

# Ocean Warming Slows Coral Growth in the Central Red Sea

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Sea surface temperature (SST) across much of the tropics has increased by 0.4° to 1°C since the mid-1970s. A parallel increase in the frequency and extent of coral bleaching and mortality has fueled concern that climate change poses a major threat to the survival of coral reef ecosystems worldwide. Here we show that steadily rising SSTs, not ocean acidification, are already driving dramatic changes in the growth of an important reef-building coral in the central Red Sea. Three-dimensional computed tomography analyses of the massive coral *Diploastrea heliopora* reveal that skeletal growth of apparently healthy colonies has declined by 30% since 1998. The same corals responded to a short-lived warm event in 1941/1942, but recovered within 3 years as the ocean cooled. Combining our data with climate model simulations by the Intergovernmental Panel on Climate Change, we predict that should the current warming trend continue, this coral could cease growing altogether by 2070.

**H**ermatypic corals contribute up to 75% of the calcium carbonate (CaCO<sub>3</sub>) budget of modern reefs through the process of

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skeleton building (1). Today, rates of CaCO<sub>3</sub> production by reef corals, thought to be enhanced by the photosynthetic activities of symbiotic algae (zooxanthellae) (2, 3), far exceed carbonate production rates in the absence of biological activity and ensure that rates of reef accretion exceed natural rates of bioerosion, dissolution, and off-

shore transport (4). For individual corals, rapid rates of skeletal growth are essential for successful recruitment, in order to reach a size refuge from mortality (5) and to maximize colony surface area for photosynthesis (6).

Predictions based on experimental and field observations indicate that the combined effects of rising temperatures and ocean acidification could increase the frequency of bleaching events and reduce coral calcification by 80% of modern values when atmospheric CO<sub>2</sub> concentrations reach 560 parts per million around 2055 (7, 8, 9). At this point, if rates of CaCO<sub>3</sub> production by corals and other reef calcifiers cannot keep up with rates of erosion, the majority of coral reefs could switch from net accreting to net eroding structures. Elevated temperatures suppress the calcification rates of reef-building corals (10) by affecting the relationship between the coral host and its algal symbionts (zooxanthellae). As temperatures rise above threshold summertime values, the photosynthetic capacity of the symbiotic zooxanthellae declines (11), reducing the availability of algal-derived photosynthate that fuels light-enhanced calcification (12). A prolonged increase of ~1°C or more above historical maximum sea surface temperatures (SSTs)

(13) can result in substantial loss of zooxanthellae or “bleaching,” cessation of calcification, and in some cases coral mortality. The model predictions in (8, 9) consider the temperature at which bleaching occurs as the “threshold” temperature at which coral calcification begins to decline. However, elevated temperatures can negatively affect calcification long before bleaching is evident. Indeed, laboratory-based culture studies and field observations have shown the optimum temperature for calcification by several tropical coral species to be several degrees below their ambient summertime SSTs (14–16).

Mean annual SSTs across much of the global tropics and subtropics have increased between 0.4° and 1°C in the past four decades (17). However, in the central Red Sea, home to extensive reef growth and a high diversity of scleractinian corals, the extent of warming exceeds the observed mean tropical warming. For the past decade, summertime SSTs [July, August, and September (JAS)] in this region have remained on average 1.46°C above the historical mean [relative to 1950–1997 National Oceanic and Atmospheric Administration (NOAA) Extended Reconstructed Sea Surface Temperature (ERSST) v3b climatology]. Nevertheless, although localized bleaching to depths of 20 m was reported in 1998 (18), large-scale bleaching and the mortality typically associated with persistent warm SST anomalies have not been observed, suggesting that Red Sea corals may be naturally adapted to extremes of temperature and salinity. The lack of empirical data documenting the effects of thermal stress on coral growth in this region limits our ability to predict how future increases in SST will shape the coral reef landscape of the central Red Sea over the next century.

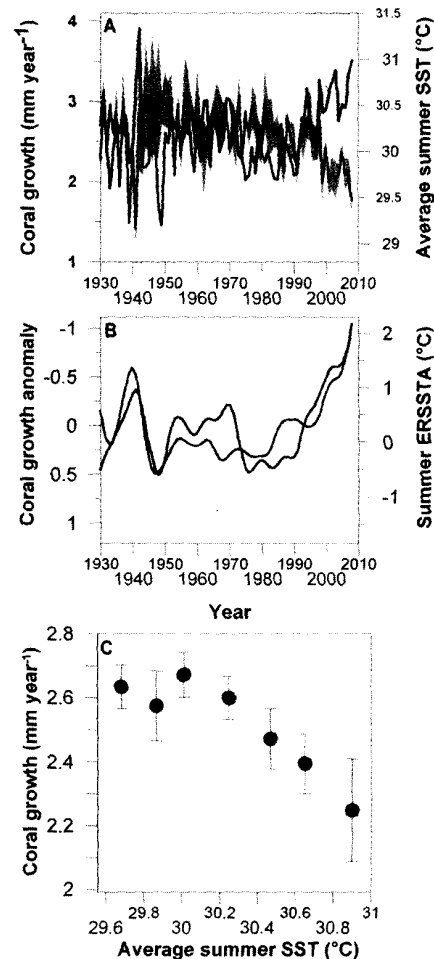
We used historical temperature records to quantify the temperature dependence of skeletal growth and calcification rates of the massive reef-building coral *Diploastrea heliophora* in the central Red Sea and to investigate the potential for subliminal (nonvisible) effects of recently rising SSTs. The coral colonies showed no outward signs of thermal stress, bleaching, or disease at the time of sampling. Skeletal cores were

removed from six colonies with a submersible hydraulic drill, and the holes were filled with pre-made cement plugs. In the lab, the intact cores were scanned with a Siemens Volume Zoom Spiral Computerized Tomography (CT) Scanner to reveal the annual growth bands (19). In *D. heliophora*, as with other architecturally complex coral skeletons, annual growth bands can be difficult to visualize and quantify with conventional two-dimensional (2D) x-ray techniques. The 3D imaging capabilities of the CT scanner allow us to digitally rotate the reconstructed core images to accurately identify the maximum vertical growth axis of the coral and to then slice the 3D image electronically to an optimal thickness, thus revealing the high- and low-density couplets that constitute each annual growth band.

By sampling colonies at different times of the year (20), we deduced that *D. heliophora* at this Red Sea site forms a narrow high-density skeletal band in the spring and that ~75% of skeletal extension occurs over the remainder of the year, as a wide low-density band (Fig. 1). We established the age of each coral by counting the number of high-density bands visible in the CT images and obtained a precise measure of their annual linear extension (upward growth) rates ( $SE \pm 0.5$  mm) by measuring the distance between successive high-density bands [see the supporting online material (SOM)]. Using the NOAA ERSST v3b (21), we quantified the relationship between coral growth and SST over the collective time period represented by the cores [1930 to 2008; see (20) for the age of each individual core]. Coral growth and summertime (JAS) SSTs are significantly coherent (95%) at periods longer than 10 years (fig. S1). A second-order Butterworth low-pass filter with a cutoff frequency of 10 years was applied to the coral and SST data sets to remove high-frequency variability and reveal the temperature-dependent signal. Average JAS SSTs account for 68% of the variance in *D. heliophora* skeletal growth on decadal time scales ( $R^2 = 0.676$ ,  $P < 0.001$ , effective number of samples = 7; Fig. 2B). Skeletal growth correlates inversely with temperature, and growth rates are highest when JAS SSTs remain

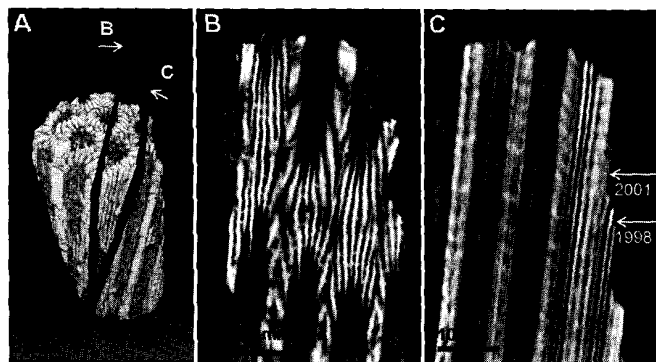
below 30.25°C. When the average JAS SST exceeds 30.5°C, *D. heliophora* growth declines rapidly, by 0.12 mm (5%) for every 0.2°C increase in summer SST (Fig. 2C).

Average summertime SSTs have exceeded 30.5°C at our study site twice in the past 85



**Fig. 2.** Calibration of the coral growth dependence on SST. (A) Averaged annual growth of six corals  $\pm 1$  SE (red line  $\pm$  gray shading) measured from CT scans compared with average annual summer SSTs (JAS, ERSST v3b, blue line), 1925–2008. SSTs exceeded 30.5°C twice in the past 83 years (vertical blue shading). (B) 10-year filtered coral growth anomaly (red line) and ERSST anomaly (ERSSTA, blue line) (coral growth and ERSST anomalies relative to the 1950–1997 mean for each time series) data show inverse correlation on multi-year time scales ( $r^2 = 0.68$ ). (C) Model I regression of mean annual coral growth  $\pm 1$  SE against average summer SST ( $\pm 1$  SE for each SST bin) from six *D. heliophora* colonies ( $n = 318$  total observations of unfiltered data). The red circles indicate the regression of average coral extension rate within each SST range indicated by the SE bars. The optimum temperature for *D. heliophora* skeletal growth,  $<30.5^\circ\text{C}$ , was determined as the point at which average annual skeletal growth deviates from the mean annual baseline extension rate [2.69 mm year<sup>-1</sup>, model I regression,  $F_{5,300} = 2.73$ ,  $P < 0.05$ ].

**Fig. 1.** Quantification of annual coral growth by 3D CT scanning. (A) 3D CT scan reconstruction of the skeleton of *D. heliophora* from a small core. Virtual 2D slices (B and C), 2.5 mm thick, are cut digitally along two planes. (B) Slice B is subparallel to the upward growth axis, and the annual growth bands are not visible. (C) Slice C, cut parallel to the upward growth axis, reveals annual growth bands, including two anomalously high-density bands coincident with the 1998 and 2001 high-temperature events.



## REPORTS

years (Fig. 2A). In the early 1940s, SSTs remained  $+3^{\circ}\text{C}$  above the historical mean for two successive summers (1941 and 1942). In both coral cores that span this time, average annual growth rates decreased by 44% over the corresponding period (Fig. 2A). In this case, however, the anomaly was short-lived; summer SSTs dropped below the historical average JAS SST in the following year, and coral growth rates quickly recovered. Conversely, the most recent warm SST anomaly is persistent. Since 1998, JAS SSTs at our study site have remained at  $0.9^{\circ}$  to  $2.2^{\circ}\text{C}$  above historical mean values. A 30% decline in mean linear extension [ $F_{1,27} = 32.04$ ,  $P < 0.001$ ,  $n = 6$  coral colonies] relative to pre-1997 extension rates is recorded over this time period. Using the CT scan images, we also calculated the change in average annual calcification rate—that is,  $\text{CaCO}_3$  production—by each coral associated with the drop in skeletal extension. Skeletal densities (in grams per cubic millimeter) were quantified from the CT images of each core by converting grayscale values to apparent absolute density using hydroxyapatite standards of known density [see the CT scanning methods (20)]. Average annual calcification by *D. heliopora*, defined as the product of annual linear extension and annual density (14), declined by  $0.05 \text{ g mm}^{-2} \text{ year}^{-1}$  [ $F_{1,29} = 8.04$ ,  $P = 0.008$ ] or 18% from 1998 to 2008 relative to the 1976–1997 mean.

This decline in coral growth rates is probably a consequence of the impact of thermal stress on the coral host–symbiont relationship. The NOAA degree heating weeks (DHWs, see SOM) product provides a measure of the likelihood that thermal stress will induce coral bleaching [loss of symbiotic zooxanthellae (22)]. Over a 12-week period,  $\text{DHWs} \geq 4^{\circ}\text{C weeks}$  indicate that some coral bleaching is likely, and as  $\text{DHWs}$  reach  $\geq 8^{\circ}\text{C weeks}$ , widespread and severe bleaching and some coral mortality can be expected (23). Weekly SST data are available at our study site from 1982 through 2008 [from the Integrated Global Ocean Services System (IGOSS) nmc Reyn\_SmithOlv2 data set (24)], allowing us to calculate the DHW index for this time period (Fig. 3). A significant increase in the duration as well as the intensity of heat stress over the past decade corresponds directly with the decline in skeletal growth and calcification measured in our coral cores (Fig. 3). Thus, although the coral colonies sampled for this study exhibited no obvious signs of thermal stress, such as bleaching or disease, the skeletal growth histories provide evidence for prolonged thermal stress that has inhibited the recovery of *D. heliopora* skeletal growth since 1998. Indeed, rates of skeletal growth and calcium carbonate production are lower now than they have been since at least 1940.

The aragonite saturation state values [ $\Omega_{\text{arag}}$ ] of seawater at the coral sampling sites are relatively high in both summer (4.08) and winter (3.94) (SOM). Calculations using the few available historical data suggest that  $\Omega_{\text{arag}}$  values in the

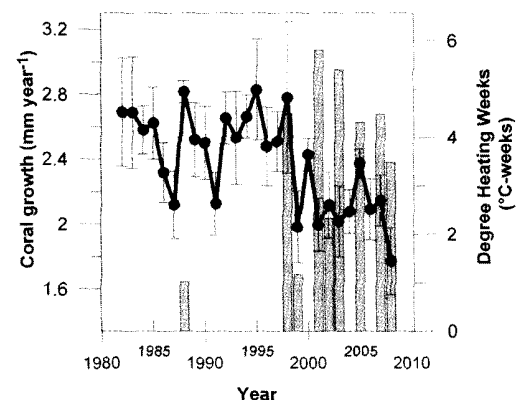
Red Sea have risen over the past 30 years; apparently, the effect of rising SST [which tends to increase  $\Omega_{\text{arag}}$ ] has more than offset the effect of rising atmospheric  $\text{CO}_2$  [which tends to lower  $\Omega_{\text{arag}}$ ]. We therefore think it is unlikely that ocean acidification has caused or contributed to the observed drop in Red Sea *D. heliopora* calcification over the past decade. Instead, the timing and intensity of the decline in skeletal growth are most consistent with the impact of thermal stress on physiological processes involved in calcification.

The skeletal growth response to historical SST variability shows that these corals can recover from major warming anomalies if the episodes are short-lived. What, then, is the likelihood that summer temperatures in the Red Sea will return to pre-1998 values fostering coral recovery? Using the output from a suite of 17 global, fully coupled climate model simulations from the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR4), we examined projections of future trends in summer

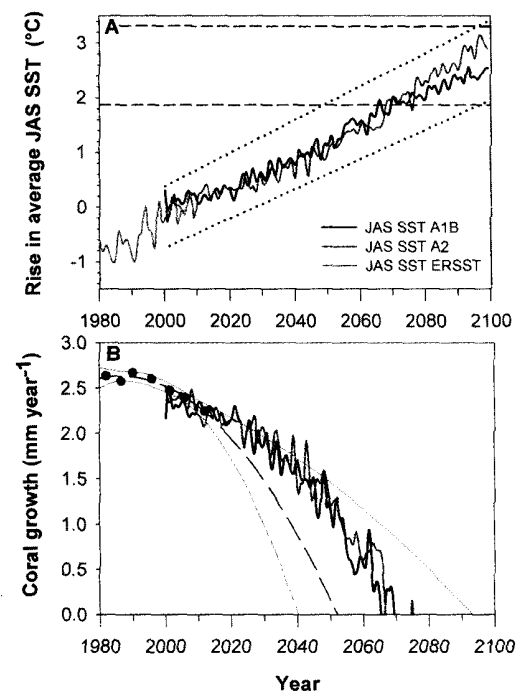
SSTs in the Saudi Red Sea ( $20^{\circ}$  to  $24^{\circ}\text{N}$ ) under the IPCC AR4 A1B and A2  $\text{CO}_2$  emissions scenarios. The multimodel mean results (Fig. 4) indicate that summer SSTs in the central Red Sea will continue to rise as atmospheric  $\text{CO}_2$  concentration rises through the 21st century, reaching a high of  $2.5^{\circ}$  to  $3^{\circ}\text{C}$  relative to the 2000–2008 mean by 2099. Extrapolating our empirically derived coral growth–SST relationship, we expect that *D. heliopora* will cease calcifying altogether by 2070, when summer SSTs will exceed current summer values by  $1.85^{\circ}\text{C}$  (Fig. 4B). This is probably a conservative estimate, given that the corals studied were not visibly bleached at the time of sampling. As temperatures continue to rise, events that cause significant loss of zooxanthellae and depletion of energetic reserves will become more frequent, and coral mortality from the effects of bleaching may occur long before calcification rates approach zero.

Recent work suggests that photoprotective mechanisms of both the coral host and symbionts (25), as well as shuffling of the dominant

**Fig. 3.** Impact of accumulated thermal stress on coral growth. Annual growth rates of *D. heliopora* (red circles, mean  $\pm 1$  SE) versus the annual DHWs product (blue bars) for this site. In general, moderate coral bleaching is expected above 4 DHWs and severe bleaching and mortality above 8 DHWs. The corals in this study were not visibly bleached at the time of sampling. However, their skeletal growth record reveals the significant impact of chronic thermal stress over the past decade.



**Fig. 4.** Predicted rise in summertime SST in the central Red Sea: 1980–2100. (A) JAS SST trajectory ( $0^{\circ}\text{C}$  is the average 2000–2008 JAS SST) averaged over 17 IPCC AR4 climate models for two midrange emissions scenarios (A1B and A2,  $\pm 1$  SE, dotted black lines). Dashed red lines depict the SST threshold for zero coral growth for *D. heliopora* [ $1.85^{\circ}\text{C}$  above average 2000–2008 JAS SST, upper 95% confidence limit], using the SST–coral growth relationship derived in Fig. 2C. (B) Statistical inverse model to predict future coral growth rates based on the current rate of SST rise (1980–2008, black dashed line) and the projected coral growth rates based on IPCC model A1B and A2 SSTs (2000–2100). Gray lines are the 95% confidence interval surrounding the inverse model coral growth projection. Red circles indicate coral growth (in millimeters per year).



symbiont assemblage to more thermally tolerant zooxanthellae genotypes (26–28), could increase the tolerance of reef-building corals to future ocean warming. However, existing data suggest that symbiont shuffling to thermally tolerant genotypes would increase thermal tolerance by 1° to 1.5°C, which is insufficient to cope with the magnitude of SST change predicted for the Red Sea and much of the tropical oceans over this century (29). Indeed, our data do not suggest that *D. heliopora* has acquired enhanced resistance, despite a decade of exposure to persistent thermal stress. Continued efforts to quantify the thermal tolerances of other coral species and important reef calcifiers will improve our predictions of how climate change will affect coral reefs of the central Red Sea. However, the data in hand suggest that without immediate, aggressive global intervention to reduce carbon emissions below IPCC A1B and A2 scenarios, the pressures of predicted annual heat stress will most certainly result in further deterioration of coral health in the central Red Sea over this century.

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#### Supporting Online Material

[www.sciencemag.org/cgi/content/full/329/5989/322/DC1](http://www.sciencemag.org/cgi/content/full/329/5989/322/DC1)

Materials and Methods

SOM Text

Fig. S1

References

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