How do coral reefs recover?
John F. Bruno
Science **345**, 879 (2014);
DOI: 10.1126/science.1258556

toward sugars (see the figure). Importantly, some of these residues are apparently under positive selection.

In behavioral taste testing with both captive and wild hummingbirds, Baldwin *et al.* observed a general agreement between these results and the results of in vitro receptor assays. One exception occurred for the sweet-tasting (to humans), non-nutritive sweetener, sucralose. Although sucralose was a potent agonist for the hummingbird T1R1-T1R3 receptor, hummingbirds behaviorally exhibited no avidity for it and seemed to reject sucralose-sucrose mixtures. The latter indicates that sucralose may actually have negative, perhaps bitter, taste properties. Another, alternative possibility to explain the absence of agreement between behavior and in vitro assays is that a T1R-independent mechanism such as sugar transporters and metabolic sensors located on taste receptor cells (*6*) may also contribute to the sweet taste perception of hummingbirds. The possibility of using new techniques (*7*) to genetically ablate the hummingbird T1R1-T1R3 taste receptor to test for sweet taste perception, presuming such animals are viable, would be fascinating.

Much of the recent work designed to match taste receptor function and feeding ecology has focused on sweet taste. For amino acid or umami taste, the correlations between diets and T1R1 function have received less attention. However, in giant pandas, the *T1R1* gene is mutated and nonfunctional (a "pseudogene"), and this could be related to the animal's unique monophagous herbivorous diet (*8*). For sea lions, dolphins, and whales, mammals that migrated back to the sea from land 25 to 55 million years ago, all T1Rs are no longer functional (*4*, *9*). It remains a puzzle as to what aspects of the return to sea life underlies their independent loss of sweet, amino acid, and even bitter (detected by the T2R family of receptors) taste perception. How bitter, salty, and sour taste perception relate to species variation in diet is even less well understood but is likely to also vary in interesting and illuminating ways. ■

REFERENCES

1. P. H. Barrett, P. J. Gautrey, S. Herbert, D. Kohn, S. Smith, *Charles Darwin's Notebooks, 1836–1844: Geology, Transmutation of Species, Metaphysical Enquiries* [British Museum (Natural History) and Cornell Univ. Press, London/Ithaca, NY, 1987).
2. M. W. Baldwin *et al.*, *Science* **345**, 929 (2014).
3. E. R. Liman, Y. V. Zhang, C. Montell, *Neuron* **81**, 984 (2014).
4. P. Jiang *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 4956 (2012).
5. H. Zhao *et al.*, *Mol. Biol. Evol.* **27**, 2642 (2010).
6. K. K. Yee, S. K. Sukumaran, R. Kotha, T. A. Gilbertson, R. F. Margolskee, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 5431 (2011).
7. P. D. Hsu, E. S. Lander, F. Zhang, *Cell* **157**, 1262 (2014).
8. R. Li *et al.*, *Nature* **463**, 311 (2010).
9. P. Feng, J. Zheng, S. J. Rossiter, D. Wang, H. Zhao, *Genome Biol. Evol.* **6**, 1254 (2014).

10.1126/science.1259175

ECOLOGY

How do coral reefs recover?

Experiments on juvenile coral and fish behavior may have implications for reef restoration efforts

By **John F. Bruno**

A key challenge for ecologists is to understand why ecosystems are being degraded and how to restore their natural structure and function. On page 892 of this issue, Dixson *et al.* (*1*) use an impressive series of experiments to determine whether chemical signals in seawater from corals and seaweeds affect the behavior and settlement choices of juvenile corals and fish. The results reveal the surprising ability of dispersing reef larvae to detect habitat quality under well-controlled conditions. However, differences with previous research suggest that we are a long way from understanding where this ability fits into the complex settlement process and what it means for reef restoration and recovery.

Larvae from neighboring or distant reefs can replenish populations wiped out by natural disturbances or overharvesting. Working in Fiji, Dixson *et al.* used water from healthy (coral-dominated) and degraded (seaweed-dominated) reefs to examine the potential role of chemical cues in the recovery of coral and fish populations. Their findings suggest that odors from degraded reefs are repulsive, whereas those from healthy reefs are an attractant. In one experiment, coral larvae were placed in a Y-shaped tank, from which they could swim toward waters with different odors. By a large margin, they swam toward the smells of their own kind.

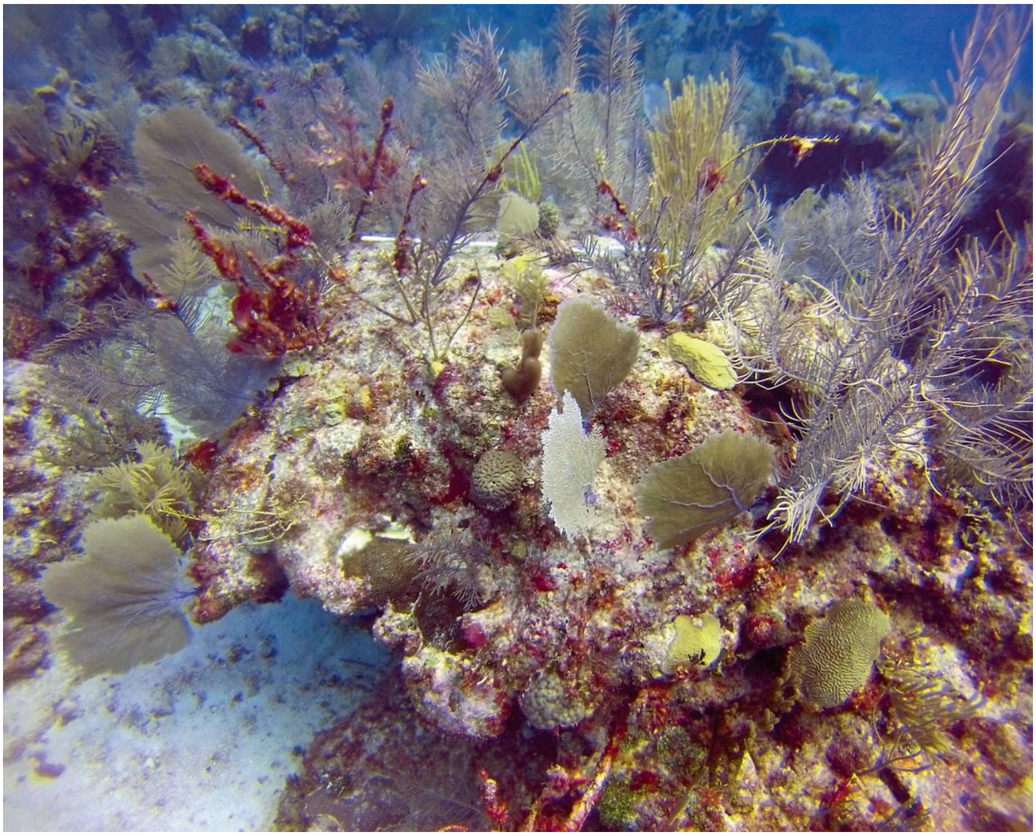
The study elaborates on a chemically based explanation for a frequently observed pattern: high concentrations of juvenile corals on seaweed-free sea floor (*2*). Other factors affecting coral larval settlement and survival include light, current velocity, predators, competition, disease, sound, and physical abrasion and shading by large, fleshy seaweeds that can kill small corals (*3*). Multifactorial experiments and field manipulations of the putative odor signals will be needed to determine the relative importance of odor relative to other mechanisms.

Dixson *et al.* also report a more surprising finding: The water source and odors can affect the choices made by juvenile fishes arriving from distant reefs. In one experiment, several reef fish species were deterred by the presence of brown seaweed often prevalent on disturbed reefs. If fish larvae behave similarly in nature, then overfished, seaweed-dominated reefs could be difficult to restore even when fishing is regulated, because fish would choose to settle in coral-dominated areas.

Dixon *et al.*'s results suggest that degraded reefs might have trouble recovering because fewer fish larvae will choose to settle there. Reconciling these findings with the broader marine ecological literature will be challenging, however. Recent evidence indicates that fisheries restrictions

Reef recovery. Most elkhorn corals (*Acropora palmata*) in the Mesoamerican Barrier Reef were killed off by disease, storms, and ocean warming. Some are now recovering, as shown by this coral colony near Akumal, Mexico.

PHOTO: JOHN BRUNO



Dead and overgrown. A dead colony of *Orbicella sp.* near Akumal, Mexico, is overgrown by invertebrates such as sponges, gorgonians, and weedy corals. The *Orbicella* colony is over 1 m tall and 2 m wide and was centuries old when it was killed by yellow band disease in the early 2000s. Note the absence of seaweed on the colony surface due to intense grazing by urchins and fish.

can restore coral reef fish (*4*, *5*), regardless of the abundance of corals and seaweed. Adam *et al.* have reported that increases in seaweed boosted parrotfish populations on the reefs of Mo'orea in French Polynesia (*6*), providing a positive feedback that could return a reef to coral dominance. Furthermore, as seawater warms due to climate change, herbivorous coral reef fishes are invading temperate ecosystems despite the absence of corals and the dominance of large algae (*7*). Many tropical fishes first recruit into mangroves, seagrass beds, and other plant-dominated habitats before migrating onto the reef as they mature (*8*); the response of juvenile fishes to seaweed or coral odors may not be relevant in those cases. Finally, Edmunds and Carpenter (*9*) found that small, algae-free surfaces are quickly colonized by juvenile corals even on reefs with few fish and large amounts of seaweed. These previous studies suggest that the dynamics controlling reef colonization are complex and not easily described by any single set of results.

In the regions studied by Dixson *et al.*, seaweed heavily dominated the degraded sites (49 to 91% coverage of the sea floor) and was essentially absent on the healthy reefs (1 to 2%). Although such conditions exist in nature, average seaweed cover on reefs is just 15 to 25% on Caribbean reefs and typically lower across much of the Indo-Pacific; in 2006, just 10% of Caribbean reefs and 1% of Indo-Pacific reefs had seaweed coverage of more than 50% (*10*). It remains to be shown whether the odor signal can also be detected under the less extreme conditions found on most reefs.

I am writing this article in Akumal, Mexico, while working on the restoration of reefs off the Yucatán Peninsula. Most massive boulder corals and branching corals of the 1000-km-long Mesoamerican Barrier Reef have been killed by disease, storms, and ocean warming since the 1980s. The reefs are degraded by any measure, yet there are signs of hope. Abundant herbivorous fishes and sea urchins consume seaweed, resulting in minimal seaweed coverage. Elkhorn coral (*Acropora palmata*, a formerly dominant species listed as threatened under the U.S. Endangered Species Act) is recovering (see the first figure), possibly enabled by the seaweed-free space.

Understanding of the dynamics of reef recovery is in a state of flux. Contrary to a common assumption, reefs in regions with high fish and coral diversity do not recover more quickly (*11*). In some locations, there appears to be a shift toward dominance by other invertebrate animals and weedy coral species rather than seaweeds (see the second figure). Coral reef scientists also once believed that reefs overgrown by seaweed would be permanently locked in to an alternative stable state, but that now appears unlikely. Once herbivores are restored, seaweed quickly disappears and coral populations usually return, although this process can take decades (*12*, *13*).

Yet, sometimes reefs fail to recover, for reasons that are often unclear. Why are the largely unprotected reefs in Mexico showing signs of recovery, whereas some in fully protected marine reserves just to the south in Belize are not? A better understanding of the factors that drive reef recovery may come from multifactor experiments, recognition of the complexity and variability of the natural world (*14*), and far more openness to unexpected discoveries, such as the possible role of odors from seaweeds in controlling reef recovery highlighted by Dixson *et al.* Results from one reef might not apply to another, and conservation strategies might be most successful if they combine global recommendations from academics with first-hand knowledge of local conditions. ■

Department of Biology, The University of North Carolina at Chapel Hill, Chapel Hill, NC 27517, USA. E-mail: jbruno@unc.edu

REFERENCES

1. D. L. Dixson, D. Abrego, M. E. Hay, *Science* **345**, 892 (2014).
2. L. J. McCook, J. Jompa, G. Diaz-Pulido, *Coral Reefs* **19**, 400 (2001).
3. G. F. River, P. J. Edmunds, *J. Exp. Mar. Biol. Ecol.* **261**, 159 (2001).
4. P. J. Mumby *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 8362 (2007).
5. K. L. Kramer, K. L. J. Heck Jr., *Mar. Ecol. Prog. Ser.* **349**, 111 (2007).
6. T. C. Adam *et al.*, *PLOS ONE* **6**, e23717 (2011).
7. A. Vergés *et al.*, *Proc. Biol. Sci.* **281**, 20140846 (2014).
8. I. Nagelkerken, C. H. Faunce, *Estuar. Coast. Shelf Sci.* **75**, 417 (2007).
9. P. J. Edmunds, R. C. Carpenter, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 5067 (2001).
10. J. F. Bruno, H. Sweatman, W. F. Precht, E. R. Selig, V. G. W. Schutte, *Ecology* **90**, 1478 (2009).
11. S. Y. Zhang *et al.*, *Peer J* **2**, e308 (2014).
12. J. A. Idjadi *et al.*, *Coral Reefs* **25**, 209 (2006).
13. G. Diaz-Pulido *et al.*, *PLOS ONE* **4**, e5239 (2009).
14. J. F. Bruno, W. F. Precht, P. S. Vroom, R. B. Aronson, *Mar. Pollut. Bull.* **80**, 24 (2014).

10.1126/science.1258556

PHOTO: JOHN BRUNO