PNAS COMMENTARY

Some coral reef communities may degrade and change but persist

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Coral reefs have waxed and waned through geological history (1), with the Anthropocene bringing far more of the latter than the former. Over the past several decades, scientists have detailed the widespread loss of live coral (50% globally by some estimates) and the resulting reduced capacity of reefs to shelter their renowned biodiversity and provide ecosystem services (2). While initially these declines were mostly the consequence of pollution and overfishing (3), local stressors have now been joined by the twin impacts of anthropogenic greenhouse gas emissions: warming (which destabilizes the essential nutritional partnership between corals and their symbiotic algae, resulting in coral bleaching) and acidification (which interferes with the ability of corals to lay down their skeletons) (4). Warming-induced bleaching is now increasingly widespread, frequent, and severe, causing coral mortality in many locations (5, 6). Moreover, results from laboratory experiments and field observations coupled with predictions for future emissions have forecast an ever-grimmer future for reefs as sea temperatures continue to rise and pH falls (7, 8). However, some recent work has sought to test whether the most alarming predictions may have underestimated the potential for reefs to survive in some form (9). In this vein, the paper by Jury et al. (10) concludes that reefs may be able to persist in the face of near-term warming and acidification, albeit with substantial declines and changes and provided the Paris Agreement targets are met.

Their approach was to assemble small reefs in enclosures on land (mesocosms of 70 or 180 L) and compare the performance of reefs growing in today's temperature and pH conditions with those grown in likely future conditions of higher temperature and lower pH (+ 2 °C, −0.2 pH units compared to ambient), as well as higher temperature and lower pH conditions separately. Importantly, these future conditions represent states likely to be achieved in the near-term (around 2075) assuming a high emissions scenario. These values only slightly exceed the Paris Agreement targets for warming and linked acidification and are thus highly policy-relevant.

The experimental reefs (ten for each of the four treatments) were designed to resemble the local Hawai'ian reefs at 2 m depth in their composition and light levels. Each had a layer of reef sand and gravel, plus dead coral rubble, that seeded the mesocosm with local epifauna and infauna. Unfiltered flow-through seawater from the local reef replaced the mesocosms' water every hour, providing food and recruits. To these were added eight of the locally most common corals species (3 to 4 pieces per species per mesocosm, initially totaling 3% live coral cover). In addition, two small fish (one herbivore and one predator), and five herbivorous snails were added to provide realistic consumer pressure. Finally, stacked settlement plates [modified Autonomous Reef Monitoring Systems, or ARMS (11)] were added to facilitate censusing of noncoral organisms. The result was a community simpler than a natural reef but far more complex than a typical laboratory experiment. Moreover, the experiment was maintained for 2 y, again longer than a typical laboratory experiment and thereby allowing gradual adaptation to occur. The results for multiple measures taken over the course of the experiment are summarized in Table 1.

The first observation of note is that coral cover increased in all four treatments during the course of the study, and neither survivorship nor growth was affected by low pH conditions, a more positive outcome than might have been expected given previous assessments (12). Of course, not surprisingly, the high heat treatments (alone and with acidification) did take a serious toll. Some coral species suffered substantial bleaching and death (97 to 100% mortality for *Pocillopora meandrina* in heated treatments), thereby reducing coral diversity, whereas others came through the treatments largely unscathed (92 to 95% survivorship for *Porites evermanni* across all treatments). Overall, survivorship was reduced by 35% at high temperatures, and coral coverage (a function of growth, partial mortality, and colony death) increased from 3% to only 21% at high temperatures as compared to 40% at ambient temperatures. Examination of a subset of the coral species revealed considerable variation in physiological responses to the different treatments, with a suggestion that in some cases, this may be due to the corals' distinct microbiomes. Notably, two coral species reproduced during the course of the experiment with no obvious effects from the treatments.

The responses of other reef species revealed additional variability rather than uniform decline. Notably, many groups (e.g., anemones, bivalves, macroalgae, serpulid worms, sponges, and tunicates) showed no response in abundance to either high temperature or low pH alone or in combination. Others (e.g., motile invertebrates and some algae) responded in varying ways to either warming or acidification but not both [although biomass assays using a metabarcoding approach reported in a previous paper (13) revealed some responses not detected in this study; see notes to Table 1]. Vermetid snails responded positively to warmth but

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Table 1. Summary of effects of high temperature and low pH on reef communities relative to the present

Measure	Only high temperature	Only low pH	Present vs. Future
% Cover/Abundance*			
Coral	Negative	None	Present > Future
Vermetid snails	Positive	Negative	Present = Future
Motile invertebrates†	Positive	None‡	Present < Future
Algae (crustose coralline)	Positive	None§	Present < Future
Algae (encrusting green)	None	None	Present < Future
Algae (turf)	Negative	None	Present = Future
Other groups¶	None	None	Present = Future
Diversity#			
Corals	Negative	None	Present > Future
Sponges	None	Negative	Not reported separately
Motile invertebrates‖	Positive	Negative	Not reported separately
Algae**	None	None	Not reported separately
Microbes (coral)	Positive	None	Not reported separately
Microbes (water)	None	None	Not reported separately
Total	None	None	Present = Future
Calcification			
Coral	Negative	None	Present > Future
Rubble	None	Negative	Present > Future
Total mesocosm	Negative	Negative	Present > Future

*3-D cover for corals, analyses of stacked settling plates for other groups (2-D cover for sessile organisms, counts of individuals for motile invertebrates).
†Primarily amphipods and brittlestars.
‡Metabarcoding results reported previously (13) indicate a positive biomass response.
§Metabarcoding results reported previously (13) indicate a negative biomass response, supported by observation that the crusts were thinner.
¶Anemones, bivalves, macroalgae, serpulid worms, sponges, tunicates, sediment, and bare space.
#Species counts for corals, DNA sequences for other groups; diversity data were not presented separately for noncoral groups.
‖Cryptic species from settling plates, e.g., crustaceans, echinoderms, snails, annelids.
**Symbiodiniaceae from corals, crustose coralline algae, and macroalgae from stacked settling plates (data analyzed separately).
The four treatments were ambient conditions (present), elevated temperature (+2 °C), lower pH (−0.2 units), and combined elevated temperature and lower pH (future).

negatively to acidification, resulting in no change in the future ocean treatment (high temperature and low pH) as compared to ambient conditions, while encrusting green algae only responded to the combined (future ocean) treatment. These results echo conclusions of previous studies that responses to warming and acidification are complex and sometimes difficult to predict (14).

In this vein, the paper by Jury et al. (10) concludes that reefs may be able to persist in the face of near-term warming and acidification, albeit with substantial declines and changes and provided the Paris Agreement targets are met.

Diversity in noncoral organisms was similarly variable. Algae of various types (single-celled coral symbionts, crustose corallines, and macroalgae) and water column microbes showed no statistically significant response to the treatments. In contrast, the diversity of microbes associated with corals increased with high temperatures, sponge diversity decreased with low pH, and motile invertebrate diversity increased with high temperature but decreased with low pH. However, when all the diversity data were combined, the study found no significant differences in response to treatments.

Looking at community responses more generally, an analysis of community structure (combined diversity and abundance data) showed communities differing as a function of temperature but not pH [although again, more sensitive metabarcoding analyses revealed some sensitivity to acidification (13)]. Notably, there were few amplifying interactions between temperature and pH, with only encrusting green algae showing a sharp increase in abundance in future ocean conditions with no response to high temperature or low pH on their own. Calcification, important for maintaining the structural integrity of the reef, was also broadly lower, with reductions associated with high temperature in corals and low pH in other calcifying organisms, but the reefs were still net calcifying even in the combined warming and acidification treatment, albeit reduced by about 50%.

In sum, the responses of the organisms in these mesocosms did not reflect a wholesale collapse of the community, as has been predicted by other studies for similar levels of warming and acidification (12). Rather, they suggest that these Hawai'ian reefs may change and degrade but persist for the foreseeable future if the Paris Agreement targets are not greatly surpassed. There are several possible reasons for these diverging predictions. First, many previous studies of the impacts of high temperature and low pH focused on corals, particularly from the genera *Acropora* and *Pocillopora*, taxa which are known to be especially sensitive to high temperatures (4), while this study included a number of less sensitive coral species as well as a variety of noncoral taxa. A second reason for the stronger than expected performance may be that, contrary to some studies (14), there were few examples where the effects of combined warming and acidification were more severe than what would be expected based on responses to high temperature and low pH alone.

As hopeful as these results are, considerable caution is advised before assuming that reefs around the world will exhibit the same characteristics in the future as these experimental Hawai'ian reefs. First, many reefs, including the iconic Great Barrier Reef and other high diversity reefs of the Indo-west Pacific, are dominated by temperature-sensitive *Acropora* species, which were not included in this study because they are rare on the reefs of Hawai'i. Second, while the high temperatures they used represented a considerable stress, comparable overall to that experienced by reefs during the major bleaching events of 2023 (10), very extreme temperatures well above minimum bleaching thresholds, which were not tested in this study, can result in more severe bleaching and mortality (15). Finally, the experiment deliberately used fish and snails to maintain healthy levels of herbivory, and the waters bathing the experimental reefs did not have highly elevated nutrients. Because overfishing and pollution can exacerbate the effects of high temperature and limit recovery following disturbance (16–19) and local conditions remain poor on many reefs (12), these experiments provided favorable conditions for enduring warming and acidification. Indeed, on Hawai'ian reefs between 2003 and 2015, coral cover increased, as it did in the mesocosms, in areas with high herbivory and low pollution, but declined where local conditions were less favorable (18). Thus, as the authors note, while their results are more encouraging (or at least less depressing) than those of other studies, they hardly relieve us of the obligation to rapidly reduce greenhouse gas emissions and improve local conditions on reefs around the world if we want them to persist as viable and valuable ecosystems into the future.

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