CORAL REEFS

Spatial and temporal patterns of mass bleaching of corals in the Anthropocene

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Tropical reef systems are transitioning to a new era in which the interval between recurrent bouts of coral bleaching is too short for a full recovery of mature assemblages. We analyzed bleaching records at 100 globally distributed reef locations from 1980 to 2016. The median return time between pairs of severe bleaching events has diminished steadily since 1980 and is now only 6 years. As global warming has progressed, tropical sea surface temperatures are warmer now during current La Niña conditions than they were during El Niño events three decades ago. Consequently, as we transition to the Anthropocene, coral bleaching is occurring more frequently in all El Niño–Southern Oscillation phases, increasing the likelihood of annual bleaching in the coming decades.

The average surface temperature of Earth has risen by close to 1°C as of the 1880s (*1*), and global temperatures in 2015 and 2016 were the warmest since instrumental record keeping began in the 19th century (*2*). Recurrent regional-scale (>1000 km) bleaching and mortality of corals is a modern phenomenon caused by anthropogenic global warming (*3*–*10*). Bleaching before the 1980s was recorded only at a local scale of a few tens of kilometers because of small-scale stressors such as freshwater inundation, sedimentation, or unusually cold or hot weather (*3*–*5*). The modern emergence of regional-scale bleaching is also evident from the growth bands of old Caribbean corals: synchronous distortions of skeletal deposition (stress bands) along a 400-km stretch of the Mesoamerican Reef have only been found after recent hot conditions, confirming that regional-scale heat stress is a modern phenomenon caused by anthropogenic global warming (*10*). Bleaching occurs when the density of algal symbionts, or zooxanthellae (*Symbiodinium* spp.), in the tissues of a coral host diminishes as a result of environmental stress, revealing the underlying white skeleton of the coral (*8*). Bleached corals are physiologically and nutritionally compromised, and prolonged bleaching over several months leads to high levels of coral mortality (*11*, *12*). Global climate modeling and satellite observations also indicate that the thermal conditions for coral bleaching are becoming more prevalent (*13*, *14*), leading to predictions that localities now considered to be thermal refugia could disappear by midcentury (*15*).

Although several global databases of bleaching records are available (notably ReefBase, reefbase.org), they suffer from intermittent or lapsed maintenance and from uneven sampling effort across both years and locations (*7*). The time spans of five earlier global studies of coral bleaching range from 1870 to 1990 (*3*), 1960 to 2002 (*4*), 1973 to 2006 (*5*), 1980 to 2005 (*6*), and 1985 to 2010 (*7*). Here we compiled de novo the history of recurrent bleaching from 1980 to 2016 for 100 globally distributed coral reef locations in 54 countries using a standardized protocol to examine patterns in the timing, recurrence, and intensity of bleaching episodes, including the latest global bleaching event from 2015 to 2016 (table S1). This approach avoids the bias of the continuous addition of new sites in open-access databases and retains the same range of spatial scales through time (fig. S1). A bleaching record in our analysis consists of three elements: the location, from 1 to 100; the year; and the binary presence or absence of bleaching. Our findings reveal that coral reefs have entered the distinctive human-dominated era characterized as the Anthropocene (*16*–*18*), in which the frequency and intensity of bleaching events is rapidly approaching unsustainable levels. At the spatial scale we examined (fig. S1), the

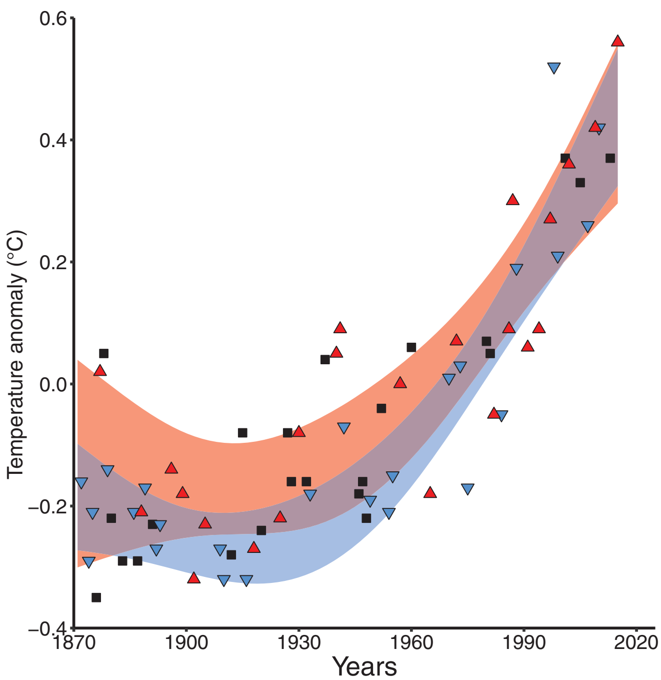

Fig. 1. Global warming throughout ENSO cycles. Sea surface temperature anomalies from 1871 to 2016, relative to a 1961–1990 baseline, averaged across 1670 1° latitude–by–1° longitude boxes containing coral reefs between latitudes of 31°N and 31°S. Data points differentiate El Niño (red triangles), La Niña (blue triangles), and ENSO neutral periods (black squares). Ninety-five percent confidence intervals are shown for nonlinear regression fits for years with El Niño and La Niña conditions (red and blue shading, respectively; overlap is shown in purple).

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number of years between recurrent severe bleaching events has diminished fivefold in the past four decades, from once every 25 to 30 years in the early 1980s to once every 5.9 years in 2016. Across the 100 locations, we scored 300 bleaching episodes as severe, i.e., >30% of corals bleached at a scale of tens to hundreds of kilometers, and a further 312 as moderate (<30% of corals bleached). Our analysis indicates that coral reefs have moved from a period before 1980 when regional-scale bleaching was exceedingly rare or absent (*3*–*5*) to an intermediary phase beginning in the 1980s when global warming increased the thermal stress of strong El Niño events, leading to global bleaching events. Finally, in the past two decades, many additional regional-scale bleaching events have also occurred outside of El Niño conditions, affecting more and more former spatial refuges and threatening the future viability of coral reefs.

Increasingly, climate-driven bleaching is occurring in all El Niño–Southern Oscillation (ENSO) phases, because as global warming progresses, average tropical sea surface temperatures are warmer today under La Niña conditions than they were during El Niño events only three decades ago (Fig. 1). Since 1980, 58% of severe bleaching events have been recorded during four strong El Niño periods (1982–1983, 1997–1998, 2009–2010, and 2015–2016) (Fig. 2A), with the remaining 42% occurring during hot summers in other ENSO phases. Inevitably, the link between El Niño as the predominant trigger of mass bleaching (*3*–*5*) is diminishing as global warming continues (Fig. 1) and as summer temperature thresholds for bleaching are increasingly exceeded throughout all ENSO phases.

The 2015–2016 bleaching event affected 75% of the globally distributed locations we examined (Figs. 2A and 3) and is therefore comparable in scale to the then-unprecedented 1997–1998 event, when 74% of the same 100 locations bleached. In both periods, sea surface temperatures were the warmest on record in all major coral reef regions (*2*, *19*). As the geographic footprint of recurrent bleaching spreads, fewer and fewer potential refuges from global warming remain untouched (Fig. 2B), and only 6 of the 100 locations we examined have escaped severe bleaching so far (Fig. 2B and table S1). This result is conservative because of type 2 errors (false negatives) in our analyses, where bleaching could have occurred but was not recorded.

After the extreme bleaching recorded from 2015 to 2016, the median number of severe bleaching events experienced across our study locations since 1980 is now three (Fig. 2C). Eighty-eight percent of the locations that bleached from 1997 to 1998 have bleached severely at least once again. As of 1980, 31% of reef locations have experienced four or more (up to nine) severe bleaching events (Fig. 2C), as well as many moderate episodes (table S1). Globally, the annual risk

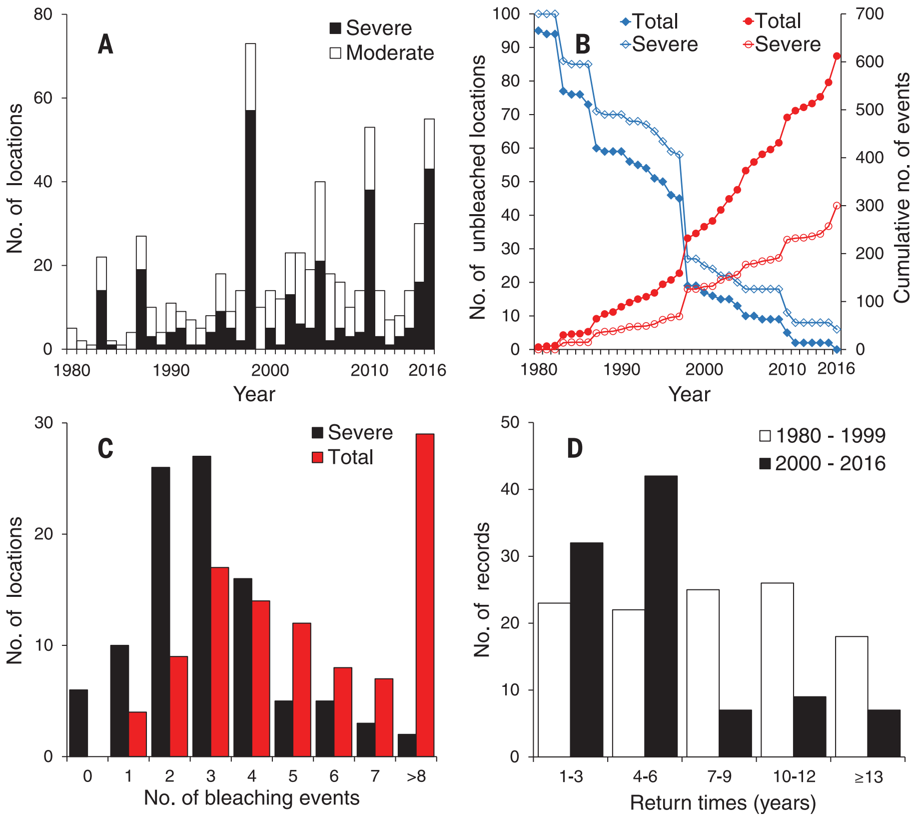

Fig. 2. Temporal patterns of recurrent coral bleaching. (**A**) Number of 100 pantropical locations that have bleached each year from 1980 to 2016. Black bars indicate severe bleaching affecting >30% of corals, and white bars depict moderate bleaching of <30% of corals. (**B**) Cumulative number of severe and total bleaching events since 1980 (red; right axis) and the depletion of locations that remain free of any bleaching or severe bleaching over time (blue; left axis). (**C**) Frequency distribution of the number of severe (black) and total bleaching events (red) per location. (**D**) Frequency distribution of return times (number of years) between successive severe bleaching events from 1980 to 1999 (white bars) and 2000 to 2016 (black bars).

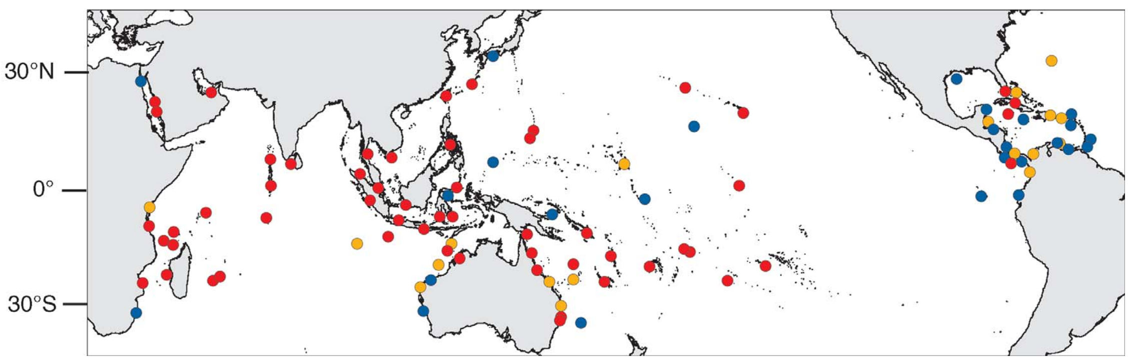

Fig. 3. The global extent of mass bleaching of corals in 2015 and 2016. Symbols show 100 reef locations that were assessed: red circles, severe bleaching affecting >30% of corals; orange circles, moderate bleaching affecting <30% of corals; and blue circles, no substantial bleaching recorded. See table S1 for further details.

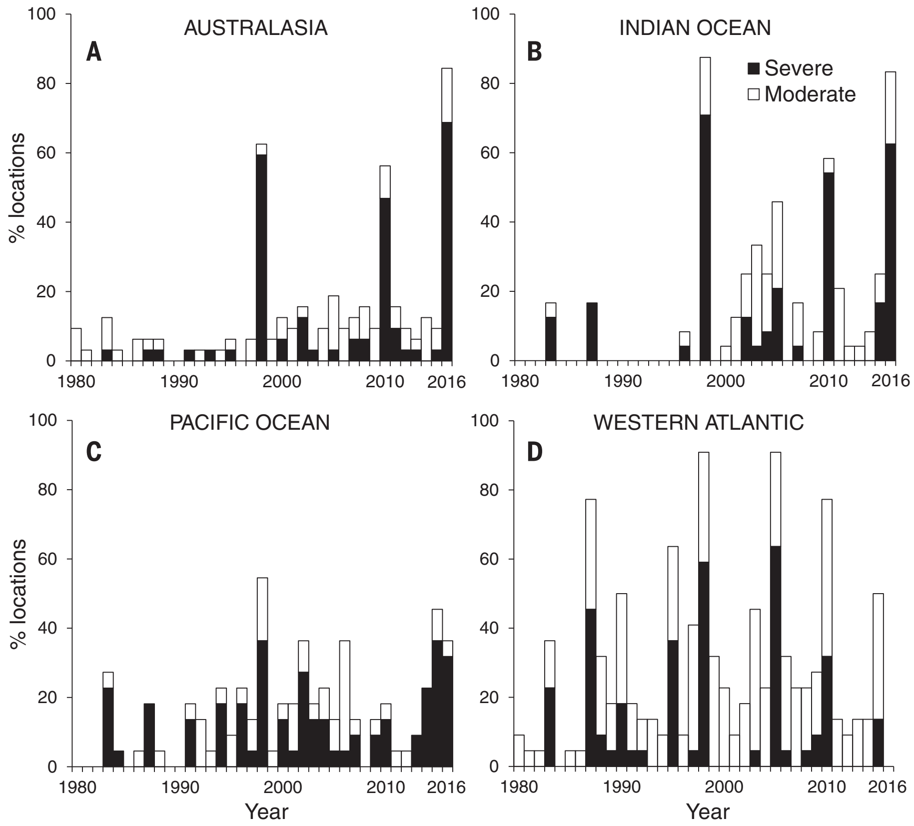

Fig. 4. Geographic variation in the timing and intensity of coral bleaching from 1980 to 2016. (**A**) Australasia (32 locations). (**B**) Indian Ocean (24 locations). (**C**) Pacific Ocean (22 locations). (**D**) Western Atlantic (22 locations). For each region, black bars indicate the percentage of locations that experienced severe bleaching, affecting >30% of corals. White bars indicate the percentage of locations per region with additional moderate bleaching affecting <30% of corals.

of bleaching (both severe and more moderate events) has increased by a rate of approximately 3.9% per annum (fig. S2), from an expected 8% of locations in the early 1980s to 31% in 2016. Similarly, the annual risk of severe bleaching has also increased, at a slightly faster rate of 4.3% per annum, from an expected 4% of locations in the early 1980s to 17% in 2016 (fig. S2). This trend corresponds to a 4.6-fold reduction in estimated return times of severe events, from once every 27 years in the early 1980s to once every 5.9 years in 2016. Thirty-three percent of return times between recurrent severe bleaching events since 2000 have been just 1, 2, or 3 years (Fig. 2D).

Our analysis also reveals strong geographic patterns in the timing, severity, and return times of mass bleaching (Fig. 4). The Western Atlantic, which has warmed earlier than elsewhere (*13*, *19*), began to experience regular bleaching sooner, with an average of 4.1 events per location before 1998, compared with 0.4 to 1.6 in other regions (Fig. 4 and fig. S2). Furthermore, widespread bleaching (affecting >50% of locations) has now occurred seven times since 1980 in the Western Atlantic, compared to three times for both Australasia and the Indian Ocean, and only twice in the Pacific. Over the entire period, the number of bleaching events has been highest in the Western Atlantic, with an average of 10 events per location, two to three times more than in other regions (Fig. 4).

In the 1980s, bleaching risk was highest in the Western Atlantic followed by the Pacific, with the Indian Ocean and Australasia having the lowest bleaching risk. However, bleaching risk increased most strongly over time in Australasia and the Middle East, at an intermediate rate in the Pacific, and slowly in the Western Atlantic (Fig. 4, fig. S3B, and tables S2 and S3). The return times between pairs of severe bleaching events are declining in all regions (fig. S3C), with the exception of the Western Atlantic, where most locations have escaped a major bleaching event from 2010 to 2016 (Fig. 2D).

We tested the hypothesis that the number of bleaching events that have occurred so far at each location is positively related to the level of postindustrial warming of sea surface temperatures that has been experienced there (fig. S4). However, we found no significant relationship for any of the four geographic regions, consistent with each bleaching event being caused by a short-lived episode of extreme heat (*12*, *19*, *20*) that is superimposed on much smaller long-term warming trends. Hence, the long-term predictions of future average warming of sea surface temperatures (*13*) are also unlikely to provide an accurate projection of bleaching risk or the location of spatial refuges over the next century.

In the coming years and decades, climate change will inevitably continue to increase the number of extreme heating events on coral reefs and further drive down the return times between them. Our analysis indicates that we are already approaching a scenario in which every hot summer, with or without an El Niño event, has the potential to cause bleaching and mortality at a regional scale. The time between recurrent events is increasingly too short to allow a full recovery of mature coral assemblages, which generally takes from 10 to 15 years for the fastest growing species and far longer for the full complement of life histories and morphologies of older assemblages (*21*–*24*). Areas that have so far escaped severe bleaching are likely to decline further in number (Fig. 2B), and the size of spatial refuges will diminish. These impacts are already underway, with an increase in average global temperature of close to 1°C. Hence, 1.5° or 2°C of warming above preindustrial conditions will inevitably contribute to further degradation of the world's coral reefs (*14*). The future condition of reefs, and the ecosystem services they provide to people, will depend critically on the trajectory of global emissions and on our diminishing capacity to build resilience to recurrent high-frequency bleaching through management of local stressors (*18*) before the next bleaching event occurs.

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ACKNOWLEDGMENTS

Major funding for this research was provided by the Australian Research Council's Centre of Excellence Program (CE140100020). The contents of this manuscript are solely the opinions of the authors and do not constitute a statement of policy, decision, or position on behalf of the National Oceanic and Atmospheric Administration or the U.S. government. Data reported in this paper are tabulated in the supplementary materials.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/359/6371/80/suppl/DC1
Materials and Methods
Figs. S1 to S4
Tables S1 to S3
References (*25*–*29*)

26 May 2017; accepted 5 December 2017
10.1126/science.aan8048

Science

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Science **359** (6371), 80-83.
DOI: 10.1126/science.aan8048

Not enough time for recovery

Coral bleaching occurs when stressful conditions result in the expulsion of the algal partner from the coral. Before anthropogenic climate warming, such events were relatively rare, allowing for recovery of the reef between events. Hughes *et al.* looked at 100 reefs globally and found that the average interval between bleaching events is now less than half what it was before. Such narrow recovery windows do not allow for full recovery. Furthermore, warming events such as El Niño are warmer than previously, as are general ocean conditions. Such changes are likely to make it more and more difficult for reefs to recover between stressful events.

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