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Global warming and recurrent mass bleaching of corals

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46

47 **In 2015-2016, record temperatures triggered a pan-tropical episode of coral bleaching,**
48 **the third global-scale event since mass bleaching was first documented in the 1980s.**
49 **Here we examine how and why the severity of recurrent major bleaching events has**
50 **varied at multiple scales, using aerial and underwater surveys of Australian reefs**
51 **combined with satellite-derived sea surface temperatures. The distinctive geographic**
52 **footprints of recurrent bleaching on the Great Barrier Reef in 1998, 2002 and 2016 were**
53 **determined by the spatial pattern of sea temperatures in each year. Water quality and**
54 **fishing pressure had minimal effect on the unprecedented bleaching in 2016, suggesting**
55 **that local protection of reefs affords little or no resistance to extreme heat. Similarly,**
56 **past exposure to bleaching in 1998 and 2002 did not lessen the severity of bleaching in**
57 **2016. Consequently, immediate global action to curb future warming is essential to**
58 **secure a future for coral reefs.**

59

60 The world's tropical reef ecosystems, and the people who depend on them, are increasingly
61 impacted by climate change¹⁻⁷. Since the 1980s, rising sea surface temperatures due to global
62 warming have triggered unprecedented mass bleaching of corals, including three pan-tropical
63 events in 1998, 2010 and 2015/16¹. Thermal stress during marine heatwaves disrupts the
64 symbiotic relationship between corals and their algal symbionts (*Symbiodinium* spp.),
65 causing the corals to lose their color²⁻³. Bleached corals are physiologically damaged, and
66 prolonged bleaching often leads to high levels of mortality⁵⁻⁸. Increasingly, individual reefs
67 are experiencing multiple bouts of bleaching, as well the impacts of more chronic local
68 stressors such as pollution and overfishing¹⁻⁴. Our study represents a fundamental shift away
69 from viewing bleaching events as individual disturbances to reefs, by focussing on three
70 recurrent bleachings over the past 18 years along the 2,300 km length of the Great Barrier
71 Reef, as well as the potential influence of water quality and fishing pressure on the severity of
72 bleaching.

73 The geographic footprints of mass bleaching of corals on the Great Barrier Reef have varied
74 strikingly during three major events in 1998, 2002 and 2016 (Fig. 1a). In 1998, bleaching was
75 primarily coastal and most severe in the central and southern regions. In 2002, bleaching was
76 more widespread, and affected offshore reefs in the central region that had escaped in 1998⁸.
77 In 2016, bleaching was even more extensive and much more severe, especially in the
78 northern, and to a lesser extent the central regions, where many coastal, mid-shelf and
79 offshore reefs were affected (Fig. 1a, b). In 2016, the proportion of reefs experiencing
80 extreme bleaching (>60% of corals bleached) was over four times higher compared to 1998
81 or 2002 (Fig. 1f). Conversely, in 2016, only 8.9% of 1,156 surveyed reefs escaped with no
82 bleaching, compared to 42.4% of 631 reefs in 2002 and 44.7% of 638 in 1998. The
83 cumulative, combined footprint of all three major bleaching events now covers almost the

84 entire Great Barrier Reef Marine Park, with the exception of southern, offshore reefs (Fig.
85 1d).

86

87 **Explaining spatial patterns**

88 The severity and distinctive geographic footprints of bleaching in each of the three
89 years can be explained by differences in the magnitude and spatial distribution of sea-surface
90 temperature anomalies (Fig. 1a, b and Extended Data Table 1). In each year, 61-63% of reefs
91 experienced four or more Degree Heating Weeks (DHW, °C-weeks). In 1998, heat stress was
92 relatively constrained, ranging from 1-8 DHWs (Fig. 1c). In 2002, the distribution of DHW
93 was broader, and 14% of reefs encountered 8-10 DHWs. In 2016, the spectrum of DHWs
94 expanded further still, with 31% of reefs experiencing 8-16 DHWs (Fig. 1c). The largest heat
95 stress occurred in the northern 1000 km-long section of the Great Barrier Reef. Consequently,
96 the geographic pattern of severe bleaching in 2016 matched the strong north-south gradient in
97 heat stress. In contrast, in 1998 and 2002, heat stress extremes and severe bleaching were
98 both prominent further south (Fig. 1a, b). In 2016, severe bleaching (defined as an aerial
99 score of >30% of corals bleached) was correctly predicted by satellite-derived DHW in a
100 statistical model, in 75% of cases (Extended Data Fig. 1 and Extended Data Table 1), similar
101 to the amount of spatial variation in bleaching explained by temperature stress in 1998 and
102 2002⁸.

103 The geographic pattern of bleaching also demonstrates how marine heatwaves can be
104 ameliorated by local weather⁹, even during a global bleaching event. Arguably, southern reefs
105 of the Great Barrier Reef would also have bleached in 2016 if wind, cloud cover, and rain
106 from ex-Tropical Cyclone Winston had not rescued them¹⁰. Winston passed over Fiji on
107 February 20th, when the southern Great Barrier Reef was only 1°C cooler than the north. By
108 March 6th, this disparity increased to 4°C (Extended Data Fig. 2). Corals in the south that had

109 begun to pale in February regained their colour in the south in March, whereas bleaching
110 continued to progress in central and northern sectors (Fig. 2a). Similarly, in western Australia
111 in 2016, Tropical Cyclone Stan cooled down mid-coast regions in early February¹¹, and the
112 Leeuwin Current (which transports warm tropical water southwards) was also weakened due
113 to El Niño conditions¹². Consequently, both sides of tropical and sub-tropical Australia,
114 including offshore atolls in the Coral Sea and Indian Ocean, exhibited continental-scale
115 latitudinal gradients in bleaching (Fig. 1g).

116 The local (individual reef) scale pattern of recurrent bleaching on the Great Barrier Reef also
117 reveals the trend of increasing severity, and the erosion of potential spatial refugia. Of the
118 171 individual reefs that were aerial-surveyed three times, 43% bleached in 1998, 56% in
119 2002, and 85% in 2016. Knowing the bleaching-history of these well-studied reefs allows us
120 to investigate why they have bleached zero, one, two or three times. Only 9% of these
121 repeatedly surveyed reefs have never bleached, in most cases because they are located near
122 the southern, offshore end of the Great Barrier Reef (Fig. 1e), where they have experienced
123 relatively low temperature anomalies during each event. A further 26% of repeatedly-
124 surveyed reefs have bleached only once - ten reefs in 1998, eight in 2002, and 32 for the first
125 time in 2016. The latter were primarily in the northern sector of the Great Barrier Reef, which
126 largely escaped bleaching in the two earlier events (Fig. 1a). Thirty-five percent of the reefs
127 have bleached twice, but only one reef bleached in both 1998 and 2002, compared to 58 reefs
128 that bleached either in 1998 or 2002 and for a second time in the severe 2016 event. Finally,
129 29% of the repeatedly censused reefs bleached for a third time in 2016, primarily in central
130 areas of the Great Barrier Reef, because they experienced anomalously warm temperatures
131 during all three events (Fig. 1b, e). We conclude that the overlap of disparate geographic
132 footprints of heat stress explains why different reefs have bleached 0-3 times, i.e. the repeated
133 exposure to unusually hot conditions is the primary driver of the likelihood of recurrent

134 bleaching at the scale of both individual reefs and the entire Great Barrier Reef (Fig. 1a, b).
135 We found a similar strong relationship between the amount of bleaching measured
136 underwater, and the satellite-based estimates of heat exposure on individual reefs (Fig. 3).
137 Low levels of bleaching was observed at some locations when DHW values were only 2-3
138 °C-weeks. Typically, 30-40% of corals bleached on reefs exposed to 4 °C-weeks, whereas an
139 average of 70-90% of corals bleached on reefs that experience 8 °C-weeks or more (Fig. 3).

140 **Resistance and adaptation to bleaching**

141 Once we account for the amount of heat stress experienced on each reef, adding
142 chlorophyll-*a*, a proxy for water quality, to our statistical model yielded no support for the
143 hypothesis that good water quality confers resistance to bleaching¹³. Rather, the estimated
144 effect of chlorophyll-*a* was to significantly reduce the DHW threshold for bleaching
145 (Extended Data Table 1). However, despite the statistical significance, the effect in real terms
146 beyond heat stress alone is very small (Extended Data Fig. 1). Similarly, we found no effect
147 of the level of protection (in fished or protected zones) on bleaching ($P > 0.1$: Extended Data
148 Table 1). These results are consistent with the broad-scale pattern of severe bleaching in the
149 northern Great Barrier Reef, which affected hundreds of reefs across inshore-offshore
150 gradients in water quality, and regardless of their zoning (protection) status (Fig. 1a, b).

151 Similarly, we find no evidence for a protective effect of past bleaching (e.g. from
152 acclimation or adaptation): reefs with higher bleaching scores in 1998 or 2002 did not
153 experience less severe bleaching in 2016, after accounting for the relationship between the
154 2016 temperature stress and bleaching propensity ($P > 0.9$ in all cases; Extended Data Figure
155 3). Thus, while several studies have indicated that prior exposure can influence the
156 subsequent bleaching responses of corals¹⁴⁻¹⁷, our comprehensive analysis of 171 repeatedly

157 censused reefs indicates that any such historical effects on the Great Barrier Reef were
158 masked by the severity of bleaching in 2016 (Fig. 2).

159 **Winners and losers**

160 Individual coral taxa bleached to different extents, especially on less affected reefs, creating
161 both winners and losers, but the disparity among species diminished in the worst affected,
162 northern regions. (Fig. 4). At the population and assemblage level, when and where bleaching
163 is severe, even century-old corals can bleach (Fig. 2b-d). In contrast, where bleaching is less
164 intense, it is highly selective, with a broad spectrum of responses shown by resistant corals
165 (so-called winners) versus susceptible species (losers); winners by definition bleach less and
166 have higher survivorship¹⁸⁻²¹. On lightly and moderately bleached reefs (<10% or 10-30% of
167 corals affected), predominantly in the southern Great Barrier Reef, many of the more robust
168 coral taxa escaped with little or no bleaching in 2016. In contrast, on extremely bleached
169 reefs in the north (60-80% or >80% overall bleaching), we found far fewer lightly-bleached
170 winners (Fig. 4). The rank order of winners versus losers also changed as the severity of
171 bleaching increased (Extended Data Table 2), reflecting disparate responses by each taxon to
172 the range of bleaching intensities. Thus, even species that are winners on relatively mildly
173 bleached reefs joined the ranks of losers where bleaching was more intense (Fig. 4), creating
174 a latitudinal gradient in the response of the coral assemblages.

175 The recovery time for coral species that are good colonizers and fast growers is 10-15 years²²⁻
176 ²⁴, but when long-lived corals die from bleaching their replacement will necessarily take
177 many decades. Recovery for long-lived species requires the sustained absence of another
178 severe bleaching event (or other significant disturbance), which is no longer realistic while
179 global temperatures continue to rise²⁵. Therefore, the assemblage structure of corals is now
180 likely to be permanently shifted at severely bleached locations in the northern Great Barrier
181 Reef.

182 **Implications for reef management**

183 Our analysis has important implications for the management and conservation of coral reefs.
184 We found that local management of coral reef fisheries and water-quality affords little if any
185 resistance to recurrent severe bleaching events: even the most highly protected reefs and
186 near-pristine areas are highly susceptible to severe heat stress. On the remote northern Great
187 Barrier Reef, hundreds of individual reefs were severely bleached in 2016 regardless of
188 whether they were zoned as no-entry, no-fishing, or open to fishing, and irrespective of
189 inshore-offshore differences in water quality (Fig. 1a and Extended Data Fig. 1). However,
190 local protection of fish stocks and improved water quality may, given enough time, improve
191 the prospects for recovery^{3,4,26-29}. A key issue for all coral reefs is the frequency, or return
192 time, of recurrent disturbance events, and whether there is sufficient time between successive
193 bleachings for the re-assembly of mature coral assemblages. The chances of the northern
194 Great Barrier Reef returning to its pre-bleaching assemblage structure are slim given the scale
195 of damage that occurred in 2016 and the likelihood of a fourth bleaching event occurring
196 within the next decade or two as global temperatures continue to rise.

197 Identifying and protecting spatial refugia is a common strategy for conservation of threatened
198 species and ecosystems, including coral reefs³⁰. However, our analyses indicate that the
199 cumulative footprint of recurrent bleachings is expanding, and the number of potential
200 refugia on the Great Barrier Reef is rapidly diminishing. Indeed, the remote northern region
201 escaped serious damage in 1998 and 2002, but bore the brunt of extreme bleaching in 2016.
202 Rather than relying on the premise of refugia, our results highlight the growing importance of
203 promoting the recovery of reefs to recurrent bleaching events through local management of
204 marine parks and water quality. However, bolstering resilience will become more challenging
205 and less effective in coming decades because local interventions have had no discernible
206 effect on resistance of corals to extreme heat stress, and, with increasing frequency of severe

207 bleaching events, the time for recovery is diminishing. Securing a future for coral reefs,
208 including intensively managed ones such as the Great Barrier Reef, ultimately requires urgent
209 and rapid action to reduce global warming.

210

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295 paper. All authors contributed to writing subsequent drafts. JTK coordinated data
296 compilation, analysis and graphics. Aerial bleaching surveys in 2016 of the Great Barrier
297 Reef and Torres Strait were executed by JTK, TPH and TS, and in 1998 and 2002 by RB and
298 DRW. Underwater bleaching censuses in 2016 were undertaken on the Great Barrier Reef by
299 MAN, AHB, DRB, MB, NEC, CYK, GDP, ASH, MOH, EVK, MMcW, RJP, MSP, GT and
300 BLW, in the coral Sea by TCB and HBH, in subtropical Queensland and New South Wales
301 by MB, IRB, RCB, SJD, WFF, HAM, JMP, and BS, off western Australia by RCB, SC, JPG,
302 JPH, MMcC, VS and SKW. JGA-R, SRC, CME, SFH, GL, JML, and WJS undertook the
303 analysis matching satellite data to the bleaching footprints on the Great Barrier Reef

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306 welcome to comment on the online version of the paper. Correspondence and requests for
307 materials should be addressed to T.P.H. (terry.hughes@jcu.edu.au)

308 **Figure legends**

309 **Figure 1.** Geographic extent and severity of recurrent coral bleaching at a regional scale,
 310 Australia. (a) The footprint of bleaching on the Great Barrier Reef in 1998, 2002 and 2016,
 311 measured by extensive aerial surveys: dark green (<1% of corals bleached), light green (1-
 312 10%), yellow (10-30%), orange (30-60%), red (>60%). The number of reefs surveyed in each
 313 year was 638 (1998), 631 (2002), and 1,156 (2016). (b) Spatial pattern of heat stress (Degree
 314 Heating Weeks, DHWs, °C-weeks) during each mass bleaching event. (c) Frequency
 315 distribution of maximum DHWs on the Great Barrier Reef, in 1998, 2002 and 2016. White
 316 bars indicate 0-4 °C-weeks, grey bars 4-8 °C-weeks, black bars >8 °C-weeks. (d) Locations
 317 of individual reefs that bleached (by >10% or more) in 1998, 2002 and/or 2016, showing the
 318 most severe bleaching score for reefs that were censused more than once. Yellow (10-30%
 319 bleaching), Orange (30-60%), Red (>60%). (e) Location of reefs that were censused in all
 320 three years that bleached zero (white), one (light grey), two (dark grey) or three times (black).
 321 (f) Frequency distribution of aerial bleaching scores for reefs surveyed in 1998 (left bar),
 322 2002 (middle), and 2016 (right). Colour bleaching scores as in (a). (g) Bleaching severity
 323 during March to early April 2016 on both sides of Australia, including the Coral Sea and the
 324 eastern Indian Ocean. Colour bleaching scores as in (a). Bar graphs show mean sea-surface
 325 temperatures during March for each year from 1980 to 2016 for northern and southern
 326 latitudes on either side of Australia. The red bar highlights the north-south disparity in 2016.

327 **Figure 2.** Recurrent severe coral bleaching. (a) Aerial view of severe bleaching in Princess
 328 Charlotte Bay, NE Australia, March 2016. Close to 100% of corals are bleached on the reef
 329 flat and crest. Bleaching occurs when algal symbionts (*Symbiodinium* spp.) in a coral host are
 330 killed by environmental stress, revealing the white underlying skeleton of the coral. (b)
 331 Severe bleaching in 2016 on the northern Great Barrier Reef affected even the largest and
 332 oldest corals, such as this slow-growing *Porites* colony. (c) Large, old beds of clonal staghorn

333 corals, *Acropora pulchra*, on Orpheus Island, Queensland photographed in 1997 were killed
334 by the first major bleaching event on the Great Barrier Reef in 1998. (d) Eighteen years later
335 in May 2016, corals at this site have never recovered, with the original assemblages still
336 visible as dead, unconsolidated and muddy rubble that is unsuitable for successful
337 colonization by coral larvae. (e-f) Mature stands of clonal staghorn corals were extirpated by
338 heat stress and colonized by algae over a period of just a few weeks in 2016 on Lizard Island,
339 Great Barrier Reef. Before (e) and after (f) photographs were taken on February 26th and
340 April 19th 2016. Photo credits: (a) JTK, (b) J. Marshall, (c) BW, (d) AHB, (e-f) R. Streit.

341 **Figure 3.** The relationship between heat exposure (satellite-based Degree Heating Weeks in
342 2016) and the amount of bleaching measured underwater (percent of corals bleached) in
343 March/April. Each data point represents an individual reef ($n = 69$). The fitted line is $y =$
344 $48.6\ln(x) - 21.6$, $R^2 = 0.545$.

345 **Figure 4.** Spectrum of bleaching responses by coral taxa on the Great Barrier Reef in 2016,
346 with relative winners on the right, and losers on the left. Species or genera (58,414 colonies)
347 are plotted in rank descending order along the x-axis from high to low levels of impact, for
348 reefs that are lightly bleached (bottom spectrum) or more severely bleached (top). Reef-scale
349 bleaching severities are (blue) 1-10% of all corals bleached, (green) 10-30%, (yellow) 30-
350 60%, (orange) 60-80%, and (red) >80% bleached. See Extended Data Table 2 for taxonomic
351 details.

352

353 **Methods**

354 **Recurrent bleaching on the Great Barrier Reef**

355 For 2016, comprehensive aerial surveys of the Great Barrier Reef Marine Park and Torres
356 Strait reported in Fig. 1a were conducted on ten days between 22nd March 2016 and 17th April
357 2016 when bleaching was highly visible. We used light aircraft and a helicopter, flying at an
358 elevation of approximately 150 m. A total of 1,156 individual reefs from the coast to the edge
359 of the continental shelf were assessed along 14° of latitude (Extended Data Fig. 4). Each reef
360 was assigned by visual assessment to one of five categories of bleaching severity, using the
361 same protocols as earlier aerial surveys conducted in 1998 and 2002 by RB⁸: (0) less than 1%
362 of corals bleached, (1) 1-10%, (2) 10-30%, (3) 30-60%, and (4) more than 60% of corals
363 bleached. The accuracy of the scores was assessed by underwater ground-truthing (see next
364 section). The aerial scores are presented in Fig. 1a as heat-maps (Stretch type: Minimum-
365 Maximum) using inverse distance weighting (IDW; Power: 2, Cell Size: 1000, Search
366 Radius: variable, 100 points) in ArcGIS 10.2.1.

367 **Underwater surveys of eastern and western Australia**

368 To ground-truth the accuracy of aerial scores of bleaching on the Great Barrier Reef (Fig. 1a),
369 we conducted in-water surveys on 104 reefs during March and April 2016 (Extended Data
370 Fig. 5). We also measured differential species responses (winners-losers; Fig. 4) on 83 reefs,
371 spanning the 1200 km long central and northern Great Barrier Reef, from 10-19°S. We
372 surveyed two sites per reef, using five 10 x 1 m belt transects placed on the reef crest at a
373 depth of 2 m at each site. Observers identified and counted each coral colony and recorded a
374 categorical bleaching score for each individual: (1) no bleaching, (2) pale, (3) 1-50%
375 bleached, (4) 51-99% bleached, (5) 100% bleached, (6) bleached and recently dead. The site-
376 level amount of bleaching for each taxon in Figure 4 is the sum of categories 2-5. The

377 number of colonies assessed was 58,414. A similar standardised protocol was used to
378 measure amounts of bleaching for the Coral Sea, on sub-tropical reefs south of the Great
379 Barrier Reef, and across 18 degrees of latitude along the west coast of Australia (Fig. 1g).

380 **Temperature and Thermal Stress**

381 The spatial pattern of thermal stress on the Great Barrier Reef during each of the three major
382 bleaching events (1998, 2002 and 2016; Fig. 1b, c) was quantified using the well-established
383 Degree Heating Week (DHW) metric³¹. The DHW values were calculated using the
384 Optimum Interpolation Sea Surface Temperature (OISST)³², because it provides a consistent
385 measure of thermal stress for all three major bleaching events on the Great Barrier Reef. The
386 baseline climatology for the DHW metric was calculated for 1985-2012, following Heron et
387 al.³³. DHW values are presented in Fig. 2b as heat-maps (Stretch type: Minimum-Maximum)
388 using inverse distance weighting (IDW; Power: 2, Cell Size: 1000, Search Radius: variable,
389 100 points) in ArcGIS 10.2.1. For Fig. 2g, March temperatures were compiled from
390 *HadISST1*³⁴ from 1980-2016 for four regions: northwest Australia, 10.5-20.5°S; mid-west
391 20.5-30.5°S; northern Great Barrier Reef (10.5°S-16.5°S), and southern Great Barrier Reef
392 (21.5°S-24.5°S).

393 **Water Quality Metrics**

394 We considered remotely-sensed chlorophyll-*a* and secchi depth proxies as water quality
395 metrics, measured for the Great Barrier Reef³⁵ over different averaging windows.
396 Specifically, we used four averaging windows with respect to 2016 (1, 2, or 4 years prior to
397 bleaching, and a long term 1997-2016 average), and two different time periods (summer
398 months only [December through May] and the entire year [June through May]). We also
399 considered derived quantities from these estimates: the proportion of time that reefs exceeded
400 an estimated water quality chlorophyll-*a* threshold of 0.45µg/L¹³ and secchi depth exposure,

401 again for four different averaging windows, and for the full year and for summer only. All of
402 these metrics were significantly correlated with one another. In particular, long-term (1997-
403 2016) average chlorophyll-*a* concentration was very highly correlated with all other metrics
404 (absolute value of Spearman's rank correlation coefficient averaged $r=0.81$, and was never
405 lower than 0.7). Therefore, to minimize the risk of Type I error, we used it as the water
406 quality proxy in our analyses of bleaching, log-transformed to obtain a symmetric distribution
407 of values.

408 **Analysis of spatial patterns, resistance and adaptation**

409 To model the factors affecting bleaching in 2016, we used aerial bleaching scores as a
410 response variable; whether a reef was severely bleached (57% of reefs had a bleaching score
411 of 3-4) or not (the remaining 43% of reefs had a bleaching score of 0-2), for all surveyed
412 reefs in the Great Barrier Reef Marine Park. We considered temperature stress (measured as
413 DHW, described above), water quality (measured as the natural logarithm of long-term
414 chlorophyll-*a* concentration), and marine protection status. Reefs in three zones classified as
415 Marine National Park, Preservation, Scientific Research, and Buffer were considered to be
416 Protected in the model, whereas all other zones were Fished. We repeated our test using other
417 splits of bleaching scores (0 versus 1-4, 0-1 versus 2-4, and 0-3 versus 4), although these led
418 to more uneven splits of the data. Regardless of how the bleaching scores were binned, the
419 severity of bleaching was significantly correlated with DHW, while the additional variables
420 had effects that were similar to our original analysis: small in magnitude or statistically non-
421 significant.

422 To calibrate the relationship between temperature and bleaching, we fit a generalized linear
423 model (GLM) with binomial error structure, using Degree Heating Weeks (DHW) as the
424 explanatory variable. To test the hypothesis that high water quality confers bleaching

425 resistance¹³, we fit a model including both DHW and chlorophyll-*a* as explanatory variables,
426 and asked whether the effect of chlorophyll-*a* concentration was significantly positive (that
427 is, if reefs with higher chlorophyll-*a* concentrations had a higher probability of bleaching).
428 Similarly, to test the hypothesis that fishing increases bleaching resistance, we fit a model
429 including DHW and protection status as explanatory variables, and asked whether the effect
430 of protection was significantly negative (Protected reefs had a lower probability of bleaching,
431 at a given level of temperature stress, than Fished reefs, see Extended Data Fig. 1 and
432 Extended Data Table 1).

433 To test for evidence of acclimation or adaptation, we extracted the residuals from our DHW-
434 only generalized linear model (Extended Data Table 1), and we tested for a negative
435 correlation between the residuals and the aerial bleaching scores recorded during prior events:
436 1998, 2002, or the higher of the two earlier scores (Extended Data Fig. 1). That is, we tested
437 the hypothesis that reefs that bleached more severely in prior events were less likely to bleach
438 at a given temperature stress in 2016, compared to reefs that bleached less in prior events.
439 Because bleaching score is ordered and categorical, we tested this hypothesis with Kendall's
440 tau.

441 **Methods References**

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455 **Data and code availability**

456 Data and code available on request from the authors.

457

458 **Extended Data Figure Legends**

459 **Extended Data Figure 1.** A General Linear Model to explain the severity of coral bleaching.
460 Curves show the estimated relationships between probability of severe bleaching (>30%) on
461 individual reefs of the Great Barrier Reef in 2016 and three explanatory variables (Degree
462 Heating Weeks, chlorophyll-*a*, and Reef Zoning, see Extended Data Table 1): The DHW-
463 only model is shown in black. For the DHW plus chlorophyll-*a* model, the blue threshold
464 shows the estimated relationship between probability of severe bleaching and DHW for the
465 25th percentile of chlorophyll-*a*, and the brown threshold shows the same for the 75th
466 percentile of chlorophyll-*a*. For the DHW plus Reef Zoning model, the red threshold, shows
467 the relationship for fished reefs, and the green for unfished reefs. Water quality metrics and
468 level of reef protection make little if any difference.

469 **Extended Data Figure 2.** Difference in daily sea surface temperatures between the northern
470 and southern Great Barrier Reef, before and after ex-Tropical Cyclone Winston. The
471 disparity between Lizard Island (14.67°S) and Heron Island (23.44°S) increased from 1°C in
472 late February to 4°C in early March, 2016.

473 **Extended Data Figure 3.** A test for the effect of past bleaching experience on the severity of
474 bleaching in 2016. The relationship between previous bleaching scores (in 1998 or 2002,
475 whichever was higher) and the residuals from the DHW generalized linear model (Extended
476 Data Table 1). Each data point represents an individual reef that was scored repeatedly. There
477 is no negative relationship to support acclimation or adaptation.

478 **Extended Data Figure 4.** Flight tracks of aerial surveys of coral bleaching, conducted along
479 and across the Great Barrier Reef and Torres Strait in March and April 2016.

480 **Extended Data Figure 5.** Ground-truthing comparisons of aerial and underwater bleaching
481 scores. Aerial scores are: 0 (<1% of colonies bleached), 1 (1-10%), 2 (10-30%), 3 (30-60%)

482 and 4 (60-100%) on the Great Barrier Reef in 2016 (Fig. 1a). Continuous (0-100%)
483 underwater scores are based on *in situ* observations from 259 sites (104 reefs). Error bars
484 indicate two standard errors above and below the median underwater score, separately for
485 each aerial category. The dashed horizontal grey lines show the upper and lower boundaries
486 of each bleaching category.

487 **Extended Data Table 1.** A test for the causes of coral bleaching. Generalized linear models
488 (GLM) show the relationship between severe bleaching of reefs (>30%) in 2016 on the Great
489 Barrier Reef and three explanatory variables. Explanatory variables were (A) Degree Heating
490 Weeks (DHW), (B) DHW plus water quality (natural logarithm of chlorophyll-*a*
491 concentration), and (C) DHW plus reef zoning (Protected or Fished). Note that the estimated
492 effect of chlorophyll-*a* is negative, contrary to the hypothesis that good water quality confers
493 resistance to bleaching.

494 **Extended Data Table 2.**
495
496 Winners and losers. Rank order of taxa, from most bleached to least bleached, for different
497 severities of bleaching. See Fig. 4.