events are often poorly observed, models can fail to represent them adequately, and their relationship with climate variability and change is often not well understood (*4*). Improved climate models, observational data sets, and theoretical understanding will be needed to improve the reliability of attribution findings for such events.

Recent initiatives, including the European project EUCLEIA (European Climate and Weather Events: Interpretation and Attribution) and the World Weather Attribution effort, seek to develop the science of event attribution. For such science to help societies become more resilient to climate variability and change, event attribution results need to be credible and relevant (*10*). Further improvements are needed in techniques for analyzing extreme events, tools to evaluate and communicate the robustness of event attribution results (*11*, *12*), and methodologies to link the effects of extreme events to their meteorological drivers (*13*). A model-based result by itself does not guarantee its utility (*3*). A convincing physically based storyline describing the event and its effects is also needed to support the legitimate use of such information for robust decision-making (*14*).

The increasingly routine nature of some temperature-based studies points the way toward an operational attribution capability in which trusted providers issue routine updates on recent events (*15*). The National Academies of Science recommended that such a capability be linked to the provision of probabilistic forecasts of extreme events at lead times of days to seasons or longer (*4*). Placing recent extreme events in the context of past and future climate variability and change would enhance the ability of societies to manage weather and climate-related risks. ■

REFERENCES

1. N. Bindoff *et al.*, in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, T. Stocker *et al.*, Eds. (Cambridge Univ. Press, Cambridge/New York, 2013), pp. 867–952.
2. X. Zhang *et al.*, *Geophys. Res. Lett.* **40**, 5252 (2013).
3. A. Solow, *Science* **349**, 1444 (2015).
4. *Attribution of Extreme Weather Events in the Context of Climate Change* (National Academies Press, Washington, DC, 2016).
5. T. Peterson *et al.*, *Bull. Am. Meteorol. Soc.* **93**, 1041 (2012).
6. S. Herring *et al.*, Eds., Explaining extreme events of 2014 from a Climate Perspective, *Bull. Am. Meteorol. Soc.* **96**, special supplement (2015).
7. Y. Sun *et al.*, *Nat. Clim. Change* **4**, 1082 (2014).
8. N. Schaller *et al.*, *Bull. Am. Meteorol. Soc.* **95**, S69 (2014).
9. K. E. Trenberth *et al.*, *Nat. Clim. Change* **5**, 725 (2015).
10. S. Sippel, *Weather Clim. Soc.* **7**, 224 (2015).
11. O. Bellprat, F. Doblas Reyes, *Geophys. Res. Lett.* **43**, 10.1002/2015GL067189 (2016).
12. F. Lott, P. Stott, *J. Clim.* 10.1175/JCLI-D-15-0566.1 (2016).
13. F. Otto, *Nat. Clim. Change* **6**, 342 (2016).
14. T. Shepherd, *Curr. Clim. Change. Rep.* **2**, 28 (2016).
15. P. Stott *et al.*, *WIRES Clim. Change* **7**, 23 (2016).

10.1126/science.aaf7271

OCEAN BIOLOGY

Corals' microbial sentinels

The coral microbiome will be key to future reef health

By **Tracy D. Ainsworth**[1] *and* **Ruth D. Gates**[2]

In 2005, Pandolfi *et al.* (*1*) asked whether U.S. coral reefs would in the future be overgrown and dominated by algae as a result of rapid change in the marine environment. Over a decade later, an increasing number of reefs worldwide have declined, and severe and lasting environmental changes are altering the composition of coral reefs that were once pristine and resilient. In the past 2 years, many reefs around the world have suffered from repeated bleaching (see the photo) as a result of high water temperatures caused by a strong El Niño event combined with climate change. Corals that survive the multiple impacts of climate change and local disturbance will form the basis of future reefs that will differ in fundamental ways from those considered healthy today (*2*). Changes to the coral microbiome on these reefs will play a vital part in future coral reef health (see the figure).

Microbial communities play central roles in animal health and ecosystem stability. Factors such as nutritional status, stress response, and disease are linked to shifts in the taxonomic composition of—and the interactions between—microbiomes and their hosts (*3*). There are also correlations between an organism's life span and its microbial complexity, structure, and function (*4*). Corals form integral and functionally important symbioses with prokaryotic microbes (forming a core symbiotic microbiome) (*5*). The implications of altered prokaryotic microbial partnerships for coral reefs are difficult to predict because little is known about the functional complexity of the undisturbed coral microbiome. However, knowledge from other systems suggests that altered microbiomes, representing a new stable state after disturbance, impair the host's metabolic state, disease resistance, and functional capacity (*6*).

One of the most extreme examples of the impacts of environmental stress on coral function is bleaching. Temperature stress of only 1°C above the physiological upper limit, as seen on coral reefs worldwide in the past 3 years, causes tropical reef corals to bleach. Bleaching reflects a reduced density of endosymbiotic algae (belonging to the dinoflagellate genus *Symbiodinium*) in the coral tissues. When these nutritionally beneficial endosymbionts are lost, coral health suffers and nutritional resources are depleted. These effects continue as long as adverse temperature conditions persist and can ultimately lead to the death of the coral.

In corals that bleach but survive, external conditions

Microbiome shifts

The shifting microbial complexity indicates the impact of climate change on the coral microbiome, host health, and population stability on coral reefs. The challenge to coral research is to understand the microbial contribution to alternate stable states on coral reefs.

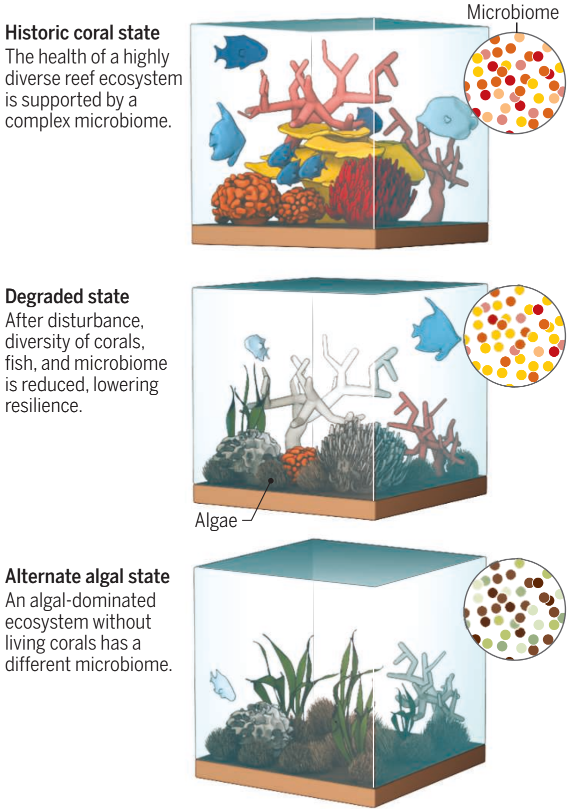

ILLUSTRATION: V. ALTOUNIAN/SCIENCE

Stress response. The past 2 years have seen widespread bleaching in coral reefs around the world, as shown here in the Maldives.

must return to normal for the repopulation of endosymbiotic algae and regeneration of the host tissue to occur. The drastic impact of bleaching on the coral animal and, ultimately, its microbiome can influence the immune system, alter the metabolic capacity, and impair the stress resistance of the surviving corals. Maintaining and/or reestablishing crucial functional contributions from the prokaryotic microbiome after events such as bleaching are key to coral survival, recovery, and prevention of disease. A microbial signature dominated by pathogens has been associated with bleaching mortality (*7, 8*), whereas in corals that survive bleaching, there is no rise in primary pathogens (*8, 9*). For example, of over 25,000 bacterial phylotypes identified on surviving Acroporid corals, only 14 bacteria of the pathogenic Vibrio genera were found; these pathogens were associated with just 2 of the 63 corals analyzed (*10*).

A shift toward a phylogenetically and functionally less diverse core symbiotic microbiome after bleaching, and in catastrophic stress survivors, would indicate the formation of a new metaorganism. As seen in other systems, new stable-state metaorganisms have altered functional capacity that can influence life history. In corals, the loss of beneficial bacteria has been linked to the development of lesions and tissue necrosis (*11*, *12*). Such changes to the surviving adult coral microbiome are likely to have far-reaching implications, including intergenerational impacts, as has been found in other organisms (*13*). As outlined by Pandolfi *et al.* (*1*), many factors shift the balance between survival and mortality on reefs. The influence of these environmental factors on the coral microbiome is not yet accounted for in estimates of coral response to climate change (*14*, *15*).

"The emergence of new ecosystem norms on coral reefs will be underpinned by changes to the microbiome...."

The coral microbiome is a critical element to the health of the corals that can influence the reef-wide response to growing environmental pressures. The emergence of new ecosystem norms on coral reefs will be underpinned by changes to the microbiome and the microbial contribution to organism health and stress resistance, under new environmental norms. Accounting for the influence of microbes in coral ecosystem stability will require an advance in our fundamental understanding of the establishment, diversity, and complexity of prokaryotic symbioses. Differentiating the elements of the microbiome that signify a loss of functional redundancy, altered stress resistance, mortal states (such as the rise of opportunistic microbes and primary pathogenesis), and disease will be crucial. ■

[1]*ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Australia, 4811.* [2]*Hawai'i Institute of Marine Biology, University of Hawai'i at Manoa, Honolulu, HI 96744, USA. Email: tracy.ainsworth@jcu.edu.au*

REFERENCES AND NOTES

1. J. M. Pandolfi *et al.*, *Science* **307**, 1725 (2005).
2. I. A. van de Leemput, T. P. Hughes, E. H. van Nes, M. Scheffer, *Coral Reefs* 10.1007/s00338-016-1439-7 (2016).
3. S. Krause *et al.*, *Front. Microbiol.* **5**, 251 (2014).
4. L. Fontana, L. Partridge, *Cell* **161**, 106 (2015).
5. T. D. Ainsworth *et al.*, *ISME J.* **9**, 2261 (2015).
6. C. Zhang *et al.*, *Nat. Commun.* **4**, (2013).
7. R. Vega Thurber *et al.*, *Environ. Microbiol.* **11**, 2148 (2009).
8. J. R. Zaneveld *et al.*, *Nat. Comm.* **7**, 11833 (2016).
9. R. Littman, B. L. Willis, D. G. Bourne, *Environ. Microbiol.* **3**, 651 (2011).
10. D. Ogawa, thesis, James Cook University, Townsville, Australia (2014).
11. J. L. Meyer, V. J. Paul, M. Teplitski, *PLOS ONE* **9**, e100316 (2014).
12. B. Glas, G. J. Herndl, P. R. Frade, *ISME J.* 10.1038/ismej.2016.9 (2016).
13. J. K. Goodrich, E. R. Davenport, J. L. Waters, A. G. Clark, R. E. Ley, *Science* **352**, 532 (2016).
14. N. Knowlton, M. Leray, in *Coral Reefs in the Anthropocene*, C. Birkeland, Ed. (Springer, Dordrecht, Netherlands, 2015), pp. 117–132.
15. T. D. Ainsworth, R. V. Thurber, R. D. Gates, *Trends Ecol. Evol.* **25**, 233 (2010).

ACKNOWLEDGMENTS

We acknowledge funding from the Australian Research Council (Discovery Program Grant DP130101421; Super Science Program FS110200046; and Centre of Excellence for Coral Reef Studies CE0561435) and the University of Hawai'i. We thank B. Leggat for editorial assistance and D. Tracy for graphic design.

10.1126/science.aad9957

Science
AAAS

Corals' microbial sentinels

Tracy D. Ainsworth and Ruth D. Gates (June 23, 2016)
Science **352** (6293), 1518-1519. [doi: 10.1126/science.aad9957]

Editor's Summary