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Global warming and recurrent mass bleaching of corals

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

The world's tropical reef ecosystems, and the people who depend on them, are increasingly impacted by climate change[1-7]. Since the 1980s, rising sea surface temperatures due to global warming have triggered unprecedented mass bleaching of corals, including three pan-tropical events in 1998, 2010 and 2015/16[1]. Thermal stress during marine heatwaves disrupts the symbiotic relationship between corals and their algal symbionts (Symbiodinium) spp.), causing the corals to lose their color[2-3]. Bleached corals are physiologically damaged, and prolonged bleaching often leads to high levels of mortality[5-8]. Increasingly, individual reefs are experiencing multiple bouts of bleaching, as well the impacts of more chronic local stressors such as pollution and overfishing[1-4]. Our study represents a fundamental shift away from viewing bleaching events as individual disturbances to reefs, by focussing on three recurrent bleachings over the past 18 years along the 2,300 km length of the Great Barrier Reef, as well as the potential influence of water quality and fishing pressure on the severity of bleaching.

The geographic footprints of mass bleaching of corals on the Great Barrier Reef have varied strikingly during three major events in 1998, 2002 and 2016 (Fig. 1a). In 1998, bleaching was primarily coastal and most severe in the central and southern regions. In 2002, bleaching was more widespread, and affected offshore reefs in the central region that had escaped in 1998[8]. In 2016, bleaching was even more extensive and much more severe, especially in the northern, and to a lesser extent the central regions, where many coastal, mid-shelf and offshore reefs were affected (Fig. 1a, b). In 2016, the proportion of reefs experiencing extreme bleaching (>60% of corals bleached) was over four times higher compared to 1998 or 2002 (Fig. 1f). Conversely, in 2016, only 8.9% of 1,156 surveyed reefs escaped with no bleaching, compared to 42.4% of 631 reefs in 2002 and 44.7% of 638 in 1998. The cumulative, combined footprint of all three major bleaching events now covers almost the entire Great Barrier Reef Marine Park, with the exception of southern, offshore reefs (Fig. 1d).

Explaining spatial patterns

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

The geographic pattern of bleaching also demonstrates how marine heatwaves can be ameliorated by local weather[9], even during a global bleaching event. Arguably, southern reefs of the Great Barrier Reef would also have bleached in 2016 if wind, cloud cover, and rain from ex-Tropical Cyclone Winston had not rescued them[10]. Winston passed over Fiji on February 20th, when the southern Great Barrier Reef was only 1°C cooler than the north. By March 6th, this disparity increased to 4°C (Extended Data Fig. 2). Corals in the south that had begun to pale in February regained their colour in the south in March, whereas bleaching continued to progress in central and northern sectors (Fig. 2a). Similarly, in western Australia in 2016, Tropical Cyclone Stan cooled down mid-coast regions in early February[11], and the Leeuwin Current (which transports warm tropical water southwards) was also weakened due to El Niño conditions[12]. Consequently, both sides of tropical and sub-tropical Australia, including offshore atolls in the Coral Sea and Indian Ocean, exhibited continental-scale latitudinal gradients in bleaching (Fig. 1g).

The local (individual reef) scale pattern of recurrent bleaching on the Great Barrier Reef also reveals the trend of increasing severity, and the erosion of potential spatial refugia. Of the 171 individual reefs that were aerial-surveyed three times, 43% bleached in 1998, 56% in 2002, and 85% in 2016. Knowing the bleaching-history of these well-studied reefs allows us to investigate why they have bleached zero, one, two or three times. Only 9% of these repeatedly surveyed reefs have never bleached, in most cases because they are located near the southern, offshore end of the Great Barrier Reef (Fig. 1e), where they have experienced relatively low temperature anomalies during each event. A further 26% of repeatedly-surveyed reefs have bleached only once - ten reefs in 1998, eight in 2002, and 32 for the first time in 2016. The latter were primarily in the northern sector of the Great Barrier Reef, which largely escaped bleaching in the two earlier events (Fig. 1a). Thirty-five percent of the reefs have bleached twice, but only one reef bleached in both 1998 and 2002, compared to 58 reefs that bleached either in 1998 or 2002 and for a second time in the severe 2016 event. Finally, 29% of the repeatedly censused reefs bleached for a third time in 2016, primarily in central areas of the Great Barrier Reef, because they experienced anomalously warm temperatures during all three events (Fig. 1b, e). We conclude that the overlap of disparate geographic footprints of heat stress explains why different reefs have bleached 0-3 times, i.e. the repeated exposure to unusually hot conditions is the primary driver of the likelihood of recurrent bleaching at the scale of both individual reefs and the entire Great Barrier Reef (Fig. 1a, b). We found a similar strong relationship between the amount of bleaching measured underwater, and the satellite-based estimates of heat exposure on individual reefs (Fig. 3). Low levels of bleaching was observed at some locations when DHW values were only 2-3 ^{o}C-weeks. Typically, 30-40% of corals bleached on reefs exposed to 4 ^{o}C-weeks, whereas an average of 70-90% of corals bleached on reefs that experience 8 ^{o}C-weeks or more (Fig. 3).

Resistance and adaptation to bleaching

Once we account for the amount of heat stress experienced on each reef, adding chlorophyll-a, a proxy for water quality, to our statistical model yielded no support for the hypothesis that good water quality confers resistance to bleaching[13]. Rather, the estimated effect of chlorophyll-a was to significantly reduce the DHW threshold for bleaching (Extended Data Table 1). However, despite the statistical significance, the effect in real terms beyond heat stress alone is very small (Extended Data Fig. 1). Similarly, we found no effect of the level of protection (in fished or protected zones) on bleaching ($P > 0.1$: Extended Data Table 1). These results are consistent with the broad-scale pattern of severe bleaching in the northern Great Barrier Reef, which affected hundreds of reefs across inshore-offshore gradients in water quality, and regardless of their zoning (protection) status (Fig. 1a, b).

Similarly, we find no evidence for a protective effect of past bleaching (e.g. from acclimation or adaptation): reefs with higher bleaching scores in 1998 or 2002 did not experience less severe bleaching in 2016, after accounting for the relationship between the 2016 temperature stress and bleaching propensity ($P > 0.9$ in all cases; Extended Data Figure 3). Thus, while several studies have indicated that prior exposure can influence the subsequent bleaching responses of corals[14-17], our comprehensive analysis of 171 repeatedly censused reefs indicates that any such historical effects on the Great Barrier Reef were masked by the severity of bleaching in 2016 (Fig. 2).

Winners and losers

Individual coral taxa bleached to different extents, especially on less affected reefs, creating both winners and losers, but the disparity among species diminished in the worst affected, northern regions. (Fig. 4). At the population and assemblage level, when and where bleaching is severe, even century-old corals can bleach (Fig. 2b-d). In contrast, where bleaching is less intense, it is highly selective, with a broad spectrum of responses shown by resistant corals (so-called winners) versus susceptible species (losers); winners by definition bleach less and have higher survivorship[18-21]. On lightly and moderately bleached reefs (<10% or 10-30% of corals affected), predominantly in the southern Great Barrier Reef, many of the more robust coral taxa escaped with little or no bleaching in 2016. In contrast, on extremely bleached reefs in the north (60-80% or >80% overall bleaching), we found far fewer lightly-bleached winners (Fig. 4). The rank order of winners versus losers also changed as the severity of bleaching increased (Extended Data Table 2), reflecting disparate responses by each taxon to the range of bleaching intensities. Thus, even species that are winners on relatively mildly bleached reefs joined the ranks of losers where bleaching was more intense (Fig. 4), creating a latitudinal gradient in the response of the coral assemblages.

The recovery time for coral species that are good colonizers and fast growers is 10-15 years[22-24], but when long-lived corals die from bleaching their replacement will necessarily take many decades. Recovery for long-lived species requires the sustained absence of another severe bleaching event (or other significant disturbance), which is no longer realistic while global temperatures continue to rise[25]. Therefore, the assemblage structure of corals is now likely to be permanently shifted at severely bleached locations in the northern Great Barrier Reef.

Implications for reef management

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

Identifying and protecting spatial refugia is a common strategy for conservation of threatened species and ecosystems, including coral reefs[30]. However, our analyses indicate that the cumulative footprint of recurrent bleachings is expanding, and the number of potential refugia on the Great Barrier Reef is rapidly diminishing. Indeed, the remote northern region escaped serious damage in 1998 and 2002, but bore the brunt of extreme bleaching in 2016. Rather than relying on the premise of refugia, our results highlight the growing importance of promoting the recovery of reefs to recurrent bleaching events through local management of marine parks and water quality. However, bolstering resilience will become more challenging and less effective in coming decades because local interventions have had no discernible effect on resistance of corals to extreme heat stress, and, with increasing frequency of severe bleaching events, the time for recovery is diminishing. Securing a future for coral reefs, including intensively managed ones such as the Great Barrier Reef, ultimately requires urgent and rapid action to reduce global warming.

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

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Figure legends

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

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

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

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

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

Methods

Recurrent bleaching on the Great Barrier Reef

For 2016, comprehensive aerial surveys of the Great Barrier Reef Marine Park and Torres Strait reported in Fig. 1a were conducted on ten days between 22nd March 2016 and 17th April 2016 when bleaching was highly visible. We used light aircraft and a helicopter, flying at an elevation of approximately 150 m. A total of 1,156 individual reefs from the coast to the edge of the continental shelf were assessed along 14^{o} of latitude (Extended Data Fig. 4). Each reef was assigned by visual assessment to one of five categories of bleaching severity, using the same protocols as earlier aerial surveys conducted in 1998 and 2002 by RB[8]: (0) less than 1% of corals bleached, (1) 1-10%, (2) 10-30%, (3) 30-60%, and (4) more than 60% of corals bleached. The accuracy of the scores was assessed by underwater ground-truthing (see next section). The aerial scores are presented in Fig. 1a as heat-maps (Stretch type: Minimum-Maximum) using inverse distance weighting (IDW; Power: 2, Cell Size: 1000, Search Radius: variable, 100 points) in ArcGIS 10.2.1.

Underwater surveys of eastern and western Australia

To ground-truth the accuracy of aerial scores of bleaching on the Great Barrier Reef (Fig. 1a), we conducted in-water surveys on 104 reefs during March and April 2016 (Extended Data Fig. 5). We also measured differential species responses (winners-losers; Fig. 4) on 83 reefs, spanning the 1200 km long central and northern Great Barrier Reef, from 10-19^{o}S. We surveyed two sites per reef, using five 10 x 1 m belt transects placed on the reef crest at a depth of 2 m at each site. Observers identified and counted each coral colony and recorded a categorical bleaching score for each individual: (1) no bleaching, (2) pale, (3) 1-50% bleached, (4) 51-99% bleached, (5) 100% bleached, (6) bleached and recently dead. The site-level amount of bleaching for each taxon in Figure 4 is the sum of categories 2-5. The number of colonies assessed was 58,414. A similar standardised protocol was used to measure amounts of bleaching for the Coral Sea, on sub-tropical reefs south of the Great Barrier Reef, and across 18 degrees of latitude along the west coast of Australia (Fig. 1g).

Temperature and Thermal Stress

The spatial pattern of thermal stress on the Great Barrier Reef during each of the three major bleaching events (1998, 2002 and 2016; Fig. 1b, c) was quantified using the well-established Degree Heating Week (DHW) metric[31]. The DHW values were calculated using the Optimum Interpolation Sea Surface Temperature (OISST)[32], because it provides a consistent measure of thermal stress for all three major bleaching events on the Great Barrier Reef. The baseline climatology for the DHW metric was calculated for 1985-2012, following Heron et al.[33]. DHW values are presented in Fig. 2b as heat-maps (Stretch type: Minimum-Maximum) using inverse distance weighting (IDW; Power: 2, Cell Size: 1000, Search Radius: variable, 100 points) in ArcGIS 10.2.1. For Fig. 2g, March temperatures were compiled from HadISST1[34] from 1980-2016 for four regions: northwest Australia, 10.5-20.5°S; mid-west 20.5-30.5°S; northern Great Barrier Reef (10.5°S-16.5°S), and southern Great Barrier Reef (21.5°S-24.5°S).

Water Quality Metrics

We considered remotely-sensed chlorophyll-a and secchi depth proxies as water quality metrics, measured for the Great Barrier Reef[35] over different averaging windows. Specifically, we used four averaging windows with respect to 2016 (1, 2, or 4 years prior to bleaching, and a long term 1997-2016 average), and two different time periods (summer months only [December through May] and the entire year [June through May]). We also considered derived quantities from these estimates: the proportion of time that reefs exceeded an estimated water quality chlorophyll-a threshold of 0.45µg/L[13] and secchi depth exposure, again for four different averaging windows, and for the full year and for summer only. All of these metrics were significantly correlated with one another. In particular, long-term (1997-2016) average chlorophyll-a concentration was very highly correlated with all other metrics (absolute value of Spearman's rank correlation coefficient averaged r=0.81, and was never lower than 0.7). Therefore, to minimize the risk of Type I error, we used it as the water quality proxy in our analyses of bleaching, log-transformed to obtain a symmetric distribution of values.

Analysis of spatial patterns, resistance and adaptation

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

To calibrate the relationship between temperature and bleaching, we fit a generalized linear model (GLM) with binomial error structure, using Degree Heating Weeks (DHW) as the explanatory variable. To test the hypothesis that high water quality confers bleaching resistance[13], we fit a model including both DHW and chlorophyll-a as explanatory variables, and asked whether the effect of chlorophyll-a concentration was significantly positive (that is, if reefs with higher chlorophyll-a concentrations had a higher probability of bleaching). Similarly, to test the hypothesis that fishing increases bleaching resistance, we fit a model including DHW and protection status as explanatory variables, and asked whether the effect of protection was significantly negative (Protected reefs had a lower probability of bleaching, at a given level of temperature stress, than Fished reefs, see Extended Data Fig. 1 and Extended Data Table 1).

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

Methods References

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Data and code availability

Data and code available on request from the authors.

Extended Data Figure Legends

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

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

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

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

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

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

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

Extended Data Table 2.

Winners and losers. Rank order of taxa, from most bleached to least bleached, for different severities of bleaching. See Fig. 4.