palm Islands on 3 February 2011 as a category 5 system (Australian Bureau of Meteorology, www.bom.gov.au/cyclone/history/yasi.shtml). The nearest wave-monitoring buoy at Townsville (19.17° S, 147.07° E) recorded the highest single wave of 10.1 m at 01:00 h on 3 February 2011 (Queensland Government 2015b). Based on the track of Cyclone Yasi, it would have been expected to affect sites in the Palm Islands (Fig. 1). Finally, a strong La Niña event in the Pacific Ocean, with the highest recorded December Southern Oscillation Index since 1973 of +27.1, caused heavy rainfall in the Fitzroy River catchment, resulting in a major

Table 1. Dates of sampling trips conducted over 2 yr in 3 regions of the Great Barrier Reef, Australia

Region	Trip				
	1	2	3	4	5
Palm Islands	02–03 April 2009	28 October 2009	21 April 2010	30 September 2010	17 April 2011
Whitsunday Islands	13–14 May 2009	24 October 2009	19 April 2010	27 September 2010	14 April 2011
Keppel Islands	24–25 April 2009	1 November 2009	18 April 2010	28 September 2010	13 April 2011

flood event in January 2011 (Australia Bureau of Meteorology 2011). More than 15 million Ml of water flowed past The Gap station on the Fitzroy River in January, contributing to a total flow of 33 million Ml recorded in the 2010–2011 wet season. This was the largest flood of the Fitzroy since 1991, and the third biggest on record (Australian Bureau of Meteorology 2011). The resulting flood-plume extended >300 km north to Mackay on 25 January 2011 (Brodie et al. 2012). The flood was expected to affect sites in the Keppel Islands.

Environmental variables

To characterize the environmental conditions at each site throughout the study period, a suite of environmental metrics were collated. *In situ* temperature data were obtained from the Australian Institute of Marine Science (AIMS) from the following locations in each region: Palm Islands (Pioneer Bay, 18.61° S, 146.48° E), Whitsunday Islands (Daydream, 20.26° S, 148.81° E) and Keppel Islands (Halfway, 23.20° S, 150.97° E). Data was collected using 'Sensus SST' temperature loggers (AIMS 2018).

To compare variation in heat stress among sites during the wet seasons in 2009–2010 and 2010–2011, the GPS coordinates of each site were used to extract site-specific seasonal sea surface temperature anomaly (SSTA) values (mean seasonal minimum, maximum and median), using the Australian Bureau of Meteorology's (BOM) eReefs Marine Water Quality Dashboard website (www.bom.gov.au/marinewater quality/) and ReefTemp Next Generation (RTNG). RTNG is a monitoring tool that uses SST data gathered by National Oceanic and Atmospheric Administration satellites and processed by BOM's Integrated Marine Observing System (IMOS) to produce high-resolution maps of thermal stress across the Great Barrier Reef (Garde et al. 2014).

Turbidity (optical backscatter) and chlorophyll fluorescence data were provided by AIMS's Marine Monitoring Program. These data were not available for each of the sites so we used data from the following collection stations to represent each region: Palm Islands (18.54° S, 146.49° E), Whitsunday Islands (20.26° S, 148.81° E) and Keppel Islands (23.22° S, 150.96° E). For details on methods of collection of the turbidity and chlorophyll fluorescence measures, see Schaffelke et al. (2012).

Daily river discharge data were obtained from the Queensland Government Department of Natural Resources and Mines Water Monitoring Portal (https://www.dnrm.qld.gov.au/water/water-monitoring-and-data/portal). The rivers and GPS coordinates of the loggers for each region were: the Herbert River (18.63° S, 146.14° E) for the Palm Islands, the Don River (20.15° S, 148.16° E) for the Whitsunday Islands and the Fitzroy River (23.09° S, 150.11° E) for the Keppel Islands.

Statistical analysis

Mortality was highly patchy both spatially and temporally; we therefore present these results qualitatively. To determine if the relationship between colony size and survival of *A. millepora* colonies was the same at all sites, a generalized linear model with binomial error structure was fit to survival data for background and catastrophic mortality. The relationship between catastrophic mortality and colony size was tested using survival at 3 sites: Orpheus and Pelorus Islands following Cyclone Yasi and Hook Island following Cyclone Ului. The relationship between size and catastrophic mortality was not tested following flooding in the Keppel Islands because all colonies were killed at both sites. The relationship between background mortality and colony size was tested using mortality values in the 18 mo period between April 2009 and October 2010 at Orpheus and Pelorus Islands. Again, it was not possible to test this relationship quantitatively in either the Keppel or Whitsunday Islands because there was too little background mortality (no change in survival between sampling intervals at these sites; Table 2) or too few colonies remaining (e.g. Hook Island between October 2010 and April 2011; Table 2). Initially, a maximal model with both surface area (log10 transformed to reduce positive skewness in size) and site as fixed factors was fit to survival following each type of disturbance. Model terms were simplified and Akaike's information criterion (AIC) was used to select the model with the best fit to the data. All analyses were conducted in R 3.1.2 (R Core Team 2014).

RESULTS

Spatial and temporal patterns of whole-colony mortality

A very high incidence of whole-colony mortality was recorded in the 2 yr of this study, with >80 % of individuals dead or lost at 5 of the 6 sites (Table 2, Fig. 2). Most mortality was associated with catastro-

Table 2. Patterns of whole-colony mortality in *Acropora millepora* at 6 sites in 3 regions on the Great Barrier Reef between April 2009 and April 2011

Region/site	n (Apr-09)	Number dead (%)	n (Oct-09)	Number dead (%)	n (Apr-10)	Number dead (%)	n (Oct-10)	Number dead (%)	n (Apr-11)
Palm Islands									
Orpheus	30	4 (13)	26	10 (39)	16	5 (31)	11	9 (82)	2
Pelorus	30	4 (13)	26	8 (31)	18	5 (28)	13	8 (62)	5
Whitsunday Islands									
Hook	30	1 (3)	29	22 (76)	7	0	7	4 (57)	3
Mid-Molle	30	1 (3)	29	0	29	2 (7)	27	1 (4)	26
Keppel Islands									
Miall	30	0	30	0	30	0	30	30 (100)	0
Halfway	30	0	30	1 (3)	29	0	29	29 (100)	0

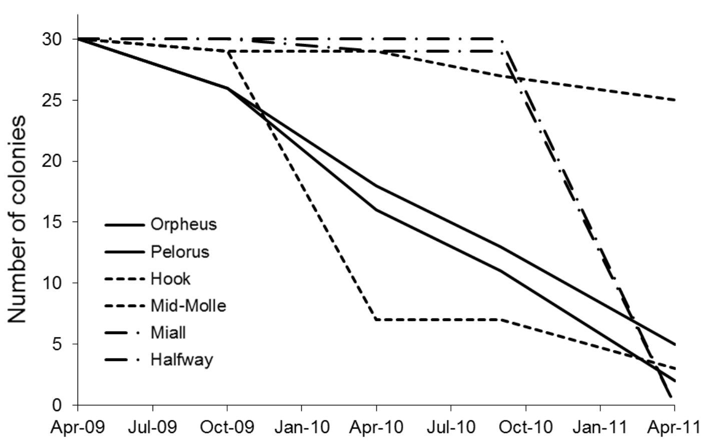

Fig. 2. Change in the number of *Acropora millepora* colonies alive through time at each study site on the Great Barrier Reef. Cyclone Yasi crossed the coast close to Orpheus and Pelorus Islands in March 2011 and Cyclone Ului crossed the coast close to Mid-Molle and Hook Islands in March 2009 (see Fig. 1 for the tracks of these cyclones)

phic disturbances: 68% of colonies died in the intervals that included Cyclone Ului or Yasi or the flooding of the Fitzroy River (Table 2, Fig. 2). Cyclone Yasi affected both sites in the Palm Islands, causing 62 and 82% mortality, respectively (Table 2). In contrast, the effects of Cyclone Ului were patchy, with 76% mortality at Hook Island compared to 0% at Mid-Molle Island (Table 2, Fig. 2). The Fitzroy flood was particularly destructive, with all 59 colonies that were alive in the previous census in the Keppel Islands dying in the interval that included the flood (Table 2, Fig. 2).

Background mortality rates varied substantially among sites (Table 2). There was almost no background mortality in either the Whitsunday or the Keppel Islands: only 10 of the original 120 colonies died in intervals that were not affected by catastrophic disturbance, and 4 of these deaths occurred at Hook Island between October and April in 2010–2011 (Table 2). In contrast, rates of background mortality in the Palm Islands ranged from 13–39% (Table 2). In the Palm Islands, deaths that occurred in intervals unaffected by catastrophic disturbance were more than twice those that occurred in affected intervals (36 vs. 17) (Table 2).

Colony size and mortality

Colony size was not associated with survival in response to either catastrophic or background mortality (Fig. 3, Tables 3 & 4). For catastrophic mortality, the model with the best fit to the data was the null model with no effect of colony size or site (Table 3). For background mortality, even though the best fitting model had size as the only explanatory variable, none of the parameter estimates were significant (Table 4). Nonetheless, the 14 colonies out of the original 30 tagged at Orpheus Island that died in the 18 mo interval between April 2009 and October 2010 included the 6 largest colonies at this site (Fig. 3).

Environmental variables and correlations with background mortality

Average annual SSTs varied predictably with latitude and season. Mean daily SSTs were higher in the summer and increased from south to north (Table 5). No SSTAs were detected during summer in the course of the study at the regional scale (Table 6).

Turbidity was higher on average and more variable in the Whitsunday Islands and higher during the wet season (October–April) than the dry season (April–October) (Fig. 4a, Table 7). A prominent peak in tur-

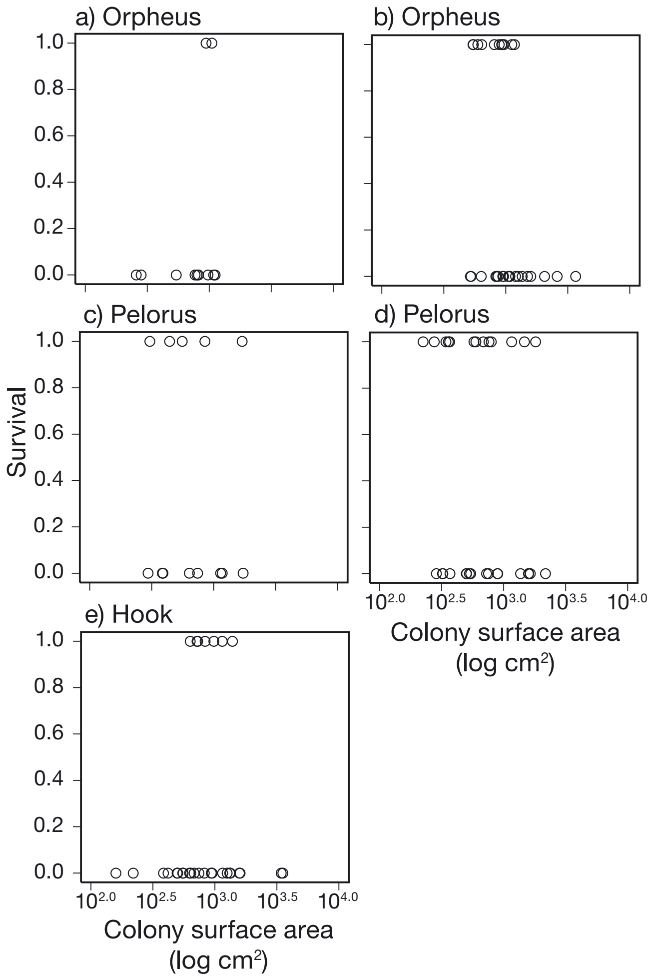

Fig. 3. Survival of *Acropora millepora* colonies at Orpheus, Pelarus and Hook Islands, Great Barrier Reef, as a function of size during (a,c,e) acute and (b,d) chronic disturbances

bidity in the Whitsunday Islands was associated with Cyclone Ului in late January 2010; otherwise, there were no obvious peaks in turbidity in the first year of the study (Fig. 4a, Table 7).

Chlorophyll was on average very similar among the regions and throughout the year, with the exception of a peak in the Keppel Islands between October 2009 and April 2010 following the flooding of the Fitzroy River in January 2010 (Fig. 4b, Table 7). There were also a number of peaks in chlorophyll in the Palm Islands between April 2009 and 2010 (Fig. 4b).

DISCUSSION

Patterns of whole-colony mortality in the 6 populations of *Acropora millepora* were dominated by catastrophic mortality following 3 large disturbance events: Cyclone Ului that killed 76% of colonies at Hook Island; Cyclone Yasi that killed 70% of colonies at 2 sites in the Palm Islands; and the flooding of the Fitzroy River that killed 100% of colonies in the Keppel Islands. Overall, deaths following catastrophic disturbance outnumbered background whole-colony mortality by more than 2 to 1 (98 vs. 46; Table 2). Nonetheless, there were striking differences in the rates of background mortality in periods between these catastrophic events amongst the regions. Rates of background mortality were at least 14-fold higher at sites in the Palm Islands than at sites in the other 2 regions (43 vs. 3% yr^{-1} in the first year of the study; Table 2). Only 36 (20%) of the original 180 colonies were alive after 2 yr, and 26 of these colonies were at 1 site (Mid-Molle Island; Table 2).

Whole-colony mortality following catastrophic disturbances, such as cyclones, is generally high but patchy (Woodley et al. 1981, Done 1992, Connell et al. 1997). In this respect, Cyclone Ului was typical, with 76% mortality at Hook Islands and 0% at Mid-Molle Island, only 8 km to the south-east (Table 2, Fig. 2). In contrast, Cyclone Yasi caused very high mortality at both sites in the Palm Islands, and the flooding of the Fitzroy River killed 100% of colonies in the Keppel Is-

Table 3. Parameter estimates for the catastrophic disturbance binomial regression models and Akaike's information criterion (AIC) used for model comparison. **Bold** type indicates significant ($p < 0.05$) parameter estimates and lowest AIC. Sites used in the analysis are Palm Island, Orpheus Island and Hook Island. (–) Variable not included in the model

Parameter	(1) Size × Site		(2) Size + Site		(3) Size		(4) Site		(5) Null	
	Estimate	p	Estimate	p	Estimate	p	Estimate	p	Estimate	p
Intercept	−2.94	0.52	−3.12	0.38	−2.51	0.46	**−1.19**	**0.01**	**−1.05**	**0.01**
log (Size)	0.60	0.70	0.66	0.58	0.50	0.67	–	–	–	–
SiteOrpheus	−34.21	0.41	−0.27	0.76	–	–	−0.31	0.72	–	–
SitePelorus	3.72	0.63	0.78	0.28	–	–	0.72	0.31	–	–
log(Size) : SiteOrpheus	11.49	0.41	–	–	–	–	–	–	–	–
log(Size) : SitePelorus	−1.04	0.70	–	–	–	–	–	–	–	–
AIC	70.21		68.05		65.62		66.35		**63.81**	

Table 4. Parameter estimates for the background disturbance binomial regression models and Akaike's Information Criterion (AIC) used for model comparison. **Bold** type indicates lowest AIC. Sites used in the analysis are Palm Island and Orpheus Island. (–) Variable not included in the model

Parameter	(1) Size × Site Estimate	p	(2) Size + Site Estimate	p	(3) Size Estimate	p	(4) Site Estimate	p	(5) Null Estimate	p
Intercept	14.98	0.07	5.97	0.10	5.69	0.08	–0.55	0.15	–0.41	0.12
log (Size)	–5.22	0.06	–2.18	0.07	–2.10	0.06	–	–	–	–
SitePelorus	–12.02	0.19	–0.10	0.86	–	–	0.28	0.60	–	–
log(Size) : SitePelorus	4.08	0.19	–	–	–	–	–	–	–	–
AIC	82.98		82.96		**80.99**		84.48		82.76	

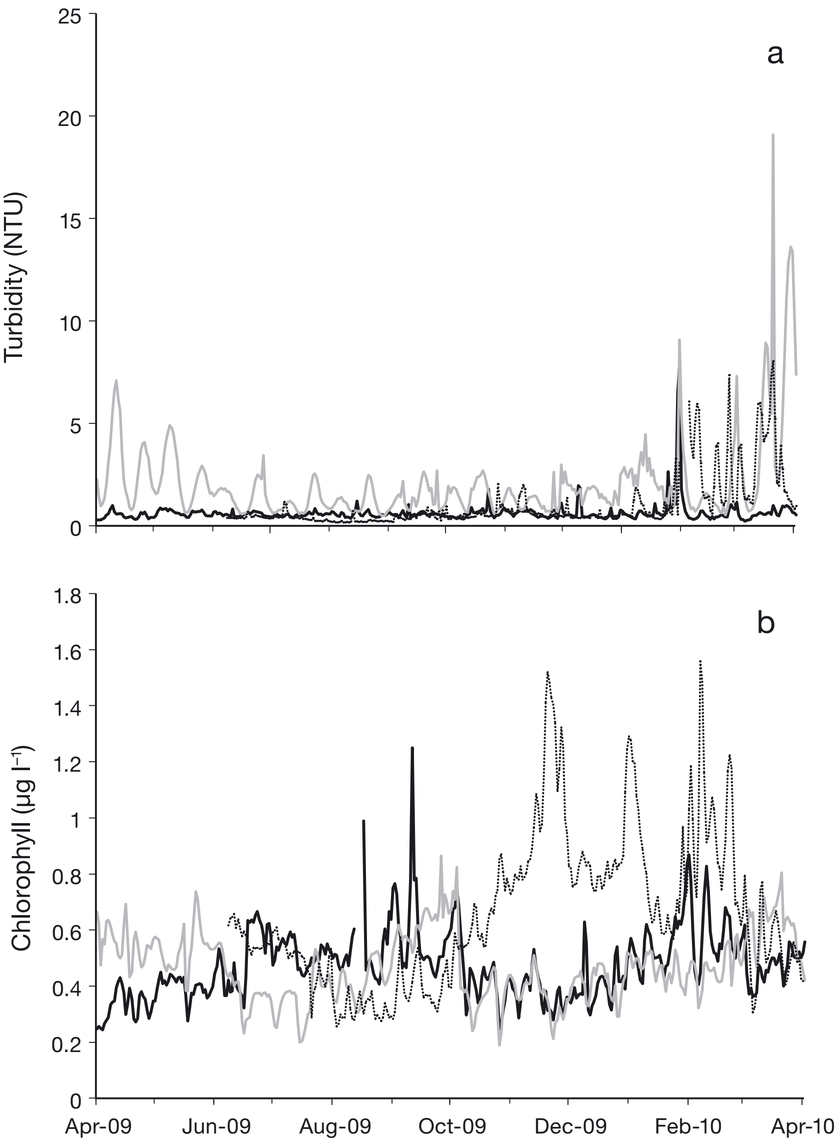

Fig. 4. Annual changes in (a) turbidity and (b) chlorophyll fluorescence among the 3 study regions. Solid black line represents Palm Islands, grey line represents Whitsunday Islands and dotted black line represents Keppel Islands

lands (Table 2). Indeed, the flood killed 100% of corals down to approximately 6 m depth at these sites in the Keppel Islands (Tan et al. 2012). These were atypical events. Cyclone Yasi was the largest cyclone to affect the Queensland coast in the last 30 yr (Australian Bureau of Meteorology, www.bom.gov.au/cyclone/history/yasi.shtml). Similarly, the flooding of the Fitzroy River in January 2011 was the third largest on record (Australian Bureau of Meteorology 2011). Both Cyclone Yasi and the floods caused extensive mortality to reefs over a very large scale (Berkelmans et al. 2012, Jones & Berkelmans 2014, Beeden et al. 2015). However, projected increases in the intensity of cyclones (Knutson et al. 2010, Cheal et al. 2017) suggest that catastrophic losses of corals as reported here will become commonplace in the future.

Despite a recent focus on catastrophic disturbance (e.g. De'ath et al. 2012), background mortality was generally thought to dominate mortality schedules in corals. For example, between 1963 and 1993, mortality attributed to catastrophic disturbance accounted for less than one-third of the whole-colony mortality in coral assemblages on Heron Island (Hughes & Connell 1999). Similar patterns were evident in St. Croix, in the Caribbean (Bythell et al. 1993). However, annualized rates of background mortality of over 40% yr^{-1}, as found in Palm Island in the current study, are high when compared to more recent estimates from similar taxa. For example, annual

Table 5. *In situ* seawater temperature (°C) in the 3 regions in the 4 sampling intervals between April 2009 and April 2011

Region	October 2009–April 2010			April–October 2010			October 2010–April 2011			April–October 2011		
	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Palm Islands	25.0	0.10	22.4–28.1	28.3	0.09	25.9–29.8	24.7	0.10	22.3–27.4	28.2	0.08	26.1–30.2
Whitsunday Islands	24.4	0.11	21.7–27.5	27.8	0.10	25.3–29.6	24.1	0.10	21.6–27.1	27.4	0.09	25.5–28.7
Keppel Islands	22.7	0.13	19.8–26.3	26.9	0.09	24.3–28.3	22.3	0.12	19.8–26.4	26.5	0.11	23.8–28.3

Table 6. Site-specific sea surface temperature anomalies (SSTAs) during the wet seasons in 2009–2010 and 2010–2011. SSTA values were calculated as the difference between mean seasonal SST values and the long-term seasonal average SST for each site. Data were extracted from the Australian Bureau of Meteorology's eReef Marine Water Quality Dashboard using IMOS climatology (www.bom.gov.au/marinewaterquality/)

Region	Site	SSTA (°C) 1 November 2009–30 April 2010			SSTA (°C) 1 November 2010–30 April 2011		
		Minimum	Maximum	Median	Minimum	Maximum	Median
Palm Islands	Orpheus	−1.48	1.51	−0.26	−1.38	0.80	−0.13
	Pelorus	−1.34	1.85	0.20	−0.92	1.34	−0.14
Whitsunday Islands	Hook	−1.02	1.64	0.28	−1.10	0.65	−0.06
	Mid-Molle	−1.71	2.53	0.26	−2.13	0.99	−0.22
Keppel Islands	Miall	−2.15	1.42	−0.04	−1.75	1.38	−0.25
	Halfway	−1.54	1.27	−0.18	−2.20	1.70	0.14

Table 7. Chlorophyll density and turbidity in the 3 regions in 2 sampling intervals between April 2009 and April 2010. Data from the Marine Monitoring Program, Great Barrier Reef Marine Park Authority (pers. comm.)

Region	Chlorophyll density (μg l^{-1}) April–October 2009			Chlorophyll density (μg l^{-1}) October 2009–April 2010			Turbidity (NTU) April–October 2009			Turbidity (NTU) October 2009–April 2010		
	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Palm Islands	0.47	0.009	0.24–1.25	0.48	0.009	0.28–0.87	0.56	0.011	0.32–1.80	0.70	0.066	0.22–7.83
Whitsunday Islands	0.47	0.009	0.19–0.86	0.46	0.009	0.21–0.80	1.70	0.080	0.48–7.08	2.51	0.229	0.54–19.08
Keppel Islands	0.48	0.011	0.26–0.87	0.83	0.021	0.31–1.56	0.42	0.019	0.16–2.05	1.60	0.142	0.34–8.03

rates of background mortality in *A. millepora* on Lizard Island in a 15 yr study were approximately 10% yr^{-1} (Wakeford et al. 2008) and rates of background mortality in 2 corymbose *Acropora* species on Lizard Island were 18% yr^{-1} over a 5 yr period (Madin et al. 2014). In addition, estimated rates of whole-colony mortality in *A. millepora* of 32% following a major bleaching event in the Palm Islands in 1998 (Baird & Marshall 2002) are lower than the 40% yr^{-1} background rates we recorded in the Palm Islands. These comparisons suggest that the rates of background mortality in the Palm Islands between 2009 and 2011 were unusually high and, just like catastrophic mortality, might also be increasing in some regions of the GBR. This combination of increased catastrophic and background mortality had resulted in the degradation of coral assemblage in the Palm Islands to the point where recovery of the former assemblage structure is unlikely (Torda et al. 2018).

The causes of high rates of background mortality in the Palm Islands are unknown. Dead colonies remained attached and covered with filamentous algae (except after Cyclone Yasi, when they were overturned or could not be relocated). COTS *Acanthaster planci* were never observed at sites in the Palm Islands, or indeed, at any of the study sites during the monitoring period. In addition, while coral disease caused high rates of tissue loss in *Montipora* spp. on the exposed side of Pelorus Island in 2008 (Sato et al. 2009), no disease was observed on any of the tagged *A. millepora* colonies in the Palm Islands, or indeed on any colonies at any of these sites during this study (C. H. Tan pers. obs.). In addition, there was no indication of thermal, sediment, nutrient or osmotic stress in periods not subject to catastrophic disturbance. Seawater temperatures were not unusually high in the summer of 2009–2010 (Fig. 4, Tables 5 & 6). While there were 4 peaks in chlorophyll in the Palm Islands between

April 2009 and April 2010 (Fig. 4b), much larger peaks in the Keppel Islands did not affect background mortality at those sites. One of these peaks also coincided with a peak in turbidity in February 2010 (Fig. 4a); however, much higher levels of turbidity in the Whitsunday Islands and the Keppel Islands did not affect rates of background mortality (Fig. 4a). The 14 deaths attributed to background disturbance at Orpheus Island included the 6 largest colonies of the original 30, suggesting senescence might be involved, but the effect of colony size was not statistically significant.

In contrast to high rates of background mortality in the Palm Islands, rates in the Whitsunday and Keppel Islands were very low. In the Whitsunday Islands, only 7 deaths could not be attributed to Cyclone Ului, and 4 of these deaths occurred between October 2010 and April 2011 at Hook Island, a per capita mortality of 57%, i.e. 50% higher than the background mortality rates during any other interval (Table 2). This suggests a more localized but intense disturbance event, such as a gale. In the Keppel Islands, only 1 of the 60 tagged colonies died in the 18 mo interval that preceded the flooding of the Fitzroy River. These rates of background mortality contrast with the high rates in the Palm Islands and indicate that background mortality rates of whole colonies can be exceptionally low when conditions are favourable. Such conditions are unlikely to prevail for long periods on reefs in the future (Hughes et al. 2017a, Frölicher et al. 2018).

These were 2 horrible years for *A. millepora* on inshore reefs on the GBR. Background rates of mortality at sites in the Palm Islands were higher than other recent estimates from the GBR, and the high proportion of mortality associated with catastrophic disturbances is also in striking contrast to earlier estimates from the GBR (Connell 1973, Connell et al. 2004). Corals have evolved to deal with a high frequency and intensity of disturbance (Richmond 1993). Indeed, most of these sites have been affected by catastrophic disturbance in the recent past, for example, bleaching in the Palm Islands in 1998 (Baird & Marshall 1998) and the Keppel Islands in 2008 (Diaz-Pulido et al. 2009) and flooding in the Keppel Islands in the early 1990s (Van Woesik et al. 1995); yet they have recovered. However, projected increases in both background mortality from sub-lethal temperature stress (Donner 2009) and the intensity of large storms (Knutson et al. 2010, Cheal et al. 2017) in response to continuing global warming suggests that disturbance regimes on reefs are changing and that there are potentially many more bad years in store for corals on the GBR and elsewhere (Frölicher et al. 2018, Hughes et al. 2018b).

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LITERATURE CITED

Álvarez-Noriega M, Baird AH, Bridge TCL, Dornelas M and others (2018) Contrasting patterns of changes in abundance following a bleaching event between juvenile and adult scleractinian corals. Coral Reefs 37:527–532

Australian Bureau of Meteorology (2011) Flood summary for the Fitzroy River at Rockhampton — December 2010 and January 2011. www.bom.gov.au/qld/flood/fld_reports/rockhampton_fact_sheet_2011.pdf

Babcock RC (1991) Comparative demography of three species of scleractinian corals using age-dependent and size-dependent classifications. Ecol Monogr 61:225–244

Baird AH, Marshall PA (1998) Mass bleaching of corals on the Great Barrier Reef. Coral Reefs 17:376

Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 237:133–141

Beeden R, Maynard J, Puotinen M, Marshall P, Dryden J, Goldberg J, Williams G (2015) Impacts and recovery from severe tropical cyclone Yasi on the Great Barrier Reef. PLOS ONE 10:e0121272

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833

Berkelmans R, Jones AM, Schaffelke B (2012) Salinity thresholds of *Acropora* spp. on the Great Barrier Reef. Coral Reefs 31:1103–1110

Brodie JE, Kroon FJ, Schaffelke B, Wolanski EC and others (2012) Terrestrial pollutant runoff to the Great Barrier Reef: an update of issues, priorities and management responses. Mar Pollut Bull 65:81–100

Bythell JC, Gladfelter EH, Bythell M (1993) Chronic and catastrophic natural mortality of three common Caribbean reef corals. Coral Reefs 12:143–152

Cheal AJ, MacNeil MA, Emslie MJ, Sweatman H (2017) The threat to coral reefs from more intense cyclones under climate change. Glob Change Biol 23:1511–1524

Clark TR, Roff G, Zhao JX, Feng YX, Done TJ, McCook LJ, Pandolfi JM (2017) U-Th dating reveals regional-scale decline of branching *Acropora* corals on the Great Barrier Reef over the past century. Proc Natl Acad Sci USA 114:10350–10355

Connell JH (1973) Population ecology of reef building corals. In: Jones OA, Endean R (eds) Biology and geology of coral reefs, Book II. Academic Press, New York, NY, p 205–245

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol Monogr 67:461–488

Connell JH, Hughes TE, Wallace CC, Tanner JE, Harms KE, Kerr AM (2004) A long-term study of competition and diversity of corals. Ecol Monogr 74:179–210

De'ath G, Fabricius K (2010) Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. Ecol Appl 20:840–850

De'ath 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 USA 109:17995–17999

Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R and others (2009) Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. PLOS ONE 4:e5239
Done TJ (1992) Phase-shifts in coral-reef communities and their ecological significance. Hydrobiologia 247:121–132
Done TJ, DeVantier LM, Turak E, Fisk DA, Wakeford M, van Woesik R (2010) Coral growth on three reefs: development of recovery benchmarks using a space for time approach. Coral Reefs 29:815–833
Donner SD (2009) Coping with commitment: projected thermal stress on coral reefs under different future scenarios. PLOS ONE 4:e5712
Edmunds PJ (2002) Long-term dynamics of coral reefs in St. John, US Virgin Islands. Coral Reefs 21:357–367
Fabricius KE, De'ath G (2004) Identifying ecological change and its causes: a case study on coral reefs. Ecol Appl 14: 1448–1465
Frölicher TL, Fischer EM, Gruber N (2018) Marine heatwaves under global warming. Nature 560:360–364
Garde LA, Spillman CM, Heron SF, Beeden RJ (2014) ReefTemp next generation: a new operational system for monitoring reef thermal stress. J Operation Oceanogr 7: 21–33
Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. Ecology 77:950–963
Hughes TP, Connell JH (1999) Multiple stressors on coral reefs: a long-term perspective. Limnol Oceanogr 44:932–940
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
Hughes TP, Baird AH, Bellwood DR, Card M and others (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933
Hughes TP, Bellwood DR, Baird AH, Brodie J, Bruno JF, Pandolfi JM (2011) Shifting base-lines, declining coral cover, and the erosion of reef resilience: comment on Sweatman et al. (2011). Coral Reefs 30:653–660
Hughes TP, Barnes ML, Bellwood DR, Cinner JE and others (2017a) Coral reefs in the Anthropocene. Nature 546:82–90
Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG and others (2017b) Global warming and recurrent mass bleaching of corals. Nature 543:373–377
Hughes TP, Anderson KD, Connolly SR, Heron SF and others (2018a) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83
Hughes TP, Kerry JT, Baird AH, Connolly SR and others (2018b) Global warming transforms coral reef assemblages. Nature 556:492–496
Jones AM, Berkelmans R (2014) Flood impacts in Keppel Bay, southern Great Barrier Reef in the aftermath of cyclonic rainfall. PLOS ONE 9:e84739
Knutson TR, McBride JL, Chan J, Emanuel K and others (2010) Tropical cyclones and climate change. Nat Geosci 3:157–163
Kroon FJ, Kuhnert PM, Henderson BL, Wilkinson SN and others (2012) River loads of suspended solids, nitrogen, phosphorus and herbicides delivered to the Great Barrier Reef lagoon. Mar Pollut Bull 65:167–181
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 17:1008–1015
Nakamura T, van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar Ecol Prog Ser 212:301–304
Osborne K, Dolman AM, Burgess SC, Johns KA (2011) Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995–2009). PLOS ONE 6:e17516
Pandolfi JM, Bradbury RH, Sala E, Hughes TP and others (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–958
Pratchett MS, Caballes CF, Rivera-Posada JA, Sweatman HPA (2014) Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster* spp.). In: Hughes RN, Hughes DJ, Smith IP (eds) Oceanogr Mar Biol Annu Rev, Vol 52. Taylor & Francis, Boca Raton, Fl, p 133–199
Queensland Government (Department of Environment and Science) (2015a) Hay Point wave monitoring. www.qld.gov.au/environment/coasts-waterways/beach/waves-sites/hay-point
Queensland Government (Department of Environment and Science) (2015b) Townsville wave monitoring. www.qld.gov.au/environment/coasts-waterways/beach/waves-sites/townsville
R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing Vienna. www.r-project.org
Richmond RH (1993) Coral reefs: present problems and future concerns resulting from anthropogenic disturbance. Am Zool 33:524–536
Richmond RH, Rongo T, Golbuu Y, Victor S and others (2007) Watersheds and coral reefs: conservation science, policy, and implementation. Bioscience 57:598–607
Sato Y, Bourne DG, Willis BL (2009) Dynamics of seasonal outbreaks of black band disease in an assemblage of *Montipora* species at Pelorus Island (Great Barrier Reef, Australia). Proc R Soc B 276:2795–2803
Schaffelke B, Carleton J, Skuza M, Zagorskis I, Furnas MJ (2012) Water quality in the inshore Great Barrier Reef lagoon: implications for long-term monitoring and management. Mar Pollut Bull 65:249–260
Sweatman H, Delean S, Syms C (2011) Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends. Coral Reefs 30:521–531
Tan CH, Pratchett MS, Bay LK, Baird AH (2012) Massive coral mortality following a large flood event. In: Yellowlees D, Hughes TP (eds) Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, 9–13 July 2012. James Cook University, Townsville, p 1–4
Torda G, Sambrook K, Cross P, Sato Y and others (2018) Decadal erosion of coral assemblages by multiple disturbances in the Palm Islands, central Great Barrier Reef. Sci Rep 8:11885
Van Woesik R, De Vantier LM, Glazebrook JS (1995) Effects of Cyclone 'Joy' on nearshore coral communities of the Great Barrier Reef. Mar Ecol Prog Ser 128:261–270
Veron JEN, Wallace CC (1984) Scleractinia of Eastern Australia. Part V. Family Acroporidae, Vol 6. ANU Press, Canberra
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 and others (1981) Hurricane Allen's impact on Jamaican coral reefs. Science 214:749–755

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