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## 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

27 was not significantly reduced by 2017, suggesting that most bleached corals survived.  
28 Moreover, bleaching was less severe in 2017 despite a higher exposure to heat stress. These  
29 results indicate that while the isolation of these oceanic reefs provides no refuge from  
30 bleaching, low nutrient levels, high wave energy and proximity to cooler deeper waters may  
31 make coral on these reefs more resistant to bleaching induced mortality.

32

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

34

## 35 **INTRODUCTION**

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

45 Unprecedented marine heatwaves, extended periods where water temperatures  
46 exceed the long-term summer maximum, disrupt the relationship between corals and their  
47 symbiotic algae (*Symbiodinium spp.*). During such events, coral polyps expel their algal  
48 symbiont, leading to a pale or 'bleached' appearance (Glynn 1984). The effects of coral  
49 bleaching are numerous, ranging from short-term physiological damage to widespread  
50 mortality (see reviews by Brown 1997; McClanahan et al. in press). The severity of bleaching

51 events is typically correlated with the intensity and duration of marine heatwaves that are  
52 measured as Degree Heating Weeks (DHW, °C-weeks) (e.g. Liu *et al.* 2014, Hughes *et al.* 2017).  
53 As global warming has progressed (Lough *et al.* 2018), and the length and frequency of  
54 marine heatwaves have increased (Oliver *et al.* 2018), so too has the geographic and  
55 ecological footprint of mass bleaching events (Hughes *et al.* 2018a).

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

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

75

## 76 MATERIALS AND METHODS

### 77 *Measuring bleaching prevalence and severity, and coral cover*

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

87 At each site, every coral colony > 5 cm in maximum diameter was counted and  
88 identified to genus following Veron (2000) in 5 to 10 replicate 1 m<sup>2</sup> quadrats at 2 m and 6 m  
89 depths to determine the severity of bleaching and any effect of depth. The level of bleaching  
90 was scored across a 6-level categorical scale following Gleason (1993): 1: no bleaching; 2:  
91 pale; 3: 1 – 50 % bleached; 4: 50 – 99 % bleached; 5: 100% bleached; 6: recently dead. A total  
92 of 8,293 individual coral colonies were surveyed in 622 quadrats throughout the region.  
93 Percent coral cover and benthic community compositions were estimated using four replicate  
94 10 m line intercept transects at 2 m and 6 m depths (Loya 1972) to measure changes in coral  
95 cover between bleaching events at each site. Transects were placed as closed to previous  
96 surveys as possible. Benthic communities were identified to nine hard-coral taxa (*Acropora*,  
97 *Faviidae*, *Isopora*, *Poritidae*, *Pocillopora*, *Montipora*, *Stylophora*, *Mussidae*, *Seriatopora*, and  
98 other scleractinians), soft corals, and other sessile fauna. Intercept distances along the  
99 transect were measured to the nearest cm.

100

101 *Bleaching probability in response to heat stress*

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

117

118 *Measuring the effect of bleaching on coral cover*

119 A linear mixed effects model was fitted to predict coral cover using the 'lmer' function from  
120 the lme4 package (Bates et al. 2015). 'Year', 'region', and an interaction between 'year' and  
121 'region' were included as fixed effects and 'site' and 'taxonomic category' were included as  
122 random effects. The function 'drop1' was used to check if eliminating fixed factors improved  
123 model fit. Two separate models, one without 'taxonomic category' as a random effect and one  
124 without 'site' as a random effect, were fitted and compared to the original model using Akaike

125 information criterion (AIC) to test whether the random effects were important. All analyses  
126 were performed in R version 3.3.2 (R Core Team 2016).

127

## 128 **RESULTS AND DISCUSSION**

129 Extensive coral bleaching occurred throughout large areas of the Coral Sea Marine Park in  
130 both 2016 and 2017 however, the response of coral colonies to heat stress, as measured by  
131 Degree Heating Weeks, differed substantially between years (Fig 1B, C). In 2016, bleaching  
132 was restricted to reefs in the central Queensland plateau of the Coral Sea and the isolated atoll  
133 of Mellish (Fig. 2, Fig S2) where between 81% and 95% of colonies bleached. In 2017, all  
134 surveyed reefs were affected, including atolls further south that escaped bleaching in 2016,  
135 and bleaching was less severe, affecting 20% to 72% of colonies. In each year, the proportion  
136 of bleached colonies at each surveyed site was strongly associated with DHW (Table 1; Fig. 3),  
137 which ranged from 0.5 to 12.5 °C-weeks. The depth of the survey and the composition of the  
138 coral assemblage were also important in determining the extent of bleaching (Table 1; Fig. 3;  
139 AIC values for models that include and do not include '*taxonomic category*' as a random effect:  
140 11991.94 vs. 13256.94, respectively). Bleaching was consistently lower at 6 m of depth than  
141 at 2 m, similar to the results of other studies (Marshall & Baird 2000; Muir et al. 2017).  
142 Bleaching was also lower at sites dominated by *Porites* and higher at sites where *Stylophora*,  
143 *Pocillopora* and *Acropora* were abundant (Fig. S3), which is also consistent with previous  
144 research (Loya et al. 2001; McClanahan et al. 2004).

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

150 *Pocillopora* on the central reefs between May 2016 and April 2017 (Fig. 4). However, together  
151 these accounted for only 6% of the overall coral cover in 2016 and does not support a shift in  
152 coral communities. Alternatively, exposure to elevated temperatures in 2016 may have pre-  
153 conditioned or acclimated corals to better cope with heat exposure in 2017 (Ainsworth et al.  
154 2016), conferring increased thermal tolerance to bleaching (e.g. Brown et al. 2000; Richards  
155 et al. 2013). However, the lower than expected levels of bleaching in 2017 at the southern  
156 atolls cannot be explained by either selective mortality or acclimation because these reefs  
157 where not exposed to elevated temperatures and did not bleach in 2016. Other possible  
158 explanations for this pattern are lower light levels (e.g., from higher cloud cover), lower  
159 nutrient levels, or higher current flow in 2017, compared to the previous summer, which may  
160 ameliorate coral bleaching (Mumby et al. 2001; Wooldridge 2009; Weidenmann et al. 2013).  
161 Spatially explicit data of sufficient quality are necessary to test these hypotheses.

162         Despite the severe and widespread bleaching on reefs in the central region of the CSMP  
163 in May 2016, there was no significant loss of coral cover on these reefs between May 2016 and  
164 April 2017 (mean  $\pm$  SE 2016 = 20.9%  $\pm$  1.2% & 2017 = 17.9%  $\pm$  1.0%; Table 2; Fig. 5). This is  
165 very different from what occurred on the Great Barrier Reef following severe bleaching in  
166 early 2016, where most heavily bleached reefs experienced > 50% loss of corals (Hughes et al.  
167 2018b). Therefore, while the isolation of the Coral Sea did not provide a refuge from  
168 bleaching, it appears to have provided a refuge from bleaching-induced mortality. Low  
169 nutrients levels in the Coral Sea compared with the Great Barrier Reef (Wiedenmann et al.  
170 2013; Wooldridge & Done 2009) may have contributed to the disparity. High rates of water  
171 flow in the Coral Sea might also have assisted post-bleaching survivorship (Nakamura et al  
172 2005), as may have the proximity of these reefs to deeper, cooler water (Done et al. 2003;  
173 Riegl & Piller 2003).



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

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

195

## 196 **Competing interests**

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

198

199 **REFERENCES**

- 200 Ayling AM, Ayling AL (1985) Report on a preliminary survey of the Lihou and  
201 Caringua/Herald Nature Reserves. Australian National Parks and Wildlife Service
- 202 Baird AH, Madin JS, Alvarez-Noriega M, Fontoura L, Kerry J, Precoda K, Torres-Pulliza D,  
203 Woods RM, Zawada K, Hughes TP (*in review*) Bathymetric patterns of bleaching on the  
204 Great Barrier Reef. Mar Ecol Prog Series (submitted November 2017)
- 205 Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: An ecological  
206 assessment of long-term impacts, recovery trends and future outlook. Estuar Coast  
207 Shelf Sci 80:435-471
- 208 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using  
209 lme4. J Stat Softw 67:1-48.
- 210 Brown BE, Dunne RP, Goodson MS, Douglas AE (2000) Bleaching patterns in reef corals.  
211 Nature 404:142-143
- 212 Brown BE (1997) Coral bleaching: causes and consequences. Coral Reefs 16:S129-S138
- 213 Ceccarelli D, Choat JH, Ayling AM, Richards Z, van Herwerden L, Ayling A, Ewels G, Hobbs J-P,  
214 Cuff B (2008) Coringa-Herald National Nature Reserve Marine Survey – 2007. Report  
215 to the Department of the Environment, Water, Heritage and the Arts by C&R Consulting  
216 and James Cook University.
- 217 Ceccarelli D, Ayling AM, Choat JH, Ayling AL, Williamson DH, Cuff B (2009) Lihou Reef National  
218 Nature Reserve Marine Survey – October 2008. Report to the Department of the  
219 Environment, Water, Heritage and the Arts by C&R Consulting Pty Ltd.
- 220 Ceccarelli DM, McKinnon AD, Andrefouet S, Allain V, Young J, Gledhill DC, Flynn A, Bax NJ,  
221 Beaman R, Borsa P, Brinkman R, Bustamante RH, Campbell R, Cappo M, Cravatte S,  
222 D'Agata S, Dichmont CM, Dunstan PK, Dupouy C, Edgar G, Farman R, Furnas M,  
223 Garrigue C, Hutton T, Kulbicki M, Letourneur Y, Lindsay D, Menkes C, Mouillot D,

224 Parravicini V, Payri C, Pelletier B, de Forges BR, Ridgway K, Rodier M, Samadi S,  
225 Schoeman D, Skewes T, Swearer S, Vigliola L, Wantiez L, Williams A, Williams A,  
226 Richardson AJ (2013) The Coral Sea: Physical Environment, Ecosystem Status and  
227 Biodiversity Assets. *Adv Mar Biol* 66:213-290

228 De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on  
229 the Great Barrier Reef and its causes. *Proc Natl Acad Sci USA*, 109:17995–17999.

230 Done T, Whetton P, Jones R, Berkelmans R, Lough JM, Skirving W, Wooldridge S (2003) Global  
231 Climate Change and Coral Bleaching on the Great Barrier Reef. Queensland  
232 Government Department of Natural Resources and Mines

233 Fisk DA, Done TJ (1985) Taxonomic and bathymetric patterns of bleaching in corals,  
234 Myrmidon Reef (Queensland). *Proc Fifth Inter Coral Reef Congress* 6:149-154

235 Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an isolated  
236 coral reef system following severe disturbance. *Science* 340:69-71

237 Gleason MG (1993) Effects of Disturbance on Coral Communities - Bleaching in Moorea,  
238 French-Polynesia. *Coral Reefs* 12:193-201

239 Glynn PW (1984) Widespread coral mortality and the 1982-83 El Nino warming event.  
240 *Environ Conserv* 11:133-146

241 Heron SF, Maynard JA, van Hooidonk R, Eakin CM (2016) Warming Trends and Bleaching  
242 Stress of the World's Coral Reefs 1985-2012. *Sci Rep* 6:38402

243 Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock  
244 RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE,  
245 Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF,  
246 Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs J-PA, Hoogenboom MO, Kennedy  
247 EV, Kuo C-y, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ,  
248 Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B,

- 249 Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017) Global warming and recurrent  
250 mass bleaching of corals. *Nature* 543:373-377
- 251 Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK,  
252 Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison HB,  
253 Hobbs J-PA, Hoey A, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M,  
254 Schoepf V, Torda G, Wilson SK (2018a) Spatial and temporal patterns of mass  
255 bleaching of corals in the Anthropocene. *Science* 359:80-83.
- 256 Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS,  
257 Hoogenboom MO, Liu G, McWilliam MJ, Pears RJ, Pratchett MS, Skirving WJ, Stella JS,  
258 Torda G (2018b) Global warming transforms coral reef assemblages. *Nature*  
259 doi:10.1038/s41586-018-0041-2
- 260 Kennedy EV, Perry CT, Halloran PR, Iglesias-Prieto R, Schönberg CHL, Wisshak M, Form AU,  
261 Carricart-Ganivet JP, Fine M, Eakin CM, Mumby PJ (2013) Avoiding Coral Reef  
262 Functional Collapse Requires Local and Global Action. *Curr Biol* 23:912–918
- 263 King AD, Karoly DJ, Henley BJ (2017) Australian climate extremes at 1.5 degrees C and 2  
264 degrees C of global warming. *Nat Clim Change* 7:412-416
- 265 Liu G, Heron S, Eakin CM, Muller-Karger FE, Vega-Rodriguez M, Guild LS, et al. (2014). Reef-  
266 Scale Thermal Stress Monitoring of Coral Ecosystems: New 5-km Global Products from  
267 NOAA Coral Reef Watch. *Remote Sens* 6:11579–11606
- 268 Lough JM, Anderson KD, Hughes TP (2018) Increasing thermal stress for tropical coral reefs:  
269 1871–2017. *Scientific Reports* 8:6079
- 270 Loya Y (1972) Community structure and species diversity of hermatypic corals at Eilat, Red  
271 Sea. *Mar Biol* 13:100-112
- 272 Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the  
273 winners and the losers. *Ecol Lett* 4:122-131

274 Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential  
275 susceptibilities among taxa. *Coral Reefs* 19:155-163

276 McClanahan T, Weil E, Cortés J, Baird AH, Ateweberhan M (2009) Consequences of coral  
277 bleaching for sessile reef organisms. In: van Oppen MJH, Lough JM (eds) *Ecological*  
278 *Studies: Coral Bleaching: Patterns, Processes, Causes and Consequences*. Springer-  
279 Verlag, Berlin, pp121-138

280 McClanahan TR, Baird AH, Marshall PA, Toscano MA (2004) Comparing bleaching and  
281 mortality responses of hard corals between southern Kenya and the Great Barrier Reef,  
282 Australia. *Mar Pollut Bull* 48:327-335

283 McClanahan TR, Ateweberhan M, Sebastian CR, Graham NAJ, Wilson SK, Bruggemann JH,  
284 Guillaume MMM (2007) Predictability of coral bleaching from synoptic satellite and in  
285 situ temperature observations. *Coral Reefs* 26:695-701

286 Mellin C, MacNeil MA, Cheal AJ, Emslie MJ, Caley JM (2016) Marine protected areas increase  
287 resilience among coral reef communities. *Ecol Lett* 19:629-637

288 Muir PR, Marshall PA, Abdulla A, Aguirre JD (2017) Species identity and depth predict  
289 bleaching severity in reef-building corals: shall the deep inherit the reef? *Proc Royal*  
290 *Soc B* 284:20171551

291 Mumby PJ, Chisholm JRM, Edwards AJ, Andrefouet S, Jaubert J (2001) Cloudy weather may  
292 have saved Society Island reef corals during the 1998 ENSO event. *Mar Ecol Prog Ser*  
293 222:209-216

294 Nakamura T, van Woesik R, Yamasaki H (2005) Photoinhibition of photosynthesis is reduced  
295 by water flow in the reef-building coral *Acropora digitifera*. *Mar Ecol Prog Ser*  
296 301:109-118

297 Oliver ECJ, Donat MG, Burrows MT, Moore PJ, Smale DA, Alexander LV, Benthuyssen JA, Feng M,  
298 Gupta Sen A, Hobday AJ, Holbrook NJ, Perkins-Kirkpatrick SE, Scannell HA, Straub SC,

- 299 Wernberg T (2018) Longer and more frequent marine heatwaves over the past  
300 century. *Nat Commun* 9:227
- 301 Oxley WG, Emslie M, Muir P, Thompson AA (2004) Marine surveys undertaken in the Lihou  
302 Reef Nature Reserve, March 2004. Department of the Environment and Heritage
- 303 Spalding MD, Brown BE (2015) Warm-water coral reefs and climate  
304 change. *Science* 350 :769–771.
- 305 Richards CL, Boruta M, Bossdorf O, Coon CAC, Foust CM, Hughes AR, Kilvitis HJ, Liebl AL,  
306 Nicotra AB, Pigliucci M, Robertson MH, Schrey AW (2013) Epigenetic mechanisms of  
307 phenotypic plasticity. *Integr Comp Biol* 53:E179-E179
- 308 Riegl B, Piller WE (2003) Possible refugia for reefs in times of environmental stress. *Int J Earth*  
309 *Sci* 92:520-531
- 310 Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T,  
311 Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE,  
312 Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and Degradation of Coral  
313 Reefs in the Northern Line Islands. *PLoS ONE* 3:e1548
- 314 van Hooidonk R, Maynard JA, Planes S (2013) Temporary refugia for coral reefs in a warming  
315 world. *Nat Clim Change* 3:508-511
- 316 Veron JEN (2000) *Corals of the world*. Australian Institute of Marine Science, Townsville
- 317 Wiedenmann J, D'Angelo C, Smith EG, Hunt AN, Legiret F-E, Postle AD, Achterberg EP (2013)  
318 Nutrient enrichment can increase the susceptibility of reef corals to bleaching. *Nat Clim*  
319 *Change* 3:160-164
- 320 Williams GJ, Knapp IS, Maragos JE, Davy SK (2010) Modeling patterns of coral bleaching at a  
321 remote Central Pacific atoll. *Mar Pollut Bull* 60:1467–1476
- 322 Wooldridge SA, Done TJ (2009) Improved water quality can ameliorate effects of climate  
323 change on corals. *Ecol Appl* 19:1492-1499

324 Wooldridge SA (2009) Water quality and coral bleaching thresholds: Formalising the linkage  
325 for the inshore reefs of the Great Barrier Reef, Australia. Marine Pollution Bulletin  
326 58:745-751

327

### 328 **Data accessibility**

329 Data are available at <https://>

330

### 331 **Authors' contribution**

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

335

336

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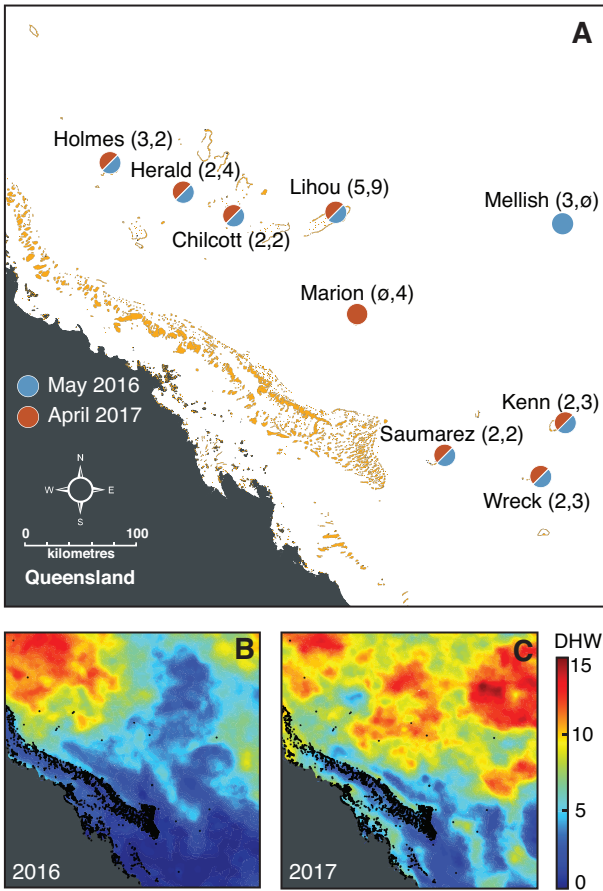
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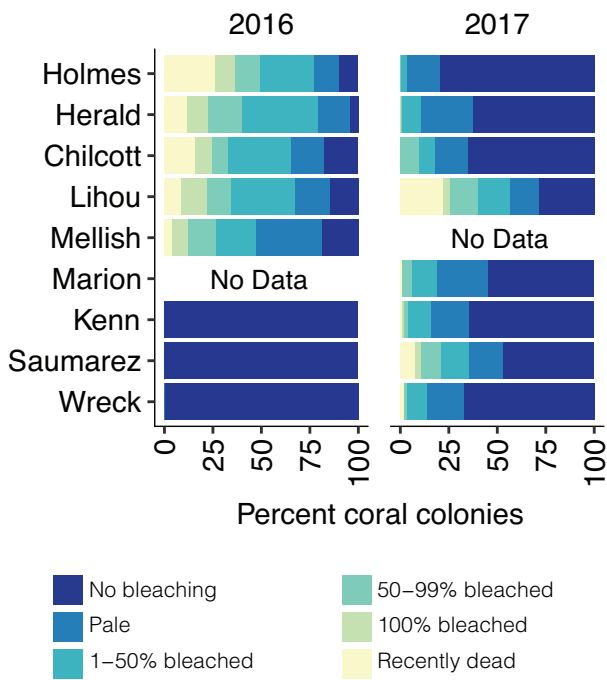
356 **Figure legends**



357

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

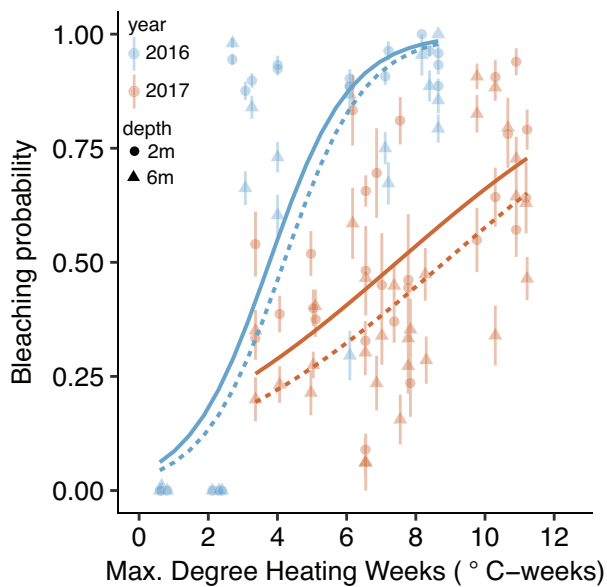
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367 **Figure 2.** The proportion of coral colonies in each of six bleaching categories, from no bleaching to  
 368 recently dead, observed at nine atolls in the Coral Sea in 2016 and 2017. Marion and Mellish were  
 369 each surveyed once only. Atolls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

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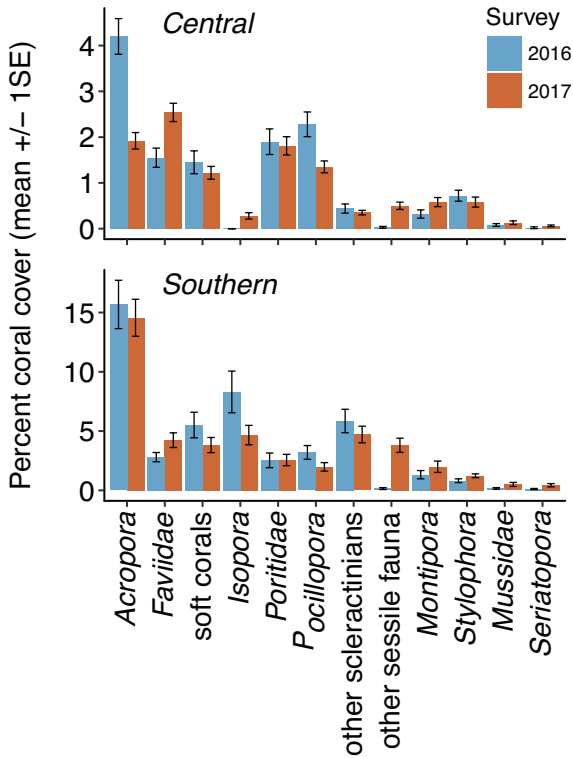


371

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

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

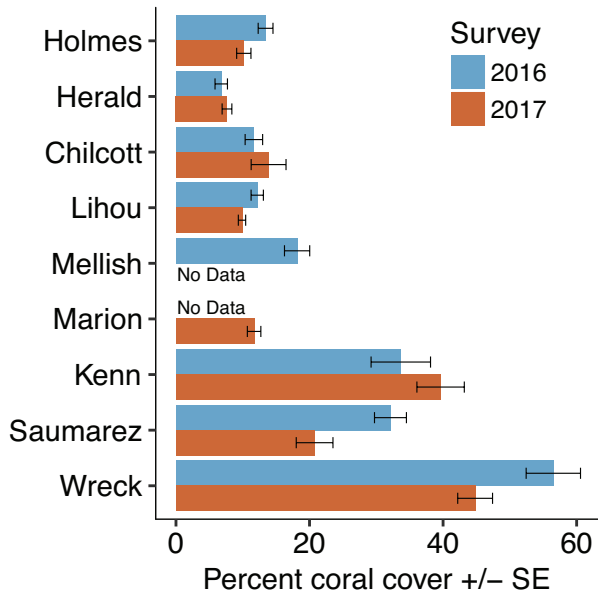
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378

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

382



383

384 **Figure 5.** The proportional coral cover at each coral reef atoll in 2016 and 2017. Marion and

385 Mellish were each surveyed once only. Atolls are ordered from northernmost to southernmost.