OCEANOGRAPHY

Nutrient-supplying ocean currents modulate coral bleaching susceptibility

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With predictions that mass coral bleaching will occur annually within this century, conservation efforts must focus their limited resources based on an accurate understanding of the drivers of bleaching. Here, we provide spatial and temporal evidence that excess nutrients exacerbate the detrimental effects of heat stress to spark mass coral bleaching in the Red Sea. Exploiting this region's unique oceanographic regime, where nutrients and heat stress vary independently, we demonstrate that the world's third largest coral reef system historically suffered from severe mass bleaching only when exposed to both unusually high temperature and nutrients. Incorporating nutrient-supplying ocean currents and their variability into coral bleaching forecasts will be critical for effectively guiding efforts to safeguard the reefs most likely to persist in the Anthropocene.

INTRODUCTION

Coral reefs are oases of productivity in low-nutrient ocean regions, providing ecosystem services such as nutrition and coastal protection to hundreds of millions of people (1). The success of coral reefs in these oligotrophic regions is due, in large part, to the efficient nutrient-recycling symbiosis that has evolved between coral hosts and symbiotic zooxanthellae algae in the family Symbiodiniaceae. Yet, under certain environmental circumstances, the host's relationship with its symbionts can be detrimental. When water temperatures become unusually high, the zooxanthellae produce reactive oxygen species that are toxic to the coral, leading to the expulsion of the symbionts and "bleaching" as the coral's white skeleton becomes visible through its translucent tissue (2, 3). If high temperatures persist, the absence of symbionts can ultimately cause mortality as the host is deprived of energy or becomes susceptible to disease (4). In controlled experiments, excess nutrients cause corals to become more susceptible to bleaching under heat because nutrients lead to denser symbiont populations and thus greater amounts of reactive oxygen species (5–7). However, field testing of the role of nutrients in coral bleaching has been precluded for two main reasons. First, nutrients and temperature often covary in the ocean, making it difficult to disentangle their effects. Second, nutrients are not directly measurable via satellite remote sensing, preventing retrospective global analyses of the role of nutrients in driving coral bleaching in the same way that can be done with satellite-derived sea surface temperature (SST) (8).

The unique oceanographic setting of the Red Sea enables both spatial and temporal tests of the isolated and combined effects of heat stress and nutrients in driving coral bleaching. With little terrestrial runoff due to the arid climate and a single narrow connection to the Indian Ocean, the dominant source of nutrients to the Red Sea can be traced to a single water mass, the Gulf of Aden Intermediate Water (GAIW) (9). The temperature and nutrient concentration of GAIW is well constrained, and GAIW only enters the Red Sea in early summer between June and August due to the reversal of monsoon winds (9). Once in the Red Sea, GAIW upwells to the surface during summer in the Farasan Banks (9), the third largest contiguous coral reef system in the world. Critically, the summer upwelling is quantifiable from satellite SST (Fig. 1), and monsoon-driven interannual variability of the GAIW intrusion establishes variability among years in the concentration of nutrients supplied to the Farasan Banks that is decoupled from the SST maximum in September to October. This oceanographic regime enables us to test the role of nutrients in modulating bleaching susceptibility both temporally and spatially. Understanding the influence of these factors in driving coral stress is key to addressing anthropogenic activities that are producing large-scale bleaching events worldwide.

We drilled skeletal cores from 60 long-lived *Porites* corals in the Farasan Banks to build a timeline of bleaching events over the past several decades (table S1). When *Porites* corals bleach, they record the event within their skeleton as either a discrete high-density "stress band" or a partial mortality scar (Fig. 2), and the proportion of *Porites* colonies with stress bands tends to correlate with bleaching severity at the community level (10–13). The use of stress bands preserved within skeletal cores to reconstruct past bleaching histories is especially useful in regions such as the southern Red Sea, where long-term observations or monitoring efforts are absent. We used cores from both living and radiometrically age-dated dead colonies to ensure an accurate bleaching reconstruction based on a representative sample of the population.

RESULTS AND DISCUSSION

Most cores (81%) showed clear evidence of stress in 2015 (Fig. 2), consistent with visual observations of bleaching at this time (fig. S1) (14). Stress bands were found in cores across the Farasan Banks (fig. S2), indicating that the bleaching event was widespread. There was no effect of *Porites* species on the stress response (χ^2 test statistic = 2.4, $P = 0.30$). Stress bands corresponding to 2015 were also present in a smaller set of *Favites* and *Platygyra* cores (fig. S3). Most of the

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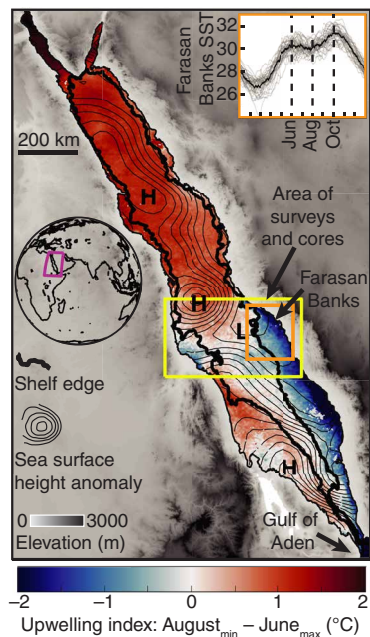
Fig. 1. Early summer upwelling in the Red Sea. SST difference between the August minimum and the June maximum reveals the influence of upwelling. Blue colors indicate upwelling, which is mostly restricted to the southeastern Red Sea. Thin contours indicate climatological SSH anomalies, which show a persistent anti-cyclonic eddy in the central Red Sea that acts as a barrier to the northward propagation of the upwelling waters. Thick black line shows the 100-m isobath that defines the shelf edge. Yellow and orange boxes show the locations of surveys and coral coring, respectively. Inset time series shows the climatology (black) of SST between 1982 and 2015 (gray) in the Farasan Banks, revealing the early summer decrease in SST due to upwelling.

Porites stress bands in 2015 were moderate or severe, and all nine dead colonies dated to 2015 (table S2). Several other *Porites* colonies that were mostly dead retained small patches of residual living tissue, and these contained clear 2015 stress bands (Fig. 2). Our cores showed no sign of bleaching in the Farasan Banks during 1998 or 2010, but other cores collected farther north near Thuwal captured the bleaching events that were observed directly at those times (fig. S4) (14, 15). Besides 2015, the only years with stress bands in the Farasan Banks were 1982, 1995, and 2002, each affecting less than 15% of corals (Fig. 2B). Thus, our results demonstrate that the 2015 bleaching event in the southeastern Red Sea was unprecedented in severity, at least over the past 70 years (95% confidence, see Materials and Methods).

The dominance of 2015 in our bleaching reconstruction is initially unexpected because it was not the warmest summer on record. Degree heating weeks (DHWs), a metric of heat stress that incorporates both the magnitude and duration above typical summer temperatures, were 75% greater in 2002 than 2015 (Fig. 3B), yet the bleaching response was 80% less in 2002 (Fig. 2B). Furthermore, 1982 stress bands were present in multiple cores, although there were four other years with higher DHW but no stress bands (Fig. 3B). Previous studies have quantified various components of heat stress to improve coral bleaching predictions beyond DHW alone (16–20). In particular, light stress, exposure to high-frequency (e.g., daily) temperature variations in shallow reef flats, and rates of heating before peak SST can all modulate bleaching responses (17, 18, 21). Because

photosynthetically active radiation (PAR) was not greater in 2015 than 2002 (fig. S5), light stress is inconsistent with the bleaching history in the Farasan Banks. Furthermore, high-frequency temperature variability is unlikely to explain our findings because cores collected both at 1-m depth on shallow reef flats and down to 11-m depth on steep reef walls facing the open ocean showed consistent stress histories. The rate of temperature change is a more plausible explanation because SST increased during a brief period in early August 2015 at a rate unprecedented since 1982. However, the warming rate was not exceptional in 2015 from the 2 weeks before SST breached the maximum monthly mean (MMM) to the time of peak DHW, with higher rates of heating in both 1982 and 2002 (fig. S8), leaving this as an unlikely cause of the especially severe bleaching in 2015.

Rather, the decoupling between heat stress and bleaching in the Farasan Banks can be explained by early summer upwelling. During 2015, the strength of June-August upwelling was the fourth greatest on record, behind only 1982 and 2 years (1983 and 1984) without any heat stress. In contrast, upwelling was effectively undetectable in 2002. Because the properties of the upwelled water are well known, we can estimate the June-August nutrient levels that preceded September-October heat stress each year (Fig. 3A). This analysis reveals that 2015 was both moderately hot and nutrient-rich, whereas 2002 was hotter but nutrient-poor, and 1982 was less hot but nutrient-rich (Fig. 3B). If bleaching were a response to temperature alone, then we would expect to find many more stress bands in 2002 than 2015, opposite to our results (Fig. 2). Therefore, the unprecedented bleaching response in 2015 is consistent with nutrients exacerbating the negative effects of heat stress to initiate bleaching. Mechanistically, this is likely to occur due to denser symbiont populations producing more reactive oxygen species (5). Although nutrient imbalance (e.g., an excess of nitrate relative to phosphate) was identified as an important factor in coral bleaching in a laboratory study (22), it is an unlikely driver of bleaching here because the N:P ratio of GAIW (~16:1; figs. S6 and S7) is more balanced, and the N:P ratio of reef water in the Farasan Banks (fig. S6) is lower than that study.

The role of nutrients in exacerbating heat stress to spark bleaching is also consistent with the spatial pattern of bleaching in the Red Sea during 2015. Coral reefs on the western side of the Red Sea along the coast of Sudan are composed of coral communities dominated by mostly the same genera as those formerly inhabiting the Farasan Banks. Before the 2015 bleaching event, *Porites*, *Pocillopora*, and *Acropora* were three of the four most common genera in both regions, together composing more than half of each coral community (fig. S9). Yet, Sudanese reefs receive little to no nutrient injection because upwelling is constrained to the eastern side of the basin (Fig. 1) (9). Some of the Sudanese reefs experienced similar or greater levels of heat stress as portions of the Farasan Banks in 2015 (Fig. 3C), but they did not bleach (Fig. 3D). Because neither Sudan nor Farasan was exposed to DHW exceeding 1°C-week during the previous 5 years (2010–2014), differential acclimatization to heat stress cannot reconcile the different bleaching response between these two regions (23).

Despite multiple laboratory studies demonstrating that nutrients exacerbate the effects of heat stress on corals (5, 22, 24), their influence has not been widely tested in the field. Because of the lack of gridded and time-resolved nutrient datasets, most studies only evaluate bleaching events in the context of various heat stress metrics
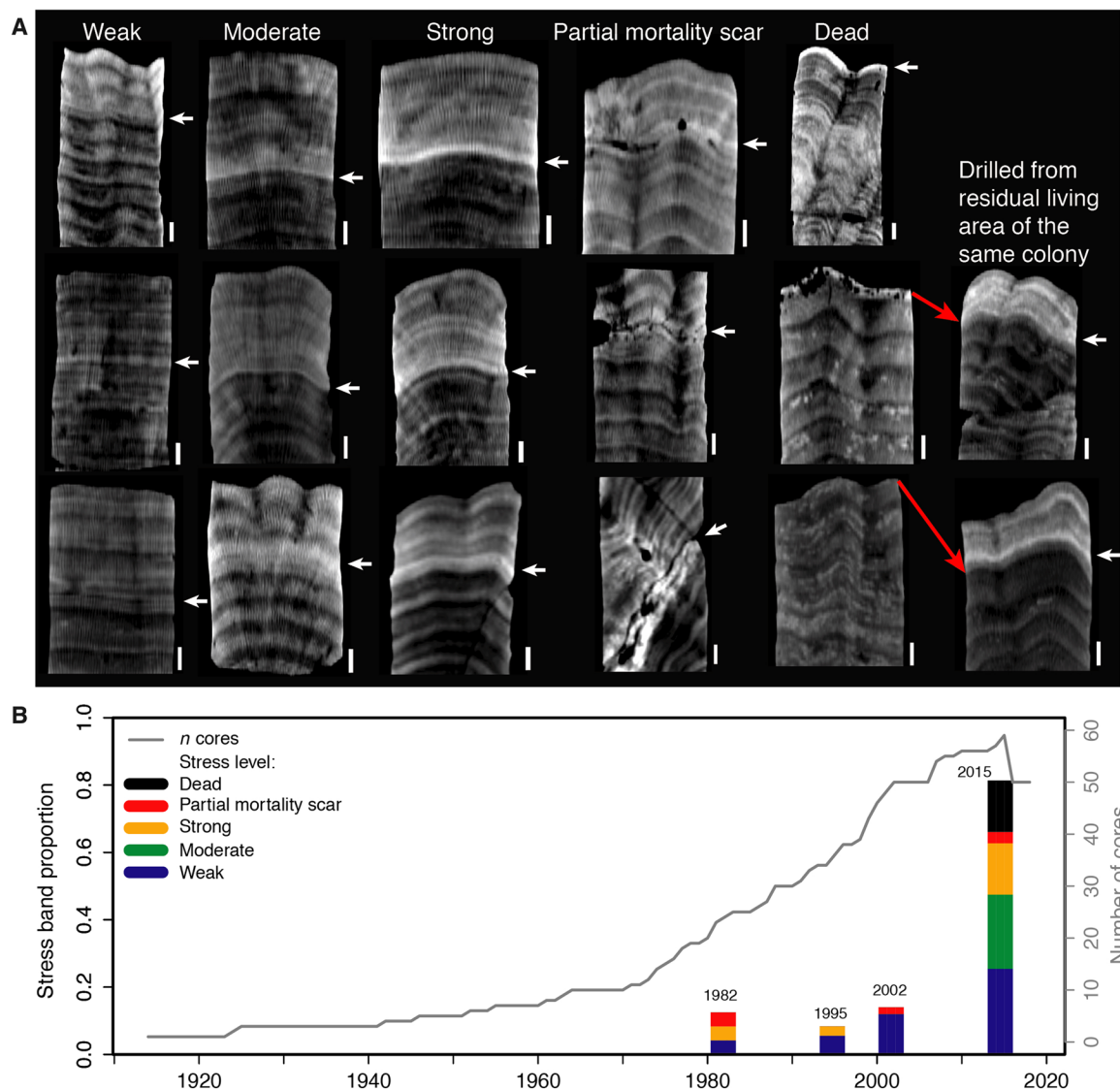
Fig. 2. Coral core evidence of past bleaching events. (A) Computerized tomography (CT) images reveal annual high (light) and low (dark) density bands and anomalous high-density stress bands or partial mortality scars (white arrows). Stress bands are weak, moderate, or strong based on the intensity of the high-density anomaly. **(B)** Dating the stress bands or partial mortality scars with the annual banding patterns reveals a timeline of past bleaching events. The thin gray line shows the number of cores in the dataset per year. Scale bars, 1 cm.

(25). Furthermore, these analyses often focus solely on bleaching events, not considering the high occurrences of false positives—times when temperature reached nominal bleaching levels, but bleaching did not occur (19, 26). For example, using a recent global bleaching database (25), we find that temperature alone correctly predicts less than half of observed bleaching events and, at the same time, predicts more false alarms than real bleaching events (fig. S10). Likewise, a variety of other bleaching reports also fail to adequately describe coral bleaching patterns solely with heat stress (26–29), indicating that other factors such as acclimatization or the interactions of multiple stressors play key roles. Last, some of the broadscale bleaching studies that have attempted to consider the role of nutrients have done so with chlorophyll a concentrations (8), which are easily accessible in time-resolved datasets but are inappropriate for shallow coral reef environments due to the overwhelming signal of bottom

reflectance (30). To date, the field studies that effectively investigated the influence of land-based nutrients on bleaching have suggested that nutrients are pivotal to coral thermal tolerance, consistent with our findings. Comparisons of bleaching histories with SST and nutrient time series in French Polynesia, Kenya, the Florida Keys, and the Great Barrier Reef all indicate that bleaching is best captured by combinations of heat and nutrient stressors (29, 31–34). Similarly, on the Mesoamerican Reef, proximity to local human populations increased coral bleaching susceptibility over the past century, with chronic nutrient pollution being one explanation for this finding (28). Here, we took advantage of the unique test bed provided by the temperature and nutrient dynamics of the Red Sea to examine the separate and combined effects of heat stress and nutrient enrichment on coral bleaching, both spatially and temporally. Our results demonstrate that while heat stress alone is capable
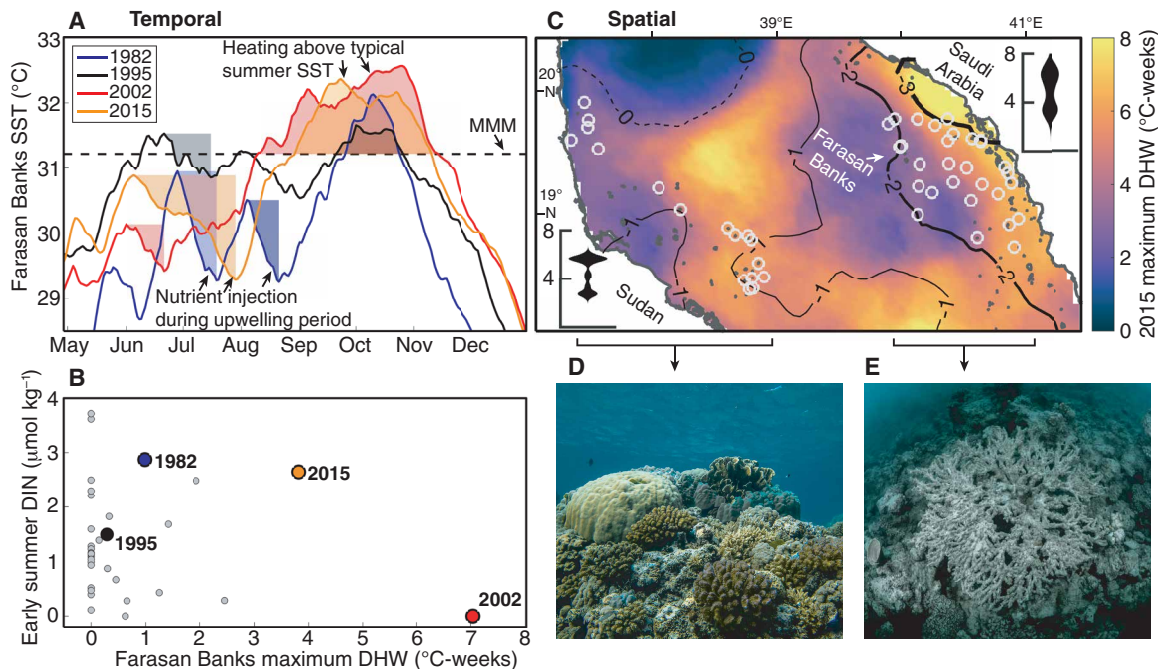
Fig. 3. Coral bleaching in response to a combination of heat and nutrient stress. (**A**) SST during the 4 years with stress bands in the Farasan Banks (1982, 1995, 2002, and 2015). Declines in SST from June to August (shading toward lower left) indicate early summer upwelling, and SST above the dashed black line indicates anomalously warm summers (shading toward upper right) above the MMM. (**B**) Summary of heat stress (DHW) and nutrients (DIN) for all years 1982–2015 in the Farasan Banks. (**C**) Spatial distribution of maximum DHW during 2015 (colors) and locations of either coral cores (eastern coast, i.e., Farasan Banks) or visual surveys (western coast, i.e., Sudan). The map corresponds to the area indicated by the yellow box in Fig. 1. The inset histograms show the relative distribution of maximum DHW (°C-weeks) per site on each side of the Red Sea. Contours show the June to August 2015 SST change, which indicates that upwelling (negative values) was constrained primarily to the Farasan Banks area. (**D** and **E**) Characteristic reefs with high live coral cover in Sudan (D) and recently dead corals with skeletons still intact in the Farasan Banks (E). Photo credits: (D) Darren Coker, King Abdullah University of Science and Technology; (E) Morgan Bennett-Smith, King Abdullah University of Science and Technology.

of causing bleaching, the addition of excess nutrients exacerbates coral bleaching.

Climate change remains the single largest threat to coral reefs (*1*), but it can only be tackled when global efforts to reduce greenhouse gas emissions are realized. In the meantime, effective actions can be taken to mitigate land-based sources of pollution (*29*, *34*, *35*) and to safeguard reefs with oceanographic conditions that protect them from either warming or excess nutrients (*36–39*). In addition, conservation agencies and scientists are now investing in major efforts to directly assist reefs through the Anthropocene, including reef restoration techniques such as seeding reefs with larvae and assisted evolution (*40*, *41*). Yet, doing so will be less effective without a complete understanding of the factors that induce mass coral bleaching. Our results provide a road map for directing conservation efforts to be most effective by incorporating oceanographic processes when deciding when and where to allocate resources or protection. Marine protected area networks in the Red Sea and elsewhere should include reefs that are oceanographically connected but that do not necessarily bleach at the same time. For example, the Farasan Banks bleached in 2015 but not 1998, whereas Sudanese reefs bleached in 1998 but not 2015 (*14*). This approach could reduce local acute disturbances to reefs that may be able to reseed each other after bleaching events. To do this effectively, projections of coral bleaching futures must move beyond solely temperature-based stress to incorporate changes in ocean current systems and their influence on coral reef nutrient enrichment.

MATERIALS AND METHODS
Climate data
We used the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation Sea Surface Temperature product (OI-SSTv2) (*42*) to assess heat stress and upwelling in the Farasan Banks (Fig. 3, A and B). OI-SSTv2 uses a single satellite source, the Advanced Very High Resolution Radiometer, to avoid long-term biases introduced by incorporating newer satellites, and it uses available in situ temperature data to adjust SSTs to further reduce biases. These features make OI-SSTv2 the most appropriate product to use for bias-free long-term assessments of SST variability. Comparison of OI-SSTv2 to Argo floats in the Red Sea since 2010 shows that it is more stable over time than NOAA's Coral Reef Watch (CRW) product for capturing summertime temperatures (fig. S11). We also compared OI-SSTv2 to in situ temperature loggers (Onset Pendant and Onset U22 models calibrated in an isothermal bath before deployment) deployed on four reefs during 2019 (fig. S12). These data show that OI-SSTv2 captures both the magnitude of cooling due to upwelling in June and July and the subsequent warming to peak SST in September and October, to within a few tenths of a degree. Nevertheless, CRW is higher resolution (5 km) than OI-SSTv2 (25 km) and provides the most precise view of the spatial distribution of temperature at one time. Thus, we used CRW to assess the spatial pattern of heat stress during summer 2015 (Fig. 3C). Last, we used the moderate resolution imaging spectroradiometer (MODIS) nighttime SST to assess the climatology of early summer upwelling (Fig. 1),

not only because it is the highest resolution data available (4 km), but also because it includes only the cloud-free data without infilling.

We calculated DHW (43) from 1982 to 2015 using OI-SSTv2 data and defining the climatological base period as 1985–2012. In analyses of heat stress over time (Fig. 3B), we calculated the maximum DHW per year. Likewise, we calculated the spatial distribution of DHW during 2015 in the same way, except using CRW data (Fig. 3C).

Upwelling of GAIW occurs in the southern Red Sea between June and August (9) and is detectable in satellite SST data (Fig. 1). We quantified the strength of upwelling as the difference between the maximum SST during June and the minimum SST during August (shading in Fig. 3A). Furthermore, we used the observed temperature (21°C) and dissolved inorganic nitrogen [DIN (nitrate + nitrite); 17 µmol kg^{-1}] properties of GAIW (fig. S6) (9) to estimate the maximum DIN concentrations during the early summer period. We used a simple mass-balance equation, $(1 - f)*T_{\text{June-max}} + f*T_{\text{GAIW}} = T_{\text{August-min}}$, where f is the proportion of GAIW at the surface and T is temperature. Assuming the normal Red Sea surface waters are depleted of DIN, we estimated the DIN concentration by August in the Farasan Banks as $f*17$ µmol kg^{-1}. This is a conservative estimate because it assumes no heating of Farasan Banks surface waters between June and August (i.e., $T_{\text{June-max}} - T_{\text{August-min}}$ represents the total effect of GAIW upwelling, although solar insolation between June and August would act to reduce the observed cooling).

In addition, we compared the marine heat wave index (44), and analogous marine cold spells, across the years with stress bands (fig. S13). These results support our analyses of DHW and upwelling strength in that 2015 is the only year with both a July-August cold spell and a September-October heat wave, due to the early summer cooling from upwelling followed by intense heating in August and September. Likewise, 1982 was characterized by repeated upwelling-driven cold spells between May and August, followed by anomalously high temperatures in October (reaching DHW levels but slightly below the criteria for a heat wave). Last, like in the DHW analyses, 2002 was the warmest summer on record and is the only year to reach a category 2 ("strong") summertime heat wave.

We used sea surface height (SSH) anomalies from the Archiving, Validation and Interpretation of Satellite Oceanographic data group to define the locations of semi-permanent eddies in the Red Sea (i.e., those that appear in the climatological mean SSH). A strong SSH peak (labeled "H" in Fig. 1) exists in the central Red Sea and appears to act as a barrier to the northward propagation of GAIW (Fig. 1A), consistent with shipboard observations (9).

PAR data from MODIS were used to assess light stress between 2002 and 2015. We calculated the climatological mean PAR during September and October (the warmest months of the year in the southern Red Sea) between 2001 and 2017 and plotted the September and October anomalies from the climatology during 2002 and 2015 (fig. S5). PAR anomalies were greater for the Farasan Banks in 2002 than 2015 and thus cannot explain the absence of bleaching in 2002. Likewise, in 2015, the southern Sudan sites were exposed to greater PAR anomalies than the Farasan Banks, making it unlikely that light stress explains the spatial pattern of bleaching in 2015 between the eastern and western Red Sea.

Seawater nutrient concentrations
We evaluated nutrient concentrations both within the core of GAIW and at 10-m depth adjacent to coral reefs within the Farasan Banks.

The GAIW sample collections and DIN concentrations were described previously (9), but we also include previously unpublished phosphate concentrations from these same samples (fig. S6). Phosphate was measured on a Lachat nutrient analyzer with a nominal detection limit of 0.05 µM, and the average difference between 40 duplicate samples was 0.02 µM. The GAIW samples were extracted from the full Red Sea database as those hydrocasts conducted adjacent to the Farasan region and shallower than 80 m [see (9) for further details]. Farasan Banks seawater samples were collected at 10-m depth with Niskin bottles in February, April, and May of 2019 and in January and February of 2020 (fig. S7). Duplicate seawater samples were each filtered through a 0.2-µm membrane filter and analyzed for nitrite, nitrate, and phosphate on a SEAL Analytical Segmented Flow Analyzer with nominal detection limits of 0.02, 0.03, and 0.01 µM, respectively. Average differences between the duplicate samples were 0.005, 0.08, and 0.03 µM for nitrite, nitrate, and phosphate, respectively. Seawater chlorophyll a concentrations were also measured for 2020 samples using Ocean Seven CTD 310 Plus.

Coral coring and CT scanning
We collected 60 skeletal cores from massive *Porites* corals in the Farasan Banks between February and May 2019, 51 of which were from living colonies and 9 from dead colonies. In addition, we collected three cores from living *Platygyra* sp. colonies and one core from a living *Favites* sp. colony in February 2020 (table S3). Last, three other *Porites* cores were collected in the Thuwal region of the central Red Sea between August 2019 and January 2020. All cores were collected with an underwater pneumatic drill, using a 5-cm-diameter diamond impregnated bit to drill downward from the top of each colony. Each core was rinsed three times with fresh water and dried before further analysis. We scanned the cores with a General Electric BrightSpeed CT scanner using 100 kV, a 9.6-cm field of view, and 1.25-mm resolution. The resulting three-dimensional images were visualized in OsiriX to inspect for anomalous high-density stress bands or partial mortality scars following previously established criteria (10, 23, 28, 45, 46). We separated the stress bands into three categories: weak, moderate, and strong, based on the intensity of the density anomaly relative to the earlier banding patterns of each core (Fig. 2). The different categories were determined visually and provide some indication of the severity of stress, but the key results are based on the presence/absence of stress bands. Three of the dead colonies had patches of living tissue on their sides, and we collected second cores from these areas, all of which showed clear stress bands dated to 2015 (Fig. 2).

To evaluate the time scale over which the 2015 bleaching event is unprecedented, we determined the number of cores required to have less than a 5% chance of a false negative, assuming that 50% of cores would record a past event of comparable intensity to 2015. This is a conservative estimate because 81% of cores showed evidence of stress in 2015. Following the calculations of (47), a sample size of at least five cores is sufficient if no core shows evidence of stress. In our study, five or more cores cover the period 1946–2015, and none have stress bands before 1982, meaning that there were not undetected bleaching events comparable to 2015 over at least the past 70 years (95% confidence).

Geochemical dating of dead-collected cores
The timing of death of the nine dead-collected cores was tested with U-Th dating. We cut 10 to 15 g of skeleton from the top 2 cm of each

core using a handheld rotary tool with a diamond-impregnated blade. To avoid any contamination of secondary minerals, we removed any discolored skeleton from the top few millimeters of each sample, retaining only the white primary skeleton. We then ground the skeletons to powders with a mortar and pestle and cleaned the samples with bleach overnight and in an ultrasonic bath for 20 min, followed by repeated rinses with deionized water. Approximately 1 g of carefully cleaned skeleton (48) from each sample was used for multi-collector inductively coupled plasma mass spectrometer U-Th dating (49, 50). To constrain the timing of coral mortality, mean ^{230}Th ages were reported with two SE bars, and averages (Tukey's biweighted means) of relative probability distributions (cumulative Gaussian plots) of U-Th ages were determined using Isoplot v.3.0.

Reef surveys

Benthic cover surveys were conducted in both the Farasan Banks (nine reefs) and along the western Red Sea (Sudan; five reefs) at similar latitudes to the Farasan Banks (table S4) during March and April of 2015, respectively. These prebleaching surveys enable a comparison of the coral communities that were exposed to heat stress later in 2015. At each reef, we conducted three point-count transects at 10-m water depth, each 50 m in length with points every 1 m. Corals were identified to genus level, and we compared which genera were the most abundant on the two sides of the Red Sea (table S5).

In May 2017, a total of 16 reefs along the western Red Sea (Sudan) were surveyed visually to assess if these Sudanese coral reefs were affected similarly to Farasan during the 2015 heat stress event. Total live coral cover and dead coral (intact dead coral structures) cover were documented at each reef. Mean live cover across the region was 43%, with dead corals comprising less than 0.1% cover. On the basis of these findings, it is clear that the stress event did not affect any of the western Red Sea reefs. We could not exclude the possibility that corals briefly bleached and recovered; however, local dive operators reported not observing any obvious signs of bleaching in the region during 2015/2016.

Species-specific responses

All *Porites* core samples with living tissue were identified to species based on corallite structure (35 *P. lutea*, 11 *P. lobata*, and 7 *P. solida*) (51). We tested whether stress responses to heat stress in 2015 varied among species using chi-square tests between species and presence/absence of any stress response.

Skill of temperature alone for predicting coral bleaching events globally

To assess the skill of temperature alone in predicting the occurrence of bleaching on reefs across the world, we used the bleaching database of Hughes *et al.* (25). The advantage of this database is that it includes bleaching occurrences and absences, both of which are necessary to fairly evaluate the skill of a predictor. We used the time period overlapping with satellite SST data (1982–2016), and we fixed 11 of 100 site coordinates that were listed incorrectly in the original database. First, we calculated maximum annual DHW for each year and each site using OI-SSTv2. We then calculated four skill scores based on DHW as the predictor and bleaching (including both moderate and severe events) as the response (fig. S10): (i) the Equitable Threat Score is commonly used in meteorology to define the optimal value of the predictor that maximizes correct predictions and minimizes false positives, (ii) bias is the ratio of the total number of pre-

dicted to observed events, (iii) the probability of detection (POD) is the proportion of observed bleaching events that were correctly predicted, and (iv) the false alarm ratio (FAR) is the proportion of predicted bleaching events that were not observed bleaching events. Last, we performed the calculations after shuffling the years of bleaching events (retaining the same number of events per site, but randomizing their timing) to demonstrate a no-skill scenario. Comparison of the DHW-predicted bleaching events with the random events confirms that DHW does have significant skill at predicting bleaching. However, the optimal DHW threshold (5.4°C-weeks) leads to a POD of 0.49 and a FAR of 0.61. This means that even with the optimal DHW predictor, most observed bleaching events are not predictable from temperature alone (POD < 0.5), and most predicted bleaching events did not actually happen (FAR > 0.6).

SUPPLEMENTARY MATERIALS

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