Coral reef bleaching and global climate change: Can corals survive the next century?

Michael P. Lesser*

Department of Zoology and Center for Marine Biology, University of New Hampshire, Durham, NH 03824

oral reef ecosystems are threatened on a worldwide basis, with overfishing, diseases, eutrophication, hurricanes, overpopulation, and global climate change all contributing to recent declines in reef-forming corals or phase shifts in community structure on time scales not observed previously (1-3). These changes are in contrast to recent periods of long-term stability in coral reef communities over geological time scales of thousands of years (4, 5). A recent meta-analysis of coral cover throughout the Caribbean has shown an 80% decline that has been both long term (e.g., decadal) in duration and region-wide (6). For the last two decades, coral reef biologists have attributed much of the increase in coral mortality to coral bleaching subsequent to elevated seawater temperatures occurring on both regional and global spatial scales (7). Coral bleaching, a stress response of reef-forming corals, results in the loss of their symbiotic algal partner that supplies a large percentage of the nutritional requirements of the coral host and causes the corals to appear white (ref. 7 and Fig. 1). Since 1979, there have been dozens of reports of coral bleaching associated with elevated sea surface temperatures (SSTs), whereas from 1876 to 1979, only three events were recorded (8). The recently released Fourth Assessment Report from the Intergovernmental Panel on Climate Change (IPCC; www.ipcc.ch) states with 90% certainty that most of the observed warming of the planet over the last half-century has been caused by human activities from the accumulation of greenhouse gases. On the heels of the IPCC report, in this issue of PNAS, Donner et al. (9) provide a quantitative assessment of the contribution of humaninduced climate change for the most devastating coral-bleaching event on record, the Caribbean-wide coral bleaching in 2005.

Donner *et al.* (9) use the extensive SST database of the Advanced Very-High-Resolution Radiometer Pathfinder satellite processed by the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch program (http://coralreefwatch.noaa.gov). The analysis of the SST data is presented in the form of degree heating weeks

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Fig. 1. Underwater photograph of coral reef taken on October 5, 2005 at Savana Island off of St. Thomas, U.S. Virgin Islands. Bleached coral is a large colony of *Montastraea faveolata*, one of the major framework species in the Caribbean. Photograph courtesy of Tyler B. Smith.

(DHWs) that are equivalent to a week of SSTs higher than the local maximum in monthly climatology. When integrated over a 12-week period, values of \geq 4.0°C-weeks indicate that coral bleaching may occur, whereas values of \geq 8.0°C-weeks indicate that severe bleaching and mortality are likely (Fig. 2). Donner et al. use this data set to develop a degree heating month (DHM), equivalent to 1 month of SSTs higher than the maximum monthly climatology, to be more compatible with the output of their global climate model (10). The simulations were conducted by using a relatively new family of climate models created by the NOAA Geophysical Fluid Dynamics Laboratory (www.gfdl. noaa.gov). In a series of simulations, Donner et al. use the output of these coupled atmosphere-ocean general circulation models to investigate the influence of anthropogenic forcing on the increase of SSTs in the Caribbean that led to the 2005 bleaching event. In addition, those investigators simulate the trajectory of changes in Caribbean SSTs to assess the probability of events similar to 2005 occurring in the future and whether thermal acclimatization or adaptation by corals (10), specifically their algal symbionts (11, 12), can prevent bleaching events.

Climate Change and the 2005 Caribbean Bleaching Event

The principal region of the study includes the eastern Caribbean where the maximum amount of thermal stress was observed (Fig. 2) and coral bleaching occurred. When Donner et al. (9) conducted multiple simulations of SSTs from the years 1870-2100, they found that simulations with and without anthropogenic forcing were consistent with the Hadley Centre (U.K. Met. Office) globally complete sea-ice and sea-surface temperature data set (HadISST) (1870-2005) of observed and reconstructed SST data (13) until the 1950s, when the two model simulations diverged significantly. The forcing model then becomes more consistent with the HadISST that shows SST observations increasing after the 1970s. The changes in SST observed in these simulations are far in excess of those observed in preindustrial "control" simulations of no forcing used to quantify the inherent variability of climate in the models, and there was no statistically significant difference between the unforced simulations and the observed variability in natural climate. Together, any inherent climate variability in the model simulations has been accounted for, and the anthropogenically forced warming signal, measured as SST or DHM, is distinguishable from that inherent variability.

These data show that there is no historical record of similar changes in SST associated with the 2005 warming of the Caribbean and the subsequent spatial scale of coral bleaching (10). The maximum DHM for the study region is 3.12°C-months in 2005. DHMs of $\geq 2.0^{\circ}$ Cmonths are equivalent in strength to a DHW of $\geq 4.0^{\circ}$ C-weeks, and 94% of the study region had DHMs of 3.12°Cmonths, which are the highest observed in the 136-year data set. Events similar to those observed in 2005 are highly unlikely to have occurred without anthropogenic forcing, but the analyses also suggest that the 2005 event is a 50- to 500-year event with anthropogenic forcing and that reasonable changes in the inherent variability associated with lowfrequency events or interannual climate variability can change the timeframe of the occurrence of another 2005 event to 10-70 years. Donner et al. (9) also con-

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^{*}E-mail: mpl@unh.edu.

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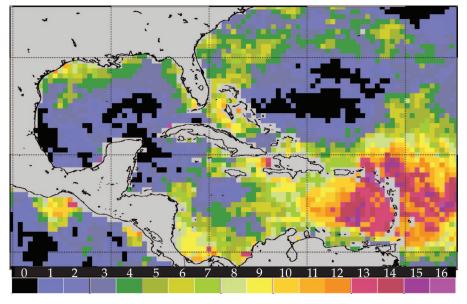


Fig. 2. NOAA Coral Reef Watch DHWs for 12 weeks before October 28, 2005 in the Caribbean Basin with the highest thermal stress ever recorded. DHW values >4 indicate that coral bleaching is expected, whereas DHW values >8 indicate that mass bleaching and mortality are expected.

ducted simulations under two different scenarios: a "business as usual" increase in atmospheric carbon dioxide and a stabilization of carbon dioxide at 550 ppm by 2100. Interestingly, both scenarios produce similar estimates of projected thermal stress on corals and will exceed the DHM values associated with the 2005 event on an annual basis by 2100. The business-as-usual scenario could result in biannual bleaching events in as little as 20–30 years.

Donner *et al.* (9) then interject another factor into their assessments: the potential for the algal symbionts of corals to acclimatize or adapt by increasing their thermal tolerance by $1.0-1.5^{\circ}$ C. If an increase of 1.0° C in thermal tolerance is acquired, the occurrence of DHMs >2.0°C-months every 5 years could be delayed until the 2040s or 2050s, and an increase in thermal tolerance of 1.5° C would further delay DHMs of >2.0°C-months every 5 years

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until the 2050s or 2060s. The ability of the algal symbionts to acclimatize or adapt to increasing SSTs and the timeframe of those processes is still being vigorously debated (10, 11). Recent studies have shown that corals can acquire a genetically diverse assemblage of symbionts (14) and "reshuffle" the genetic make-up of that assemblage in response to thermal stress (15). Although these "new" symbionts can impart increased survivability to corals, they also reduce the productivity of corals, and not all corals may be able to "shuffle" their symbionts (15). There is also evidence of long-term stability in the genetic composition of symbiotic algae in corals with little change, or reversion back to, the corals' original algal genotypes after thermal stress (16, 17).

Other factors that could affect these predictions include considerations of both the visible and UV portions of the solar spectrum that can be a significant

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synergistic factor with thermal stress and can affect the onset and magnitude of bleaching (11). Combined models of solar radiation and cloud cover, with climate change as described here, could further refine predictions of coral bleaching as thermal stress increases. Another factor that may affect the predictions of Donner et al. (9) is the response of the host to thermal stress (18) and specifically the ability of corals to respond to bleaching by increasing their capability to feed on plankton, which not all species may be able to do (19). We also do not know the effect of global climate change on the abundance of those marine organisms on which corals feed. Lastly, there is increasing concern about the secondary effects of increasing atmospheric carbon dioxide on the acid/base equilibrium of the oceans and the shift to lower pH that reduces the saturation states of carbonate minerals needed for calcifying organisms, such as corals.

Conclusions

The findings of Donner et al. (9) contribute significantly to our understanding of anthropogenic forcing of global climate change. In particular, the analyses presented use the latest data sets and models to evaluate anthropogenic forcing of climate change. Second, the quantitative analyses account for the inherent variability of global climate, distinguish the natural and anthropogenic effects on global climate, and statistically evaluate when that occurred. Lastly, the simulations take into account some of the known biology of the target organisms, reef-forming corals. Although the global climate-change models and the input data both have improved significantly, there is still much to learn about the stress response of corals and the inherent variability in those responses so we can make better predictions about the future effects of global climate change on coral reefs.

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