CORAL REEFS

Local conditions magnify coral loss after marine heatwaves

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Climate change threatens coral reefs by causing heat stress events that lead to widespread coral bleaching and mortality. Given the global nature of these mass coral mortality events, recent studies argue that mitigating climate change is the only path to conserve coral reefs. Using a global analysis of 223 sites, we show that local stressors act synergistically with climate change to kill corals. Local factors such as high abundance of macroalgae or urchins magnified coral loss in the year after bleaching. Notably, the combined effects of increasing heat stress and macroalgae intensified coral loss. Our results offer an optimistic premise that effective local management, alongside global efforts to mitigate climate change, can help coral reefs survive the Anthropocene.

Climate change is increasing the intensity and frequency of disturbances such as droughts and heatwaves (*1*), which are occurring along a backdrop of local stressors. From forests to coral reefs, these climate-driven disturbances often result in mass mortalities of foundation species (*2*). Alongside these global stressors, local stressors can also have persistent negative effects on ecosystems and can further exacerbate the mortality caused by climate-driven disturbances. For example, outbreaks of insect pests in forests can compound drought-related mortality in trees (*3*), and overfishing of predators in salt marshes can lead to population explosions of herbivorous snails, resulting in runaway consumption of marsh plants during heatwaves (*4*). The interaction between these global and local stressors suggests that effective management of local factors could lead to less-consequential impacts to ecosystems from climate-driven disturbances.

Coral reefs are sentinel ecosystems that are sensitive to both global and local disturbances (*5*, *6*). Climate change is causing marine heatwaves—periods of anomalously high seawater temperature—that induce corals to bleach. Coral bleaching is a result of the breakdown of the mutualism between corals and their endosymbiotic algae of the family Symbiodiniaceae (*7*). Extreme heatwaves cause extensive coral bleaching, resulting in widespread coral mortality and changes in reef communities (*8*). These mass coral mortality events have damaged reefs globally, and many studies have concluded that reducing global carbon emissions is the only route to conserving coral reefs (*5*, *9*, *10*). Yet local factors such as nutrient pollution (*11*) can exacerbate coral mortality associated with marine heatwaves. Identifying the local stressors that magnify coral mortality after marine heatwaves may help facilitate management strategies that boost the resistance and resilience of coral reefs to climate change (*6*, *12*).

We used a Bayesian hierarchical model to analyze the trajectories of coral cover in the year after heatwaves at 223 sites worldwide (Fig. 1). Using a suite of data on abiotic (e.g., depth, wave exposure) and biotic factors (e.g., macroalgal cover, sea urchin abundance), we investigated the effect of each factor, and its interaction with heat stress, on change in absolute coral cover. We show that, along with heat stress, key abiotic factors such as wave exposure and turbidity influenced coral mortality. We also show that increasing abundance of either sea urchins or macroalgae increased coral mortality after coral bleaching.

Not surprisingly, our results show that higher heat stress increased coral loss in the year after bleaching events (Fig. 2), consistent with other studies showing that greater heat stress results in extensive coral mortality (*5*, *13*). Our analyses show that this pattern of increasing coral mortality with increasing heat stress [ranging from 0 to 18.7 degree heating weeks (DHW), a key metric of heat stress that is known to predict coral bleaching] was robust across 26 geographic regions spanning the globe. This relationship has previously been shown at regional scales, such as within the Great Barrier Reef or Caribbean Sea (*5*, *13*), and in association with El Niño events (*14*). However, we also found interactions between heat stress and local conditions, such as macroalgae (Fig. 2), highlighting the context dependency of increasing heat stress on coral mortality.

We found that reefs with higher initial macroalgal cover experienced greater coral mortality after coral bleaching (Fig. 2). The relationship between macroalgal cover and coral loss was more negative at higher heat stress (Fig. 3A). Even at similar levels of heat stress (e.g., 4 DHW), reefs with more macroalgae experienced 10 times higher coral mortality (fig. S1). For reefs with low levels of macroalgae (<5%), there was minimal mortality even after relatively extreme heat stress (>12 DHW). There are several nonexclusive mechanisms whereby abundant macroalgae could directly lead to increased coral loss when combined with heat stress. First, macroalgae can exude dissolved organic carbon (DOC) into their environment, and exposure to excess DOC can induce coral bleaching (*15*). Algal DOC also causes areas of hypoxia on corals during coral-algal competition, often causing mortality of coral tissue (*16*). Furthermore, the microbiomes of corals exposed to macroalgae have fewer beneficial bacteria and more virulent pathogenic bacteria (*17*). These effects on the coral microbiome may contribute to a rise in coral diseases after heatwaves, leading to further coral mortality (*17*, *18*). Additionally, direct contact with macroalgae can cause coral mortality via mechanisms such as allelopathy, in the form of chemically mediated bleaching of coral tissue (*19*). Macroalgae can hinder coral recovery by limiting reproductive output (*20*), reducing coral recruitment (*21*), and increasing post-settlement mortality (*22*), thereby intensifying initial declines in coral. Higher ocean temperatures likely exacerbate many of these mechanisms, which may have contributed to the stronger relationship between

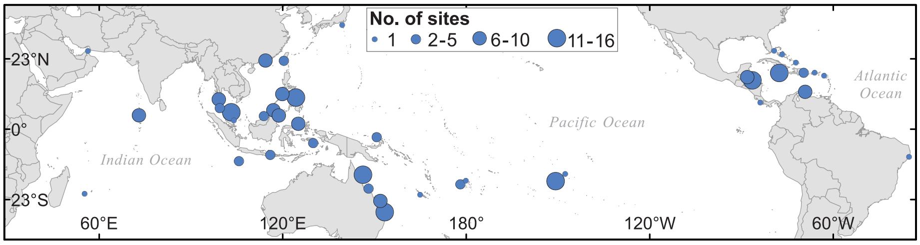

Fig. 1. Location of 223 study sites. Observations included sites from the global Reef Check dataset with coral cover both during a coral bleaching event and in the year after the bleaching event. Sites within 100 km of each other are plotted as one point, with the size of the point correlated to the number of sites.

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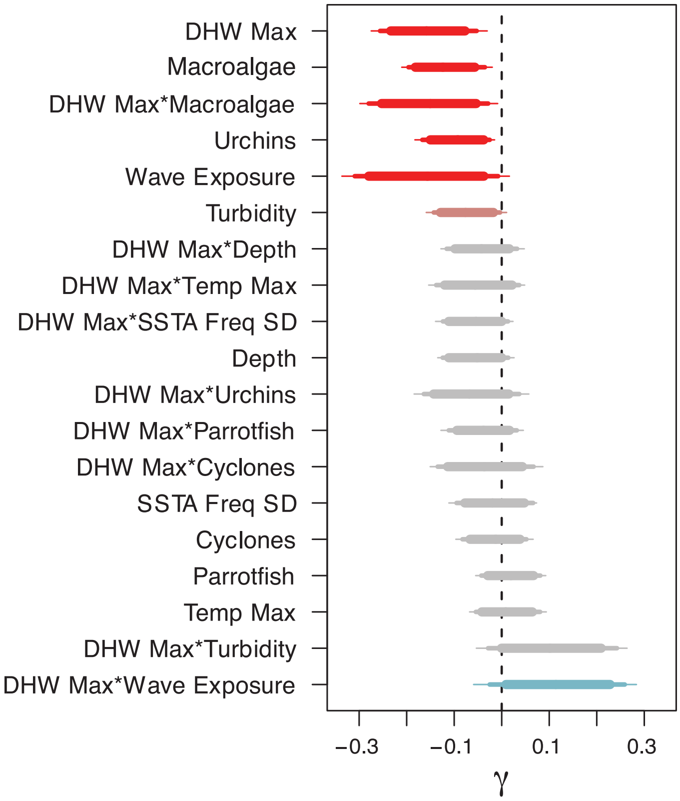

Fig. 2. Coefficients (γ) from a Bayesian hierarchical model estimating predictors of change in coral cover in the year after bleaching. Thin, medium, and thick lines represent 95, 90, and 80% credible intervals, respectively. Coefficients with negative effects are colored dark red when 90% intervals do not overlap zero, or light red when 80% intervals do not overlap zero. Coefficients with positive effects are colored light blue when 80% intervals do not overlap zero. All other effects are colored gray. Posterior distributions are plotted in fig. S2. DHW Max is the maximum degree heating weeks (a key metric of heat stress that is known to predict coral bleaching) in the 365 days preceding bleaching. Temp Max is the maximum temperature over the climatology from 1982 to 2017. SSTA Freq SD is the standard deviation of the frequency of temperature anomalies over the same climatology.

the abundance of macroalgae and coral loss at higher levels of heat stress (Fig. 3A).

Macroalgae can become abundant on coral reefs for many reasons, among which abundant nutrients and reduced herbivory are important drivers (*23*, *24*). Thus, some of the signal we show relating increased macroalgal abundance with increased coral mortality in the wake of heat stress may come as a consequence of other stressors associated with increased macroalgae. For example, increased nitrogen availability can impair the physiological relationship between corals and their symbiotic dinoflagellates (*25*), increase the severity of coral bleaching (*26*), and increase coral mortality after heatwaves (*11*). Abundant macroalgae may also be a signal of reduced herbivory from exploitation of herbivorous fishes (*6*). Not only do herbivorous fishes directly reduce the cover of algae, but they also play a role in facilitating coral recruitment (*21*) and thereby contribute to recovery after coral mortality. We did not find a direct relationship between change in coral cover and herbivorous parrotfish abundance (Fig. 2), which could be due to the indirect nature of the relationship between fishes and corals. Ultimately, there are multiple candidate drivers of macroalgal abundance that cannot be differentiated in our analyses that may have direct or indirect effects on the mortality and recovery of corals after heat stress events.

A higher density of urchins was also associated with increased coral mortality after bleaching (Figs. 2 and 3B). This result may seem surprising given that on many reefs an increasing abundance of urchins, which are important herbivores and bioeroders, is associated with a decrease in macroalgae and an increase in corals (*27*). However, urchins can become so abundant on some reefs, especially those that are heavily fished (*28*), that they suppress corals via direct predation and bioerosion of the reef matrix (*29*). In our dataset, urchin abundance varied by nearly four orders of magnitude. Reefs having higher densities of urchins, up to 1000 urchins per 100 m^2, often had negative coral trajectories in the year after coral bleaching (Fig. 3B). However, reefs with more-modest urchin densities (<18 per 100 m^2) often had positive trajectories in the year after bleaching events. Notably, although urchins often determine macroalgal cover (which also affects coral mortality after bleaching) at the local scale, they were not correlated at the global scale of our analyses (fig. S3). Thus, the context-dependent role of urchins on coral mortality after bleaching suggests that local intervention to prevent extreme urchin densities, such as reducing fishing on their predators, may help mitigate coral mortality associated with heat stress.

In addition to heat stress, we found modest evidence that several other abiotic factors were related to change in coral cover (Fig. 2), including wave exposure and turbidity. Reefs more exposed to waves lost more coral after bleaching events than more-sheltered reefs, except during the highest levels of heat stress (Fig. 3C). Bleaching and mortality may be lower on sheltered reefs owing to lower physical disturbance, the abundance of more-resistant species (*30*), or acclimation to higher temperatures (*31*). Sheltered reefs may also experience more-variable temperatures than exposed reefs, leading to higher thermal tolerance (*32*). We also found modest evidence for a negative effect of turbidity on coral mortality after bleaching (Fig. 2) and a tendency toward a positive effect of heat stress and turbidity together, which agrees with results from a recent study showing that corals may bleach less overall on turbid reefs during heat stress (*33*).

Understanding the factors that shape coral mortality in response to heatwaves will help inform management strategies that may improve the future trajectories of coral reefs. Our results suggest that abundant macroalgae are a strong predictor of whether corals survive bleaching events and that this effect is even stronger when heat stress is moderate to high. Therefore, given that local stressors such as nutrient pollution and overfishing of herbivorous fishes can lead to increases in macroalgae on reefs (*23*, *24*), reducing these stressors may provide an opportunity to reduce coral morality, especially during moderate levels of heat stress. For example, reductions in fishing of herbivorous fishes or in nutrient pollution can lead to declines in macroalgal abundance of 10 to 40% (*34*, *35*). Our analyses suggest that such reductions in macroalgal abundance could result in substantial mitigation of coral mortality under moderate heat stress (4 DHW). These types of interventions to alleviate local stressors may be key to the persistence of coral reefs given that mild-to-moderate heatwaves may occur annually in the near future (*36*). Clearly, some heatwaves will be extreme, such as what the Great Barrier Reef experienced in 2017 (*37*), overwhelming any effect of local interventions. Ultimately, combining our results with predictions of where and when both moderate and extreme heat stress events are likely to occur could prioritize decisive action at local scales (*36*, *38*).

Our results suggest that an opportunity exists to facilitate coral persistence in the face of climate-driven heatwaves by making effective local management decisions. Of course, local management is no substitute for concerted global action to limit greenhouse gas emissions and slow climate change. Yet we can take a both/and approach, strategically using local conservation actions that help ecosystems resist and recover from climate-driven

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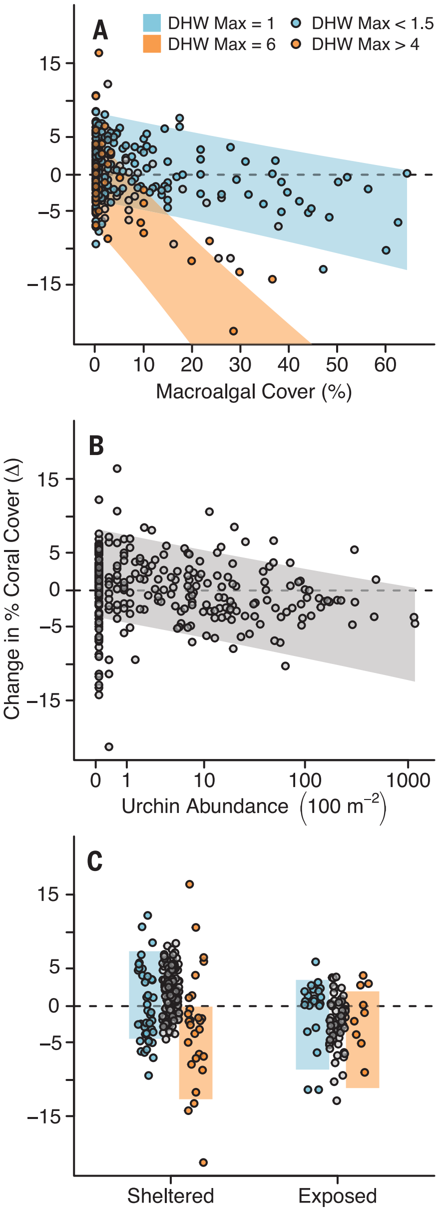

Fig. 3. Relationship between change in coral cover (Δ) over a 1-year time interval and predictors of change. (**A**) Macroalgal cover, (**B**) urchin abundance (note the log axis), and (**C**) wave exposure. Points are posterior estimates of β from equation 5 in the materials and methods (see supplementary materials). *Y* axis was back-transformed by regressing β from equation 5 against Δ in equation 4 (see supplementary materials) to reflect units of absolute change in coral cover. Shaded areas are 50% credible intervals for the predicted relationships across all regions. Given evidence for interactions with DHW Max (the 80% interval did not overlap zero), points and predicted relationships in (A) and (C) are colored. To represent mild heat stress, points are colored blue where DHW Max is <1.5, and shaded areas are blue for the relationship when DHW Max is held at 1. To represent high heat stress, points are colored orange where DHW Max is >4, and the shaded area is orange for DHW Max held at 6. All other points are colored gray.

disturbances while also working toward global reductions in carbon emissions.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S5
Tables S1 and S2
References (*40–49*)

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Think globally, act locally
Climate change–driven elevations in temperature over the past few decades have caused repeated coral bleaching and subsequent death. The impact is so widespread that it has been suggested that only climate change reversal can save coral reefs globally. Donovan *et al.* looked at the interaction between local conditions and coral reef health and found that poor conditions magnify climate impacts (see the Perspective by Knowlton). Furthermore, reefs where human stressors such as overfishing or pollution were minimized fared better. Such results suggest that caring for reefs locally may help them to persist in our warming world.
Science, abd9464, this issue p. 977; see also abi7286, p. 908

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