Harrison, Hugo B., Álvarez-Noriega, Mariana, Baird, Andrew H., Heron, Scott F., Macdonald, Chancey, and Hughes, Terry P. (2019) *Back-to-back coral bleaching events on isolated atolls in the Coral Sea.* Coral Reefs, 38 (4) pp. 713-719.

Back to back coral bleaching events on isolated atolls in the Coral Sea

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Abstract: Severe bleaching events caused by marine heatwaves over the past four decades have now affected almost every coral reef ecosystem in the world. These recurring events have led to major losses of coral cover, with adverse consequences for tropical reef ecosystems and the people who depend on them. Here, we document two consecutive and widespread coral bleaching events on remote atolls in the Coral Sea in 2016 and 2017. In each year, the proportion of colonies that bleached was strongly related to heat exposure (measured as Degree Heating Weeks, DHW, °C-weeks), depth and coral assemblage structure. Bleaching was more severe at higher DHW exposure, and at sites with a higher proportion of susceptible taxa. Bleaching was also lower at 6 m than at 2 m depth. Despite the severe bleaching in 2016 on reefs in the central section of the Coral Sea Marine Park, total coral cover was not significantly reduced by 2017, suggesting that most bleached corals survived. Moreover, bleaching was less severe in 2017 despite a higher exposure to heat stress. These results indicate that while the isolation of these oceanic reefs provides no refuge from bleaching, low nutrient levels, high wave energy and proximity to cooler deeper waters may make coral on these reefs more resistant to bleaching induced mortality.

Key words: Bleaching, coral reefs, marine heatwave, Coral Sea, Coral Sea Marine Park

INTRODUCTION

Globally, coral reefs are increasingly exposed to episodes of dangerously high sea surface temperatures (Heron et al. 2016; Hughes et al. 2017) and they are projected to experience annual bleaching events by the end of the century if global warming progresses under business-as-usual emission scenarios (van Hooidonk et al. 2013). Indeed, every major coral reef ecosystem has already been exposed to the impact of summer heatwaves associated with climate change (Hughes et al. 2018a). While isolated and remote reefs are spatial refuges from some anthropogenic stressors, such as declining water quality and overfishing (Wooldridge & Done 2009; Sandin et al. 2008), even these reefs are vulnerable to global warming (van Hooidonk et al. 2013; King et al. 2017; Hughes et al. 2017, 2018a).

Unprecedented marine heatwaves, extended periods where water temperatures exceed the long-term summer maximum, disrupt the relationship between corals and their symbiotic algae (*Symbiodinium spp.*). During such events, coral polyps expel their algal symbiont, leading to a pale or ‘bleached’ appearance (Glynn 1984). The effects of coral bleaching are numerous, ranging from short-term physiological damage to widespread mortality (see reviews by Brown 1997; McClanahan et al. in press). The severity of bleaching events is typically correlated with the intensity and duration of marine heatwaves that are measured as Degree Heating Weeks (DHW, °C-weeks) (e.g. Liu et al. 2014, Hughes et al. 2017). As global warming has progressed (Lough et al. 2018), and the length and frequency of marine heatwaves have increased (Oliver et al. 2018), so too has the geographic and ecological footprint of mass bleaching events (Hughes et al. 2018a).

The occurrence of mass coral bleaching has increased steadily since initial reports of widespread coral bleaching in the early 1980s (Glynn 1984; Fisk and Done 1985). Since these first reports, coral bleaching events are occurring more frequently and are increasingly severe (Hughes et al. 2018a). The global bleaching event of 2015/16 affected 75% of Indo-Pacific coral reefs, including 84% of Australia's tropical reefs (Hughes et al. 2018a). During this event, reefs in Australia's Great Barrier Reef (GBR) and Coral Sea were exposed to up to 14 °C-Weeks, causing extreme bleaching and mortality throughout the region (Hughes et al. 2017; Hughes et al. 2018b). A subsequent large-scale marine heatwave with even greater geographic footprint and intensity affected both the GBR and Coral Sea in the austral summer of 2017 (Fig 1; Lough et al. 2018).

In this study, we document the prevalence and severity of coral bleaching during unprecedented back-to-back bleaching events on remote atolls in the Coral Sea, a large oceanic region offshore from the Great Barrier Reef. We show that although these isolated coral reef atolls were not sheltered from coral bleaching, coral cover did not decline significantly in the aftermath of severe bleaching. Moreover, despite greater exposure to thermal stress in 2017, bleaching was less severe than in 2016. Historical data also suggest a long history of disturbance on these atolls and demonstrate the need to understand the cumulative effects of recurrent disturbance events on the current state of these remote reef systems and their potential for recovery.

MATERIALS AND METHODS

Measuring bleaching prevalence and severity, and coral cover

Surveys were conducted on nine atolls in the Coral Sea Marine Park (CSMP) during May 2016 and again in April 2017 (Fig. 1A). Surveyed atolls include four atolls in the central Queensland plateau (Holmes, Herald, Chilcott and Lihou), two isolated atolls (Mellish and Marion), as well as three atolls in the southern CSMP (Kenn, Saumarez and Wreck). Between two and nine sites were surveyed at each atoll, totalling 21 sites in 2016 and 29 sites in 2017, of which 13 were common to both years (Fig. S1; Table S1). All survey sites were selected based on the locations of previous surveys when available (Ayling & Ayling 1985; Oxley et al. 2004; Ceccarelli et al. 2008; Ceccarelli et al. 2009) and prevailing weather conditions. Our survey effort maximised site replication to reflect the available coral reef habitat at each atoll.

At each site, every coral colony > 5 cm in maximum diameter was counted and identified to genus following Veron (2000) in 5 to 10 replicate 1 m^2 quadrats at 2 m and 6 m depths to determine the severity of bleaching and any effect of depth. The level of bleaching was scored across a 6-level categorical scale following Gleason (1993): 1: no bleaching; 2: pale; 3: 1 – 50 % bleached; 4: 50 – 99 % bleached; 5: 100% bleached; 6: recently dead. A total of 8,293 individual coral colonies were surveyed in 622 quadrats throughout the region. Percent coral cover and benthic community compositions were estimated using four replicate 10 m line intercept transects at 2 m and 6 m depths (Loya 1972) to measure changes in coral cover between bleaching events at each site. Transects were placed as closed to previous surveys as possible. Benthic communities were identified to nine hard-coral taxa (*Acropora*, *Faviidae*, *Isopora*, *Poritidae*, *Pocillopora*, *Montipora*, *Stylophora*, *Mussidae*, *Seriatopora*, and other scleractinians), soft corals, and other sessile fauna. Intercept distances along the transect were measured to the nearest cm.

Bleaching probability in response to heat stress

The maximum Degree Heating Weeks (DHW, °C-weeks) values were calculated using the Coral Reef Watch Version 3, 5-km satellite coral bleaching heat stress product suite, for each site for the time period of the surveys. A generalized linear mixed effects model with a binomial error structure distinguishing bleached (categories 2-6) from unbleached corals was fitted to predict the proportion of bleached coral taxa in response to DHW using the '*glmer*' function from the 'lme4' package (Bates et al. 2015). '*Maximum DHW*', '*year*', '*depth*' and an interaction between '*maximum DHW*' and '*year*' were included as fixed effects. '*Taxonomic category*' was included as a random effect. Region and site could not be included in the analysis because no colony in the Southern reefs bleached in 2016, which caused problems with convergence. Genus was included as '*taxonomic category*' whenever there were enough replicates (≥ 80), otherwise family was used. Families with few replicates were grouped into '*other scleractinians*'. The function '*drop1*' was used to check if eliminating fixed factors improved model fit. A separate model without '*taxonomic category*' was fitted and compared to the original model using Akaike information criterion (AIC) to determine whether taxonomic category improved the model prediction.

Measuring the effect of bleaching on coral cover

A linear mixed effects model was fitted to predict coral cover using the '*lmer*' function from the *lme4* package (Bates et al. 2015). '*Year*', '*region*', and an interaction between '*year*' and '*region*' were included as fixed effects and '*site*' and '*taxonomic category*' were included as random effects. The function '*drop1*' was used to check if eliminating fixed factors improved model fit. Two separate models, one without 'taxonomic category' as a random effect and one without '*site*' as a random effect, were fitted and compared to the original model using Akaike information criterion (AIC) to test whether the random effects were important. All analyses were performed in R version 3.3.2 (R Core Team 2016).

RESULTS AND DISCUSSION

Extensive coral bleaching occurred throughout large areas of the Coral Sea Marine Park in both 2016 and 2017 however, the response of coral colonies to heat stress, as measured by Degree Heating Weeks, differed substantially between years (Fig 1B, C). In 2016, bleaching was restricted to reefs in the central Queensland plateau of the Coral Sea and the isolated atoll of Mellish (Fig. 2, Fig S2) where between 81% and 95% of colonies bleached. In 2017, all surveyed reefs were affected, including atolls further south that escaped bleaching in 2016, and bleaching was less severe, affecting 20% to 72% of colonies. In each year, the proportion of bleached colonies at each surveyed site was strongly associated with DHW (Table 1; Fig. 3), which ranged from 0.5 to 12.5 °C-weeks. The depth of the survey and the composition of the coral assemblage were also important in determining the extent of bleaching (Table 1; Fig. 3; AIC values for models that include and do not include '*taxonomic category*' as a random effect: 11991.94 vs. 13256.94, respectively). Bleaching was consistently lower at 6 m of depth than at 2 m, similar to the results of other studies (Marshall & Baird 2000; Muir et al. 2017). Bleaching was also lower at sites dominated by *Porites* and higher at sites where *Stylophora*, *Pocillopora* and *Acropora* were abundant (Fig. S3), which is also consistent with previous research (Loya et al. 2001; McClanahan et al. 2004).

The proportion of colonies affected by heat stress in 2017 was lower for a given DHW exposure than in 2016 (Fig. 3). For reefs that experienced 7-9 °C-weeks in 2016, 67-100% of coral colonies bleached, compared to only 16-81% in 2017. On the central reefs of the Queensland plateau, this shift may have been driven by the loss of colonies of susceptible taxa following bleaching in 2016. We observed a 54% decline in *Acropora* and 41% decline in

Pocillopora on the central reefs between May 2016 and April 2017 (Fig. 4). However, together these accounted for only 6% of the overall coral cover in 2016 and does not support a shift in coral communities. Alternatively, exposure to elevated temperatures in 2016 may have pre-conditioned or acclimated corals to better cope with heat exposure in 2017 (Ainsworth et al. 2016), conferring increased thermal tolerance to bleaching (e.g. Brown et al. 2000; Richards et al. 2013). However, the lower than expected levels of bleaching in 2017 at the southern atolls cannot be explained by either selective mortality or acclimation because these reefs where not exposed to elevated temperatures and did not bleach in 2016. Other possible explanations for this pattern are lower light levels (e.g., from higher cloud cover), lower nutrient levels, or higher current flow in 2017, compared to the previous summer, which may ameliorate coral bleaching (Mumby et al. 2001; Wooldridge 2009; Weidenmann et al. 2013). Spatially explicit data of sufficient quality are necessary to test these hypotheses.

Despite the severe and widespread bleaching on reefs in the central region of the CSMP in May 2016, there was no significant loss of coral cover on these reefs between May 2016 and April 2017 (mean ± SE 2016 = 20.9% ± 1.2% & 2017 = 17.9% ± 1.0%; Table 2; Fig. 5). This is very different from what occurred on the Great Barrier Reef following severe bleaching in early 2016, where most heavily bleached reefs experienced > 50% loss of corals (Hughes et al. 2018b). Therefore, while the isolation of the Coral Sea did not provide a refuge from bleaching, it appears to have provided a refuge from bleaching-induced mortality. Low nutrients levels in the Coral Sea compared with the Great Barrier Reef (Wiedenmann et al. 2013; Wooldridge & Done 2009) may have contributed to the disparity. High rates of water flow in the Coral Sea might also have assisted post-bleaching survivorship (Nakamura et al 2005), as may have the proximity of these reefs to deeper, cooler water (Done et al. 2003; Riegl & Piller 2003).

Coral cover was low in both years for reefs situated in the central Queensland plateau and on the isolated atolls of Mellish and Marion. Coral cover for these atolls ranged from 6.8% ± 0.9% to 18.1% ± 1.9% (overall 2017 mean: 10.0% ± 0.4%; Fig. 5). These observations compare with 20.8% ± 2.8% to 56.6% ± 4.1% cover in the southern CSMP (overall 2017 mean: 36.9% ± 2.1%; Fig. 5). Indeed, coral cover was already low in the Lihou and Caringa-Herald National Parks, when surveys were first conducted in 1984 (~10%), possibly due to a bleaching event in the early 1980's (Ayling and Ayling 1985) that affected outer shelf reefs of the GBR, such as Myrmidon Reef (Fisk & Done 1985). Subsequent surveys at Lihou, Herald and Chilcott atolls in 2003, 2007 and 2008 indicate that coral cover has remained below 20% in recent decades (Oxley et al. 2004; Ceccarelli et al. 2008; Ceccarelli et al. 2009).

Although remote atolls are clearly not immune to bleaching (Williams et al. 2010; Hughes et al. 2017, 2018a), isolation from other anthropogenic sources of stress, such as elevated nutrients, might provide some resistance (Wooldridge & Done 2009), albeit limited, to mortality. The lower prevalence of coral bleaching in 2017, despite higher exposure to heat stress, also indicates the need to understand the cumulative impact of disturbances events, and incorporate other factors such as incident light, light attenuation in the water column, nutrient levels and water movement (e.g., wind, waves) when predicting the ecological impact of marine heatwaves. The recovery of remote Coral Sea atolls, particularly in the already highly disturbed central reefs of the CSMP, is likely to be slow (Gilmour et al. 2013) and will require both stringent protection and global action on climate change (Kennedy et al. 2013; Mellin et al. 2016).

Competing interests

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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Data accessibility

Data are available at https://

Authors' contribution

M.A.-N., A.H.B., H.B.H. and C.MacD. collected the field observations and S.F.H. collated NOAA temperature data; A.H.B. and H.B.H. planned the study and all authors analysed the data and wrote the paper.

Funding

Funding was provided by the Director of National Parks, Parks Australia, an ACR Discovery Early Career Research Award to H.B.H. (DE160101141) and the ARC Centre of Excellence for Coral Reef Studies.

Acknowledgements

This research was jointly funded by the Director of National Parks, Australia an ACR Discovery Early Career Research Award to HBH (DE160101141) and the ARC Centre of Excellence for Coral Reef Studies. This research was conducted in the Coral Sea Marine Park under Permit No. CMR-16-000394 and CMR-16-000443. The authors wish to thank the relevant staff at Parks Australia, with particular mention given to Andy Warmbrunn, Jennifer Hoy, Bianca Priest, Samantha Fox and Jason Mundy. We thank Cpt Peter Sayre, Glenn Percy and the crew of the MV Phoenix for their assistance in the field. We are grateful to Thomas DeCarlo for producing Figures 1B and 1C and two anonymous reviewers for their thoughtful comments. The findings and views expressed are those of the authors and do not necessarily represent the views of Parks Australia, the Director of National Parks or the Australian Government. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect the views of NOAA or the US Department of Commerce.

Figure legends

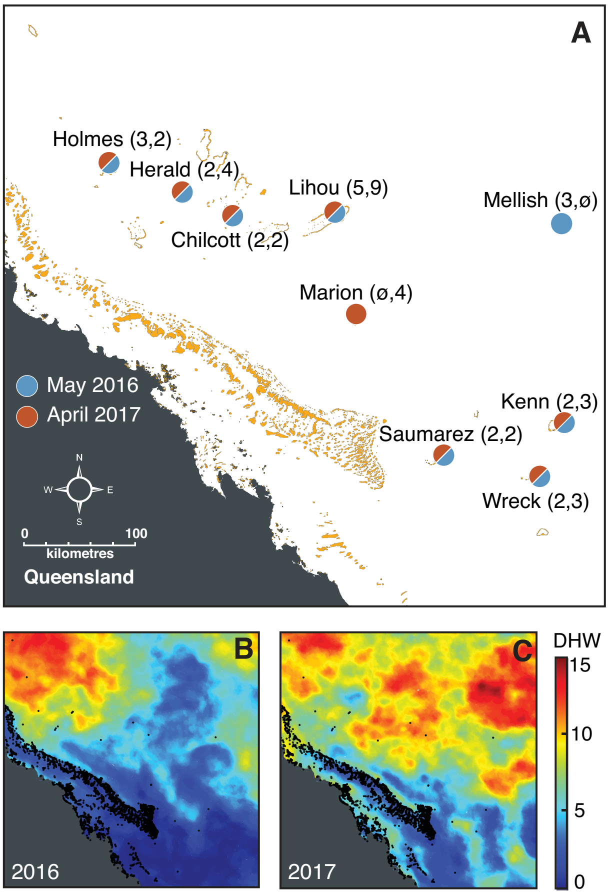

Figure 1. Marine heatwaves in 2016 and 2017 in the Coral Sea. **A.** Nine coral reef atolls were surveyed in May 2016 and/or April 2017 with number of sites per atolls in brackets (2016, 2017). All atolls are included in the Coral Sea Marine Park. Holmes, Herald, Chilcott and Lihou are referred to as the Central atolls; Marion and Mellish as Isolated atolls and Saumarez, Kenn and Wreck are referred to as Southern atolls. Spatial pattern of heat exposure (DHW, °C-weeks) during the 2016 (**B**) and 2017 (**C**) bleaching events. The maximum DHW values were calculated using the Coral Reef Watch Version 3, 5-km satellite coral bleaching heat stress product suite.

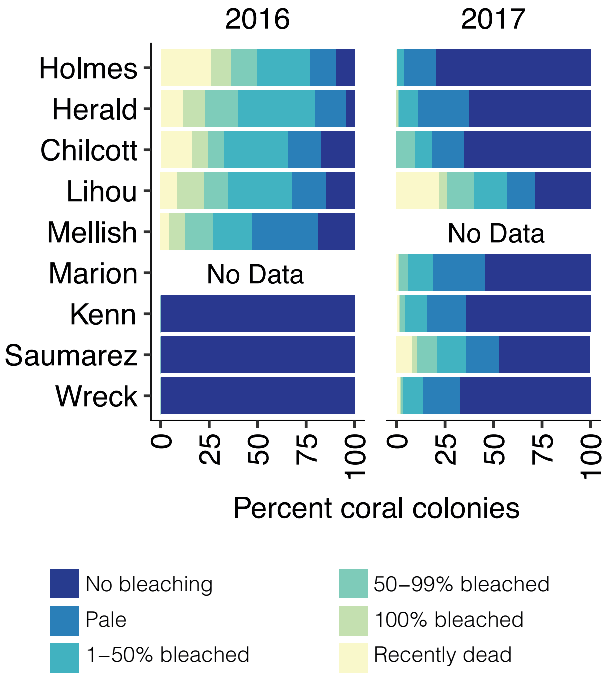

Figure 2. The proportion of coral colonies in each of six bleaching categories, from no bleaching to recently dead, observed at nine atolls in the Coral Sea in 2016 and 2017. Marion and Mellish were each surveyed once only. Atolls are ordered from northernmost to southernmost.

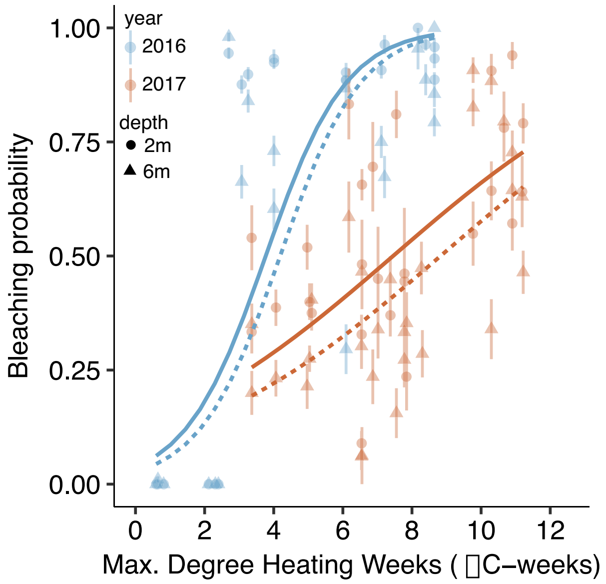

Figure 3. The relationship between heat exposure, as indicated by the maximum degree heating weeks (DHWs), and the proportion of bleached coral colonies in each year. Each data point represents a site ($N_{2016} = 21$; $N_{2017} = 29$) and the error bars show the standard errors of bleaching

probability. Solid lines and dashed lines represent the best-fit line for 2 m and 6 m depths for each year, respectively.

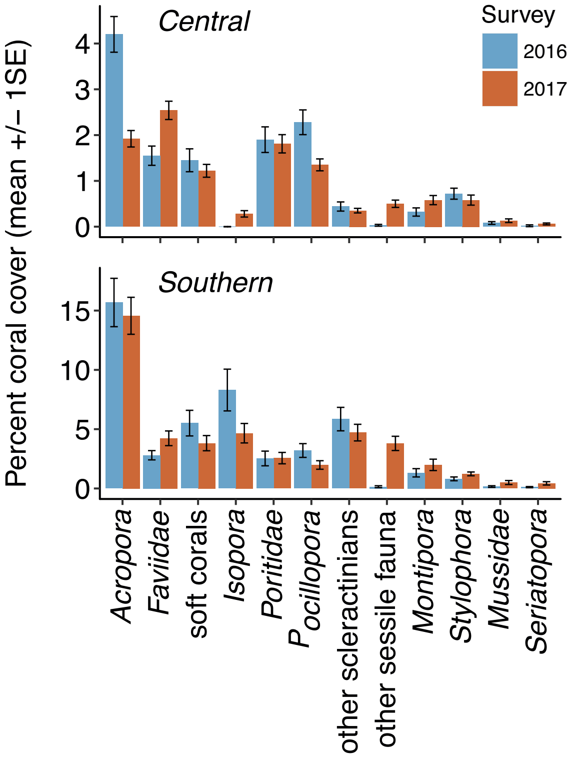

Figure 4. Percent cover of hard corals and other sessile fauna (mean ± 1 SE) in coral reef atolls in the southern and central regions of the Coral Sea Marine Park in 2016 and 2017. Coral taxa are ordered in their overall abundance in the Coral Sea Marine Park.

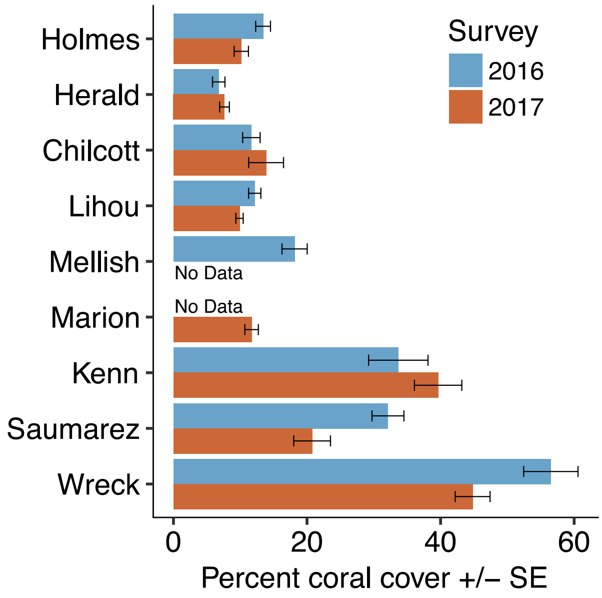

Figure 5. The proportional coral cover at each coral reef atoll in 2016 and 2017. Marion and Mellish were each surveyed once only. Atolls are ordered from northernmost to southernmost.