Coral Reef Resilience in Hot Water

LESLEY EVANS OGDEN

Researchers investigate resistance and recovery.

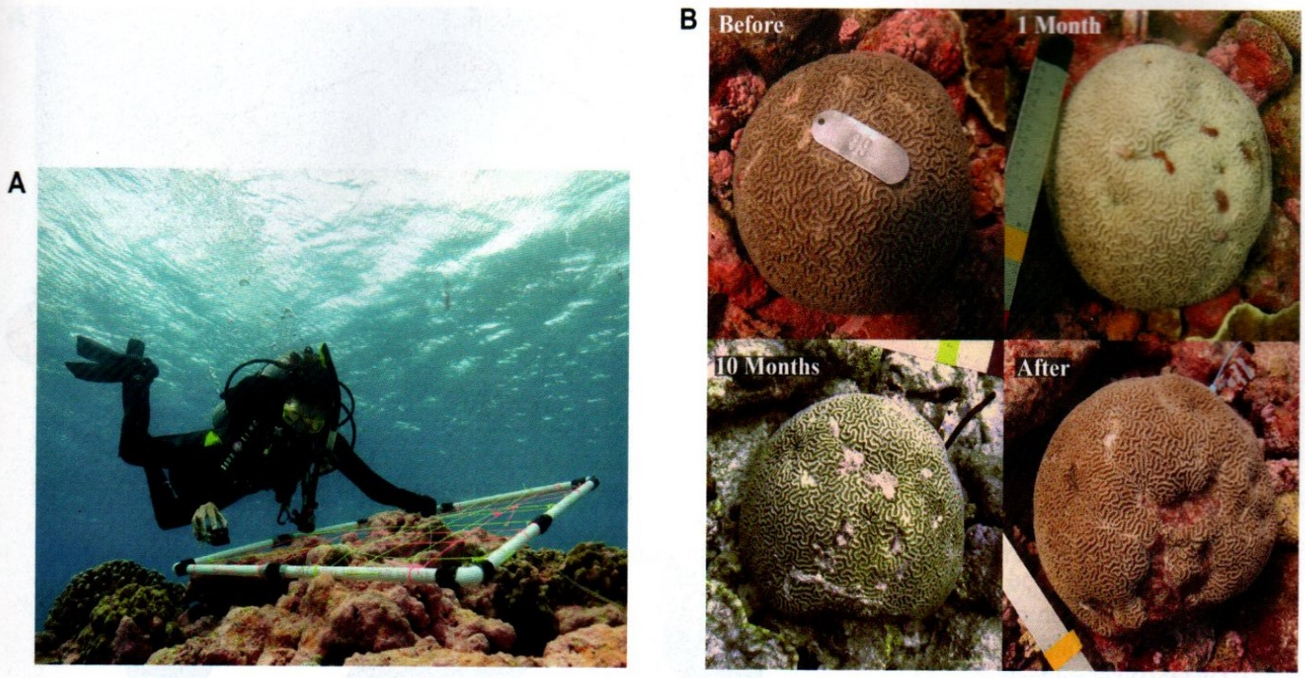
When corals are stressed, they expel the symbiotic photosynthetic algae they need for survival. This is known as* bleaching, *because without these zooxanthellae, corals lose their bright colors. Bleaching is often linked to a rise in water temperature, as has occurred in the Hawaiian Islands. Photograph: NOAA—National Marine Sanctuaries, 2015.

Reef-forming corals are struggling in warming oceans. Temperatures as little as 1 degree Celsius above normal are stressful for the delicate symbiotic relationship between corals and the tiny algae that feed them, remove their waste, and enable their beautiful colors. Heat stress can lead those algal partners to abandon their coral homes, a phenomenon called *bleaching* because it leaves reefs a ghostly white. Bleaching events are becoming increasingly common and prolonged. An estimated 94% of coral reefs have already experienced one or more episodes of severe coral bleaching since 1980 as a result of record-breaking temperature extremes.

In 2015–2016, an El Niño triggered a global bleaching event, causing mass coral mortality. Its epicenter was Kiritimati (Christmas Island), a coral atoll in the central equatorial Pacific. There, the heatwave lasted an unprecedented 12 months, and 90% of the hard corals died.

The world's media had been closely following the 2015–2016 mass bleaching event. Toward its end, journalists reached out to University of Victoria

BioScience 72: 936–944.
https://doi.org/10.1093/biosci/biac081



Coral reef ecologist Julia Baum photographs corals within a transect in Kiritimati (Christmas Island), where she has followed the survival of corals during and after marine heat waves. Photograph: Trisha Stovel. Photograph: Baum Lab.

marine ecologist Julia Baum to request follow up photographs of Kiritimati's lifeless white corals. Baum's team had been following reef health over time, tagging and treating individual corals "a bit like patients in a medical study," she says.

So Baum's graduate student Danielle Claar headed out with her camera. Surprisingly, some before and after photos were not what they expected. "We found some types of corals that recovered from bleaching and healed themselves while they were still exposed to high temperatures," says Baum. Coral recovery from bleaching had previously been observed only after heat stress subsidence. Their discovery, published in 2020 in *Nature Communications*, was "a game-changer," says Baum. It underlined the volumes still to be learned about coral resilience.

Resilience, a concept pioneered by Canadian ecologist C. S. "Buzz" Holling (1930–2019), includes resistance to and recovery from a stressor. Sampling a small cross-section of coral reef resilience research reveals work in progress in disciplines including ecology, genetics, microbiology, protected areas management, and cryobiology.

Coral 101: Life history, partnerships, and puzzles

Despite occupying a mere 1% of the ocean, reef-building warm water corals sustain a quarter of all marine life. Coral reef biodiversity supports fisheries, tourism, and recreation for hundreds of millions of people, with the corals' hard structures providing coastal storm protection for millions more. About 800 reef-building species of corals exist in the phylum Cnidaria, which also includes jellyfish and sea anemones.

Corals mainly reproduce both sexually and asexually. During sexual reproduction, males and females typically broadcast sperm and egg bundles into the seawater, where fertilization occurs. Embryos develop into swimming larvae about 4 days after conception. The corals then metamorphose and settle to begin sedentary polyp life, growing, over time, into a colony through asexual budding. Warm water corals form partnerships intracellularly with dinoflagellate algae in the family Symbiodiniaceae. The corals form these symbiotic partnerships as larvae or shortly after settling, explains Mary Hagedorn, senior research scientist with the Smithsonian Conservation Biology Institute and Hawaii Institute of Marine Biology. About 30% of coral species get symbionts from their parents, she says. The rest get symbionts from the environment. Although corals are able to acquire some food on their own with their harpoon-like tentacles, the vast majority of their nutrition comes from their single-celled algal symbionts. When under thermal stress, corals expel their symbionts, leading to bleaching.

Bleaching events are conspicuously patchy. During some bleaching events, bleached and unbleached corals are seen side by side. Scientists around the world are actively investigating why some corals are more resistant than others to losing algal partners as temperatures rise. Variation in bleaching vulnerability is hypothesized to be due to intrinsic factors such as phenotypic and genetic differences among corals and their microalgal symbionts, plus

extrinsic factors such as microhabitat differences in temperature and light.

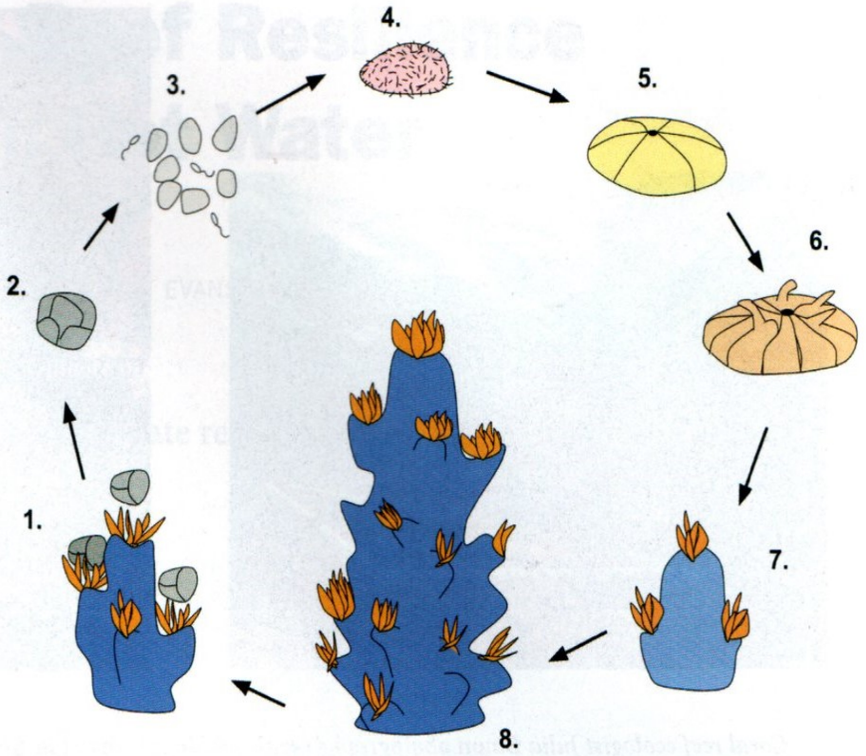
Narrowing windows for recovery

In Kiritimati, Baum established long-term reef monitoring sites in 2009 along a continuum from near villages to the remote end of the atoll. In 2014, her team tagged individual colonies of two Indo-Pacific coral species *Platygyra ryukyuensis* and *Favites pentagona* to track symbiont identities and colony fates during the heatwave. Using genetic analyses, Baum examined the influence of human disturbance on coral symbioses, bleaching timing, recovery, and symbiont community composition changes. She tested whether symbiont type mattered for bleaching and survivorship. It did. Corals on highly disturbed reefs were dominated by heat-tolerant symbionts in the genus *Durusdinium*. Reefs with lower disturbance levels had more heat-sensitive symbionts in the genus *Cladocopium*.

Two months into the heatwave, as was expected, the corals with heat-tolerant symbionts were less likely to have bleached than were those with heat-sensitive symbionts. Nevertheless, many of the heat-sensitive coral colonies recovered from bleaching while they were still at elevated temperatures, a phenomenon that had not been previously observed. Their recovery was helped by the proliferation of heat-tolerant *Durusdinium* symbionts, which the corals had adopted instead of their formerly heat-sensitive ones, a swap known as *symbiont shuffling*. The corals that started the heatwave with heat-sensitive symbionts ultimately survived at rates higher than or similar to those with thermotolerant symbionts. Recovery from bleaching during this heatwave was observed only in corals at sites without high levels of local disturbance, however, underlining that corals have multiple pathways to survival—resistance and recovery.

In follow-up work, Baum's team compared the fate of coral species with different life history strategies: the massive, tolerant, slow growing *Porites lobata* and two fast-growing but sensitive "competitive" corals *Pocillopora grandis* and *Montipora aequituberculata*. The latter two species can grow to dominate communities. With respect to survivorship at the end of the heatwave, in this case, the disturbed reefs fared better than the protected ones. That's because the disturbed sites were already composed of mainly heat-tolerant species. But the results differed between the community and species levels. For 336 coral species not eradicated by the heatwave, their survivorship declined with increasing local disturbance, underlining the complexity at different biological scales.

Although Baum's work has shown that recovery is possible even in hot water, the time windows available for recovery between consecutive mass bleaching events have shrunk from 25 to 30 years a few decades ago to 1–3 years now, far shorter than the 10–15 years that even fast-growing corals need to rebound. If climate change continues unchecked, hope for coral reef resilience may rest not on recovery but on resistance. Scientists are avidly investigating intrinsic resistance—biological traits that help the corals cope in a changing climate—and extrinsic resistance conferred by living in less vulnerable locations.

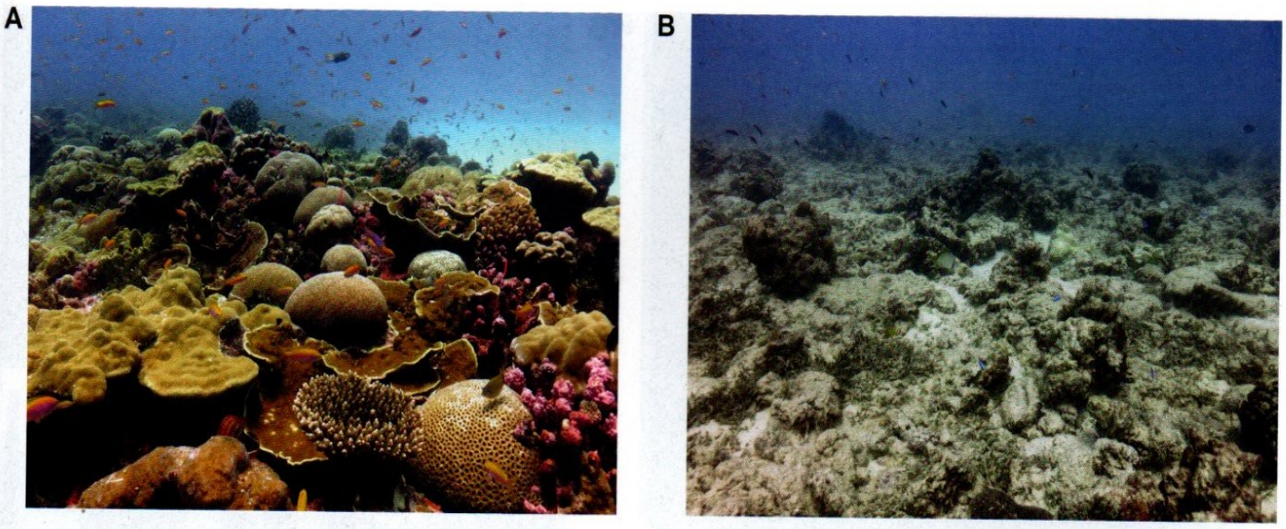


1. Sperm-egg clusters are released by polyps. 2. Gamete clusters ascend to the ocean surface. 3. Clusters break up, with gamete mixing and fertilization. 4. Embryos become larvae capable of settlement for 3–4 weeks. 5. Larvae settle and undergo metamorphosis. 6. Juvenile polyps develop a mouth and tentacles. 7. Zooxanthellae are incorporated, calcification increases, and budding begins at base of polyp to start a new colony. 8. Colony expands through calcification and budding. Image: CC BY-SA 4.0 Andcelano.

Exploring intrinsic resistance

At Stanford University, recent doctoral student Nia Walker ran experiments subjecting corals to heat stress to study resistance. Walker notes the importance of considering resilience at different levels including that of the species, the population, and the individual coral colony, because there is so much variation. "Variation is the building block material for acclimation and adaptation," says Walker.

Walker and colleagues examined *Acropora* colonies in Palau. Her team collected coral fragments and exposed



An unbleached site within Julia Baum's Kiritimati study of corals and resilience, photographed in August 2014. Photograph: Danielle Claar.

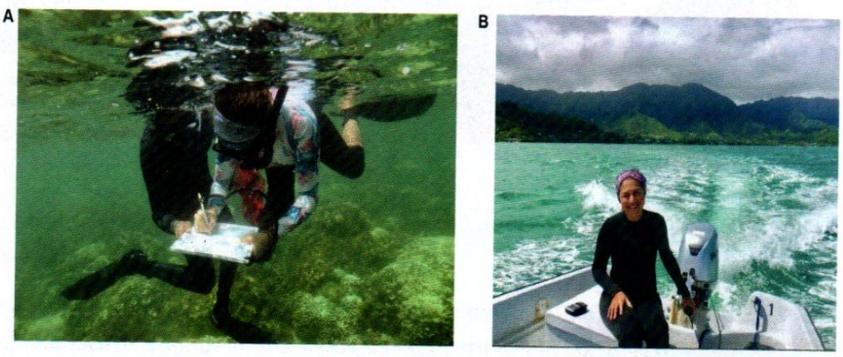
A bleached site within Julia Baum's Kiritimati study of corals and resilience, photographed in August 2014. Photograph: Danielle Claar.

them to heat pulses lasting 1–9 days. Even among corals from the same species and collection site, Walker found considerable variation in time to induce to bleaching and mortality level, categorizing the samples as low, moderate, or high in resistance. After heat stress removal, she also found variable recovery time.

If heat-resistant coral genotypes are to be used in reef restoration projects, Walker notes that there is a need to consider trade-offs. Reintroducing only thermally tolerant corals may disadvantageously create a genetic bottleneck and could have disadvantages. "Heat-resistance will likely be linked to fitness trade-offs," notes Walker. "Otherwise, all corals would be super heat resistant."

Measuring skeletal growth as a proxy for health in the recovering corals, she found that growth resumed within 4 months after bleaching in moderately resistant corals but that high- and low-resistance corals grew more slowly. High resistance but slow growth could point to a fitness trade-off, says Walker.

Not all symbionts are equally resistant to heat stress, and it has been unclear to what extent corals can switch symbionts when conditions change. Mariana Rocha de Souza, a recent PhD graduate at the University of Hawaii, investigated this in corals



Exploring vulnerability to bleaching and the influence of symbiont species, Mariana Rocha de Souza and Shreya Yadav record data on coral bleaching in Kāne'ohe Bay, Hawaii.

from Kāne'ohe Bay, Hawaii, a body of water with variable water quality, temperature, and acidity. Tagging and collecting coral fragments across the bay and logging data on temperature, she used DNA analysis to identify coral microbes, creating a symbiont DNA library. To model how the symbiont community might be affected by future ocean conditions, Rocha de Souza created a mesocosm of eight corals from three genera in four treatment groups that were heated, acidified, heated and acidified, or kept in controlled conditions for 2.5 years.

Prior to treatment, she found symbiont communities quite similar within genera. After treatment, the symbiont composition was species specific. "Even corals from the same genus didn't have the same symbiont composition," she says. Some corals had interactions with multiple symbiont species. Others were more specialized. She found that heat stress influenced symbiont composition, whereas acidification did not. The site of collection also had a major impact on symbiont composition after experimental treatments. Even after being exposed to stress for 2.5 years in the experimental setting, "corals from specific locations still had something imprinted," she says, responding differently according to their collection location. Her work contributes to broader efforts to disentangle whether local and regional variation in heat-stress vulnerability is

Adrienne Correa and colleagues, Carsten Grupstra and Alex Veglia, set up an experiment to examine the potential role of fish feces in disseminating coral symbiotic algae. Photograph: Lauren Howe-Kerr.

Adrienne Correa and her colleagues, Lauren Howe-Kerr and Carsten Grupstra process Pocillopora coral fragments in Moorea, French Polynesia, to sample viruses and assess their potential role in coral bleaching. Photograph: Rebecca Maher/Correa Lab.

due to acclimation, genetic adaptation, or heritable epigenetics.

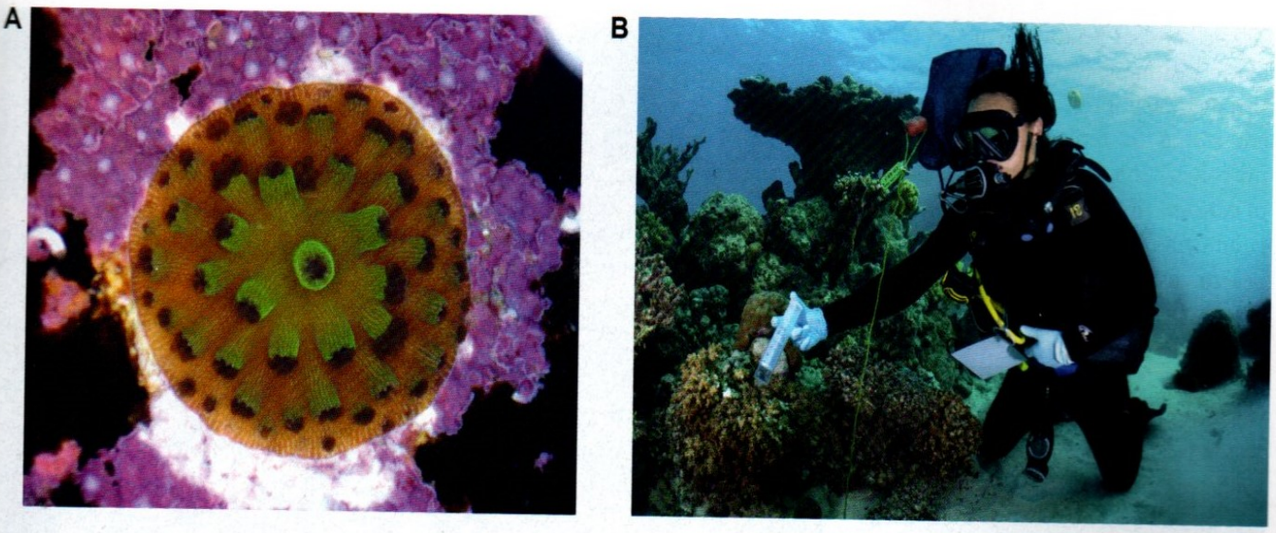
In the middle of Rocha de Souza's study, in 2019, Kāne'ohe Bay experienced a heatwave and bleaching. Heat-tolerant symbionts increased in frequency, and corals with heat-tolerant symbionts bleached less. In the north of the bay, little changed, underlining the quirks of geography. In light of suggestions by some that we infect corals with more heat-resistant symbionts to help them weather warmer conditions, "Maybe that's not going to work," says Rocha de Souza. We can try to infect corals with "preferred" symbionts, but their site of origin matters. New symbionts, she says, may not "stick."

Indeed, many questions remain regarding the basic biology of how corals and symbionts pair up, says Adrienne Correa, at Rice University. How do host and symbiont recognize each other? What triggers break ups? These are important questions in light of efforts to breed more heat-tolerant symbionts, which might evolve faster than corals because of their shorter generation times and greater abundance.

In this effort, one knowledge gap has been understanding when and how symbionts have sex. "Genetic recombination could facilitate faster generation of heat tolerance," says Correa. So she has been studying meiosis and sexual reproduction to ascertain the conditions that trigger more frequent symbiont sex.

How symbionts interact with corals and the environment is another research vein. During bleaching, there is a mass loss of symbionts to the environment, but under normal conditions, "symbionts are entering and exiting healthy hosts on a daily basis," says Correa, sparking many questions: What is the symbionts' fate if they are expelled from a host? Do they float off and die? Were they expelled because they were already dying? Are they taken up by another host? And does that change under a stressful versus normal or healthy context?

Correa is also investigating whether symbiont availability for corals is aided by fish. Following work by others, Correa's group worked in Mo'orea, French Polynesia, comparing the feces of fish with different diets, such as butterflyfish and parrotfish, which eat corals, with those of surgeonfishes, which eat algae. Examining the proportion

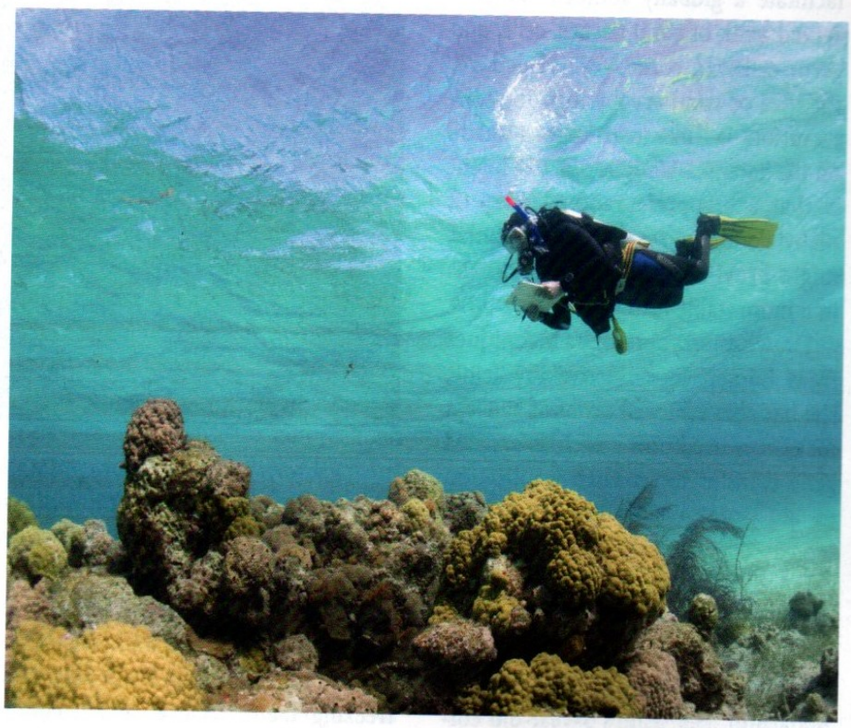


A 6-month-old assisted gene flow elkhorn coral colony produced from cryopreserved sperm crossing Florida sperm with Curaçao eggs. Photograph: Cody Engelsma, Mote Marine Laboratory, Florida.

PhD student Ines Raimundo, working in Raquel Peixoto's lab at KAUST, applies probiotics to corals in the Red Sea. Photograph: KAUST/Morgan Bennett-Smith.

of living to dead symbionts in feces, her team found that the coral-eating fish had live symbiont cell concentrations five to seven orders of magnitude higher than their concentrations in sediment and water. Correa's team speculates that fish feces might be an important source of thermotolerant symbiont cells during bleaching events.

Another focus of Correa's is coral reef viral diversity. "We are just beginning to realize what an amazing diversity of viruses are associated with coral hosts," she says. Viruses can infect corals or their symbionts, so Correa is examining whether viruses contribute to bleaching. She has observed that viruses transition to a more active infection mode during coral heat stress. Nevertheless, some viruses can be beneficial. There is even precedent for viruses to aid heat tolerance, such as in panic grass, a plant dependent on a virus to survive high temperatures in geothermal soil. "There are all sorts of different things viruses do that we have to keep our minds open for as we explore reefs," says Correa.



Isabelle Côté on a research dive in the Bahamas in 2014. Photograph: Emily Darling/WCS

Stopgap solutions leveraging intrinsic resistance

Although the only sure-fire solution for corals stressed in hot water is to cool the planet down, in the meantime, scientists seek a better understanding of a healthy coral microbiome. That's the objective of microbiologist Raquel Peixoto, at the King Abdullah University of Science and Technology, in Saudi Arabia. "Corals have a microbiome just like us," says Peixoto, an array that includes bacteria, archaea, fungi, and viruses that contribute to maintaining the intricate relationship between corals and their symbiont algae. Her team is trying to understand how bacteria affect coral and algal health.

Traditionally used for plants, for humans, and more recently for bees, frogs, and bats, might probiotics aid

stressed corals? Peixoto compares probiotic treatment with replanting trees in a degraded forest. "In this case, you are trying to replant the beneficial microbes," she says. Achieving proof of concept in the lab, her team is now running a pilot experiment in the Red Sea to test probiotic impacts on the whole reef ecosystem. How will corals respond? Will they take up provisioned microbes? Is treatment beneficial during bleaching? Which species benefit? Can it be scaled up? These are a few of the burgeoning questions.

Stopgap solutions also motivated marine biologist Mary Hagedorn to begin pioneering coral freezing (cryopreservation). Keenly aware of the coral conservation time crunch, Hagedorn is leading the Reef Recovery Initiative with Smithsonian Global to facilitate a globally sourced cryopreserved bank of coral tissues, cells, and germ cells. To some, says Hagedorn, the idea of coral cryobiology for conservation is "like rearranging chairs on the Titanic." Undeterred, her intent is that a cryopreservation library of many coral species, like seed banks, might provide stock to reseed oceans in a more stable future climate.

Drawing cryobiology techniques from human reproductive medicine, she has also achieved proof of concept for efforts used now—such as assisted gene transfer by in vitro fertilization to aid coral restoration. Her team increased genetic diversity in endangered elkhorn coral by crossing coral gametes from Curaçao, Puerto Rico, and Florida, raising them in nurseries at Florida's Mote Marine Lab and Aquarium. Her team's 3-year-old corals are now orphaned by US regulatory hurdles. But experimental restoration using coral hybrids is already in progress on some reefs in Australia.

Capturing wild coral gametes for captive breeding is challenging, says Hagedorn. Corals tend to spawn on a full moon, but their timing is unpredictable. Her team had to dive for 60 straight nights to finally net coral gametes. The team developed special techniques for freezing coral sperm and larvae without dangerous ice crystals forming, like on poorly covered ice cream, she says. "We walk this knife edge of trying to keep them alive and freezing them." Hagedorn is helping pioneer techniques such as isochoric vitrification—freezing coral microfragments into a glass-like state without expansion—enabling later growth of new corals from tiny cuttings.

Elkhorn coral (Acropora palmata) at the Limones reef in Mexico, one of the few sites supporting healthy and resilient populations of this endangered coral species which has suffered severe declines. Photograph: Lorenzo Alvarez-Filip.

Extrinsic resistance: Mapping for the future

Climate change is not the only threat to coral reefs, and efforts to create marine protected areas (MPAs) have long been advocated to protect them from local threats such as coastal development, pollution, overfishing, and harvesting for the aquarium trade. But do MPAs confer protection during marine heatwaves?

In 2010, with her doctoral student at the time Emily Darling, Simon Fraser University marine ecologist Isabelle Côté published a paper in *PLOS Biology* in which they examined whether MPAs designed for coral reef conservation increase coral reef resilience to climate disturbances. One phenomenon widely noted over time is that coral species composition varies between protected and unprotected sites. Corals such as *Acropora* and *Montipora* are particularly thermally

sensitive. Côté and Darling found that degradation can increase both the abundance of disturbance-tolerant species within a community and the ecosystem's ability to resist climate impacts.

Investigating further, Côté and colleagues tested the hypothesis that MPAs increase the resilience of coral assemblages to large-scale disturbance. Analyzing field data documenting changes in coral cover inside and outside MPAs after disturbances including storms, disease outbreaks, and acute ocean warming periods, their results indicated that MPAs have no general effect on coral loss or postdisturbance recovery. One explanation is that local stressors such as pollution and fishing get swamped by the much greater effect of ocean warming. Their analysis led them to conclude that reefs cannot be saved by local actions alone.

"Marine protected areas are not more resistant to climate change, and if anything, they can be extra vulnerable," says Darling, now director of coral reef conservation at the Wildlife Conservation Society in Toronto, Canada. Her PhD research in Kenya showed that coral communities differ in managed and unmanaged reefs. Long-term management of a reef in an MPA removes local stressors, allowing a more diverse community of corals to persist. But species flourishing in safe harbors are the same ones sensitive to climate change. "Bleaching does not stop at the boundaries of that MPA," says Darling. Reefs outside MPAs, experienced with stress and disturbance, have lost sensitive species and gained weedy or tolerant ones. Where does that conundrum leave us? "We need marine protected areas," says Darling. "But we need them in the right places."

One place so far spared the worst impacts of bleaching is the Mexican Caribbean. Lorenzo Alvarez-Filip, a coral conservation biologist at the Universidad Nacional Autónoma de México reef conservation lab in Puerto Morelos, Mexico, has been studying trends in coral cover, species composition, and functional ecology in this region. Although Mexican Caribbean coral reefs have not yet seen mass mortality from thermal stress, there are plenty of other stressors, such as coastal development, sedimentation, and pollution, says Alvarez-Filip. Diseases linked to climate change and nutrient pollution are another recent crisis.

Kay Davis samples water pH off Heron Island on the Great Barrier Reef, Australia. Photograph: Ashly McMahon.

Alvarez-Filip tracked the 2018 stony coral tissue loss disease outbreak on Mexican coral reefs. "It was very painful seeing thousands of coral die," he says. "It was like diving in a graveyard." Although it's hard to be positive about the state of coral reefs, we need to find optimism, he urges. "The problem with coral reefs is we have multiple threats," says Alvarez-Filip, with one common cause: human activity. Restoration efforts in places such as Indonesia have successfully recovered reefs over relatively large areas, he notes, but scaling up is problematic. "We are a few orders of magnitude behind what we need to do."

Alvarez-Filip underlines that the loss of corals is not random. Not all corals are created equal, and it is important that coral reef researchers avoid lumping all species together. Low-relief corals do not provide much structure or habitat, whereas branching corals do. Unfortunately, the important ones are the ones being lost at the highest rates, he says. As for knowledge gaps, Alvarez-Filip urges that we need to better understand the conditions facilitating coral resistance and recovery.

Two key coral functions are providing habitat for biodiversity and accumulating calcium carbonate—the reef framework. But the ability of corals to calcify hard skeletons puts them in trouble from the evil twin of warming seas—ocean acidification. When coral reefs grow, they take alkalinity out of the water to build their skeleton. Without constant calcification, reefs do not grow and can break down, explains Kay Davis, a postdoctoral researcher at Germany's Leibniz Centre for Tropical Marine Research who studied calcification rates on coral reefs. In a 2021 study led by Davis and published in *Nature Communications*, she and her colleagues calculated that, at 36 coral reef sites in 11 countries, reef calcification is declining by 4% per year. That suggests that reefs could become net dissolving worldwide around midcentury.

Overall, "we're seeing calcification go down and organic productivity

going up," says Davis, indicating a shift from coral- to marine algae–dominated ecosystems. Ocean acidification will likely have impacts on calcification rates, she says, but the bigger threat now is ocean warming.

Looking to the future

Moving forward, "The key is that we have to be really strategic," says Darling. She collaborated on remote sensing to identify oceanic cool spots and produced a global analysis known as the 50 Reefs approach, prioritizing avoidance refugia that are now the focus of global investments (the Global Fund for Coral Reefs, Bloomberg Philanthropies' Vibrant Oceans Initiative). But as Darling and 20 coauthors noted in *Conservation Letters* in 2018, "Investment in protecting any portfolio of reefs will be insufficient if carbon emissions are not reduced."

At the July 2022 International Coral Reef Symposium, in Bremen, Germany, long-time coral reef conservation champion Nancy Knowlton, of the National Museum of Natural History, in Washington, DC, articulated in her plenary that things are grim but not hopeless, adding that a focus on problems without solutions leads to apathy, not action. By building a biological toolbox to aid reef restoration, improving local conditions, coordinating globally, and addressing climate change, there is hope for the future for coral reefs.

If nothing changes, it is projected that the majority of coral reefs will be lost by midcentury. "It's 2022, so that's soon, and that's serious," says Darling. But she is optimistic. "Nature is plucky. Nature is resilient. And we're learning a lot more about these types of climate refugia and how corals have persisted in ways we never would have thought possible," she says. As an example, she recalls colleagues guiding her to a reef in the port of Cartagena, Colombia. The GPS point—in turbid waters in a busy shipping lane—seemed a mistake. She was incredulous that a coral reef could exist below. But as she dove down through the murk, the water suddenly cleared, revealing the largest Caribbean *Orbicella* corals she had ever seen. "It was like the underwater Alps of a coral reef," she says. They should not have been there, and they were. "It's things like that that give me hope."

Endlessly curious about the quirks of nature, Lesley Evans Ogden is a freelance science journalist, editor, and producer based in Vancouver, Canada. Find her on Twitter @ljevanso.