Marine Life on Acid

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LESLEY EVANS OGDEN

Predicting future biodiversity in our changing oceans.

The underwater vents near southern Italy's Mount Vesuvius are the closest we have to a time machine on fast-forward to the future. Carbon dioxide (CO_2) bubbles up from the seafloor like champagne as divers swim into highly acidified seawater. Outside these vent systems, the pH is a normal 8.2, and the waters are a kaleidoscope of multicolored biodiversity. Entering the aquamarine fizz, the pH drops to 7.4, and the view is a monochromatic green carpet of seagrass and algae. Plymouth University's Jason Hall-Spencer is examining these unusual waters in detail. Are these naturally acidified waters a glimpse into the future? Vent-dwelling organisms have evolved here for millennia and may indeed provide a look ahead as Earth's oceans grow increasingly acidic because of human action. If so, that vision is a 30-percent reduction in biodiversity and a significant shift away from corals and large fish, toward organisms such as algae, sea grass, and small marine worms.

Jason Hall-Spencer and his research team characterize marine life along a gradient from normal ocean acidity to the highly acidified waters near Mount Vesuvius, in the Gulf of Naples, where volcanic vents send carbon dioxide bubbling to the surface. Photograph: G. Caramanna.

The term *ocean acidification* was coined only in 2003, explains Hall-Spencer; it's a research area still in its infancy. Experts such as University of British Columbia marine ecologist Chris Harley suggest that there are knowledge gaps in at least three key areas. First, we need to understand the differential vulnerability of organisms to ocean acidification, looking at the species, geography, and life stage. Second, although single-species studies have been valuable, the impact of ocean acidification on whole ecosystems is not well understood. A third key area is understanding to what extent organisms can adapt, not just within a single lifetime but over generations, through evolution.

Ocean acidification has been dubbed "the other carbon dioxide problem" and "climate change's evil twin." The ocean is a massive carbon sink estimated to have absorbed one third of all the CO_2 produced by human activities. The tracking of carbon concentrations in the ocean, which began in the mid-1980s, has indicated that concentrations of CO_2 are increasing in parallel with the growing amount of this gas in the atmosphere. Short-term and long-term cycles continually exchange carbon among the atmosphere, the ocean, and land. CO_2 reacts with seawater to form carbonic acid, but as a weak acid, carbonic acid almost immediately dissociates to form bicarbonate ions and hydrogen ions. The increasing concentration of hydrogen ions makes seawater more acidic. Some of these extra hydrogen ions react with carbonate ions in the water to form more bicarbonate, making carbonate ions less available.

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Increased acidity makes life more difficult for species that absorb carbonate from the water to build their shells and skeletons, such as snails and corals. As acidity levels rise, those shells and skeletons begin to dissolve.

Differential vulnerability

Understanding the differential vulnerability of organisms to ocean acidification is important in order to determine the ecological and economic impacts on fisheries and aquaculture. Most biological ocean acidification studies thus far have been laboratory based, simulating different future CO_2 scenarios. But recent evidence from field studies indicates vulnerability even at current conditions in the Southern Ocean. Polar regions are particularly vulnerable to increased acidity, because colder waters absorb more CO_2, which leads to decreased availability of carbonate ions, a situation known as *undersaturation*. At a certain threshold of undersaturation, shells start dissolving.

Nina Bednaršek, formerly of the British Antarctic Survey and the University of East Anglia and now with the National Oceanic and Atmospheric Administration (NOAA), was part of a team that documented severe dissolution of the shells of marine snails, known as *pteropods*, during a 2008 ship-based expedition in the Scotia Sea, near the island of South Georgia. As pelagic zooplankton, pteropods, including the focal species of the study, *Limacina helicina antarctica*, spend their whole life cycle in the water column, never fixed to a substrate, explains Bednaršek. Ecologically, they are important as food for other zooplankton, fish, and marine mammals. Biogeochemically, they are an important component of the carbon cycle, their shells sinking to the bottom of the ocean after death. These tiny snails, reaching a maximum adult size of about 1 centimeter, were observed to have thinner, partially dissolved shells.

Undersaturation in the Antarctic was predicted to start in the winter of 2038. "So I did not expect to see evidence for dissolution already under way," says Bednaršek. "But when I began analyzing the samples and it became apparent that there was dissolution in the surface waters where there should be no dissolution whatsoever, it was a striking discovery." With dissolution at this depth clearly caused by anthropogenic CO_2 from the atmosphere, explains Bednaršek, they had discovered the first field-based evidence of human-caused ocean acidification.

Arctic work has been limited because of high costs and difficult logistics. But collaborating with Canadian scientists, a research group from the US Geological Survey (USGS) and the University of South Florida (USF) is establishing baseline pH measurements. Lisa Robbins, project chief of the USGS Arctic Ocean Acidification Research team, explains that they piggybacked their research onto US Law of the Sea cruise voyages during three summers aboard the USCGC *Healy*. Using various high-tech systems, the team obtained over 30,000 surface data points on ocean acidity and carbon parameters from water samples collected over the continental shelf up to the North Pole, vastly increasing the availability and resolution of Arctic data. The team's

Suggested reading.

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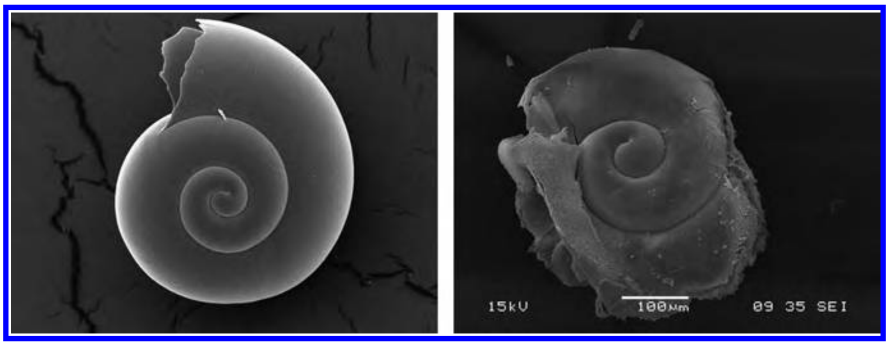


Nina Bednaršek and her colleagues documented pteropod shell dissolution in southern oceans, shown in this dramatic pair of micrographs. Micrographs: Nina Bednaršek.

A contraption called a **Niskin bottle rosette** *is pulled onto the deck of the USCGC* **Healy***, with samples from varying depths in the water column. Photograph: Lisa Robbins, US Geological Survey.*

work will provide current (baseline) acidity levels, will determine the size of the area affected by undersaturation, and will examine what is causing it. It is not only CO_2 from the air that contributes to Arctic Ocean acidification. "Isotopic data indicate that melting ice also dilutes the water, resulting in a double whammy," Robbins explains.

Large impacts are also anticipated for coral reef ecosystems. At the Australian Research Council's Center of Excellence for Coral Reef Studies and the James Cook University's School of Marine and Tropical Biology in Australia, Philip Munday's team was initially testing the idea that marine organisms in larval and juvenile life stages would be the most sensitive. Focusing on early life-history developmental patterns, growth rates, and survival in fish, they found the fish surprisingly robust to experimentally elevated CO_2. Alongside Munday's ocean acidification experiments, work was also under way by his PhD student Danielle Dixson, who was rearing clownfish to examine their sensory reef-finding systems. Out of curiosity, Munday juxtaposed his team's other experimental questions with Dixson's to test whether ocean acidification influenced these same reef-locating sensory systems—not expecting to find any relationship. Amazingly, the end-of-twentieth-century levels of dissolved CO_2 profoundly influenced fish behavior and sensory ability, making them unable to distinguish between the attractive smells of tropical trees, which are cues for suitable coral habitat, and those of swamp trees (*Melaleuca*), which are cues for inappropriate habitats.

Munday's team determined that, compared with fish reared in normal acidity, fish reared under high CO_2 could no longer distinguish the smell of their own parents and became attracted to—rather than repelled by—the smell of a predator. Their response to reef sounds was affected, too. "This is important because we know that reef sounds, like reef odors, are important in guiding baby fish back to reefs," says Munday. These and several other abnormal behaviors that the team has discovered mean reduced survival at natural reefs. They have recently attributed the strange behaviors in high-CO_2 waters to alterations in neurotransmitters ($GABA_A$ receptors) in fish brains.

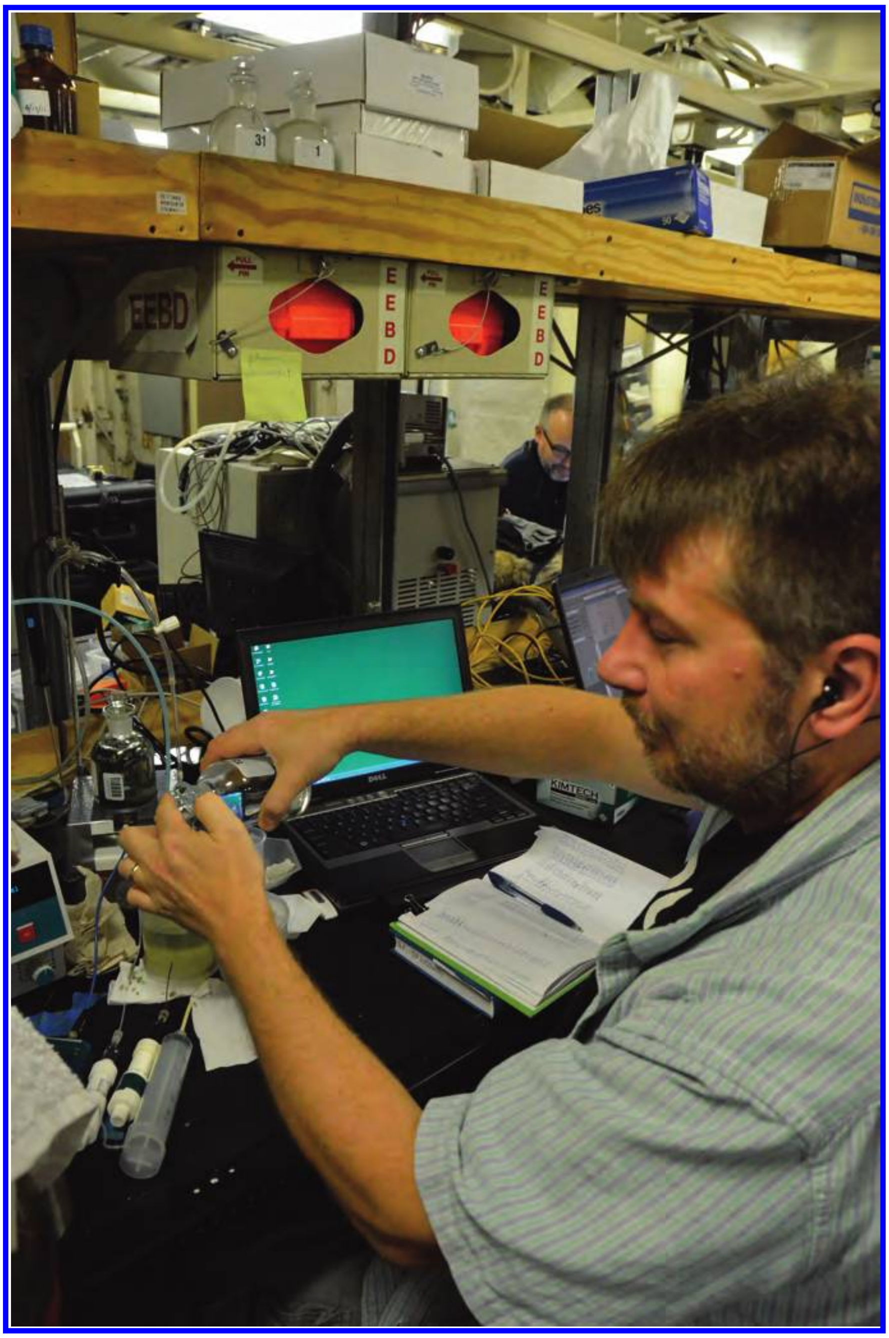
Ocean acidification may also become a bottleneck for successful reproduction. Like many marine invertebrates, the red sea urchin (*Strongylocentrotus franciscanus*) breeds by broadcast spawning, releasing its gametes directly into the water column. Experimentally tested in seawater at 400, 800, and 1800 parts per million CO_2, representing the levels of a present-day control and those expected in 2100 and 2300, fertilization efficiency respectively dropped by 72 percent and 89 percent relative to the control. Successful fertilization is facilitated by finely tuned physiological mechanisms, including a rapid change in electrical charge as soon as one sperm penetrates the external membrane, blocking entry by additional sperm. Changes to the acidity of present-day waters alter the ionic environment, slowing down the egg's reaction. In a system in which milliseconds count, that delay allows more than one sperm to traverse the egg membrane, resulting in inviable embryos.

Animals at early developmental stages are expected to be more vulnerable to ocean acidification than are those at later stages, a prediction frequently supported by experiments. But as Munday's work exemplifies, there have been some surprises, making it difficult to generalize the vulnerability of different life stages from one species to the next.

Marine shift: Ecosystems

Despite advances in the understanding of vulnerability according to species, life stage, and geographic region, there is an urgent need to move beyond single species to unravel whole-ecosystem-level impacts. That knowledge gap is beginning to be addressed by Hall-Spencer and Kristy Kroeker, of the University of California, Davis, at naturally high-CO_2 volcanic vent systems.

Originally studying deep-sea corals and the impacts of fishing gear, Hall-Spencer made an abrupt shift in focus after reading a Royal Society report on ocean acidification released in 2005. "My jaw dropped when I read it," he says. Since then, his research has been focused on understanding the impacts of ocean acidification. Hall-Spencer



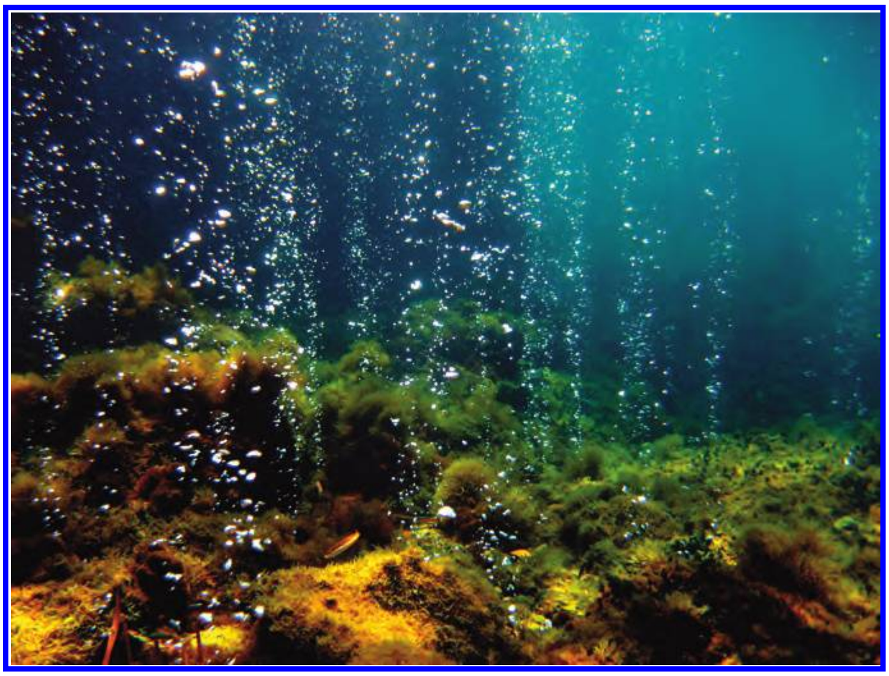
Paul Knorr, a University of South Florida graduate student, conducting research for the US Geological Survey, measures seawater alkalinity on board the USCGC Healy. *Photograph: Lisa Robbins, US Geological Survey.*

Reef fish such as these clownfish behave strangely in highly acidified waters, becoming attracted to a predator while being unable to smell their own parents. Photograph: Simon Foale.

and his colleagues are on the leading edge of research at ocean vent systems in Italy, New Guinea, and Mexico—systems that represent unique natural laboratories for examining pH impacts.

At Mediterranean vents, Kroeker is examining marine life along a gradient from current acidity levels through the low pH levels predicted for 2100, all the way to extreme low-pH zones that are way off the charts in terms of future predictions. (Note that lower pH means higher acidity.) In examining invertebrates, interestingly, says Kroeker, when you move from current to lower-pH conditions, "the community shifts a little bit, and some of the calcareous species still hang on. But when you move to the extreme low-pH zone, all those calcareous species drop out and are replaced by really high abundances of amphipods and tanaids," she explains. Shifting from normal to extremely low pH, there's a striking community reorganization, in part because these crustaceans are so tiny. "There are thousands of them, but they are much, much smaller than a rice grain. So we move from a diverse community with high biomass to a much less diverse community with much less biomass." For fish, that means less to eat, and that anticipated reduction in biomass could in turn affect economically important fisheries.

At CO_2 vent systems, Hall-Spencer says, he's surprised at the tolerance of adult fish. He sometimes sees them swimming through highly acidified waters, an observation that some of his colleagues leap on as a ray of hope for the future. But Hall-Spencer is more cautious, having never seen fish eggs or fry in these high-CO_2 waters. Through careful cataloging of species and their abundances along these underwater transects, "we think we've detected a tipping point," says Hall-Spencer, "where we see a really massive drop in biodiversity and where almost all calcified life is replaced by noncalcified life." At a pH level of 7.8, there's an abrupt shift from colorful coral ecosystems to domination by seagrasses and algae. That's the pH level that oceans are predicted to reach by 2100.



Seaweeds take over and shells dissolve as carbon dioxide levels rise. Photograph: Luca Tiberti, Associazione Nemo.

That these ecosystem shifts occur as acidification increases is clearly attributable to physiological constraints on the ability to calcify, but Kroeker's work indicates that this is not the whole story. Altered competitive interactions may also influence the suite of species present. In an experiment in which rock tiles were placed along a gradient from current to near-future (low) pH, her team observed the rates and types of colonizers that showed up. Contrary to what lab experiments had predicted, calcified species initially showed up in similar abundances on the baseline- and low-pH tiles. However, later in community development, the calcifiers were overgrown by dense mats of turf algae.

"Our conclusions are that some of these calcified species may actually be able to cope with these acidified conditions, but they may be outcompeted by the turf algae, which can… use the extra CO_2 in the system for photosynthesis and [which] may [therefore] benefit. In contrast, we never saw the calcified species in the extremely low-pH zone. They never even make it into the system," says Kroeker.

The race to evolve

A large area of uncertainty regarding ocean acidification is the extent to which organisms can adapt through evolution. Most experiments thus far have been focused on changes within a single lifetime. But to what extent do marine organisms have the genetic variability that allows the evolution of increased tolerance to a more acidified ocean? That's a question being addressed by several labs.

Jennifer Sunday, a PhD student at Simon Fraser University, in British Columbia, with collaborators, including Harley, used a breeding study to quantify standing genetic variation in heritable growth traits that might allow evolutionary adaptation to increased acidity. They examined the red sea urchin, an ecologically important grazer and sushi delicacy, and the bay mussel (*Mytilus trossulus*), a species important to global aquaculture. Because the red sea urchin can live as long as a century, whereas the mussel's life span is only a few years, they expected the mussels to be able to evolve more rapidly. Obtaining wild gametes, they cultured larvae in the laboratory under low- and high-CO_2 treatments. Under high-CO_2 conditions, larvae were smaller in both species. However, they discovered much more heritable variation in larval size in the long-lived urchin than in the short-lived mussel, which had almost none. Mathematical modeling of future generations over 50 years showed that sea urchins would have significantly higher rates of simulated evolution—the opposite of the predictions for these low-gear versus high-gear species, explains Harley.

Thorsten Reusch of the German Research Centre for Marine Geosciences (GEOMAR) Helmholtz Centre for Ocean Research Kiel, leads a team studying experimental evolution in the coccolithophore *Emiliania huxleyi*, a unicellular marine microalgae capable of forming blooms so extensive that they're visible from space. The function of the organism's calcite platelets is still a mystery. They may provide the organism with protection from viruses or grazing or may "basically act as a trash can for calcium carbonate during photosynthesis," says Reusch.

Reusch collaborated with PhD student Kai Lohbeck to examine *E. huxleyi*'s response to medium (e.g., from the end of the twentieth century) and high levels of ocean acidification (comparable to areas of upwelling) over 500 generations. *E. huxleyi*'s immediate reaction to increasing acidification was compromised growth and less calcification. But over the course of 500 generations under increased acidification, both calcification and growth rates improved, although they did not reach the levels from prior to acidification. The researchers are not sure whether coccolithophores evolve an enhanced ability to regulate their acid balance or whether they simply synthesize calcite at a faster rate. Reusch hints that more data are forthcoming in which he and his colleagues take the experiment further, to 1500 generations.

Sinead Collins also studies short-lived algae, a good model system because of their short generation times and large population sizes, not to mention, she effuses, that "they are just so cool." Collins is a Royal Society University Research Fellow at the University of Edinburgh, in Scotland. In her experimental work on marine algae, in which she has examined plastic (reversible) responses, "one really repeatable change that we are seeing is that cells get bigger in response to extra carbon, because they are getting more food," she explains. The tiny plankton *Ostreococcus tauri*, the smallest known free-living eukaryote, is normally 1 micrometer (μm) in size, but under increased CO_2, it increases to 1.5 μm in size. That change could make a huge difference for food chains. "If an organism is used to eating food the size of an orange, but then suddenly [its] food is the size of a cantaloupe, you can imagine that this becomes a feeding problem," says Collins. She has found that over many generations, the plastic response becomes fixed and no longer plastic.

The next steps, says Collins, include simulations and more experiments to figure out the theory. "It's not sexy," she says, "but it has to be done." Collins is determined to figure out how short-term plastic responses can be used to predict long-term evolutionary responses. She has begun collaborating with an international team of researchers to study tiny diatoms responding to increasing CO_2 in enclosures (mesocosms) in Gullmar Fjord, Sweden, part of the German-led BIOACID (Biological Impacts of Ocean Acidification) project coordinated by GEOMAR.

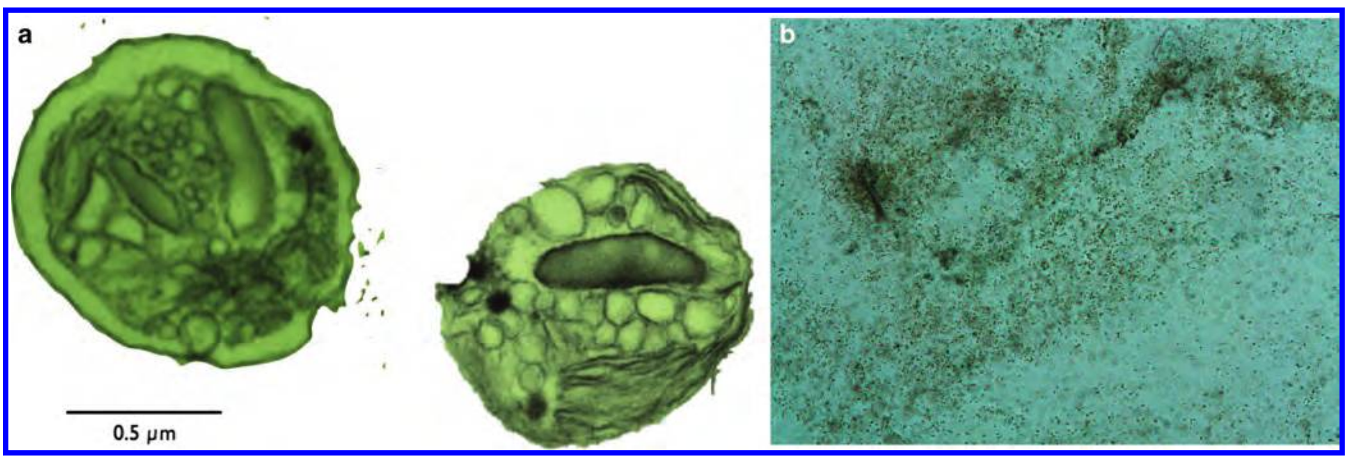
The human angle

One serendipitous "experiment" providing evidence that marine organisms can evolve in response to ocean acidification comes from unintended artificial selection in aquaculture-bred Australian oysters (*Saccostrea glomerata*). Certain lines suffered reduced shell growth compared with nonselected lines. But on the US West Coast, oyster farmers have not been so lucky. At Taylor Shellfish, a century-old aquaculture company based in Washington State that specializes in oysters, clams, muscles, and geoducks, shellfish farmer Bill Dewey recalls that, around 2007, Washington's aquaculture industry began to realize "that we had a big problem on our hands." In areas like Willapa Bay, oyster production failed over an 8-year period. Suspicion of ocean acidification as a cause directed the industry's monitoring and research focus toward adaptation.

State-funded sophisticated instrumentation now allows real-time monitoring of CO_2 levels at hatcheries, instead of samples' having to be sent out for analysis. With NOAA scientists helping the aquaculture industry to better understand the influence of the time of day and wind and weather patterns on CO_2 levels and on the upwelling of acidified waters, the industry has adaptively shifted water intake times to avoid exposing tanks of shellfish to corrosive water. And for times when corrosive water cannot be avoided, Taylor Shellfish Farms, in collaboration with the University of Washington and NOAA scientists, is researching at its hatcheries the chemical buffering of seawater with additives such as sodium carbonate.

Washington State is a leader in addressing ocean acidification. In February 2012, Governor Christine Gregoire convened a blue-ribbon panel to report on the impact of ocean acidification on Washington's marine biodiversity and on the state's $270 million aquaculture industry. Before her term ended, Gregoire included $3.3 million in the state budget to implement the November 2012 report's recommendations. Other states, including California, are beginning similar processes, and in January, the National Research Council released a report reviewing the Federal Ocean Acidification Research and Monitoring Plan mandated by Congress in 2009.

One point among many highlighted in the federal report is a widespread lack of public awareness of the problem, with more than 90 percent of Americans unaware of ocean acidification. Review panel chair George



The tiny plankton* Ostreococcus tauri *grows by a whopping 50 percent when exposed to elevated carbon dioxide levels. (a) Two cells seen with transmission electron microscopy. (b) Cells seen through a phase contrast microscope. Abbreviation: μm, micrometers. Micrographs: Elisa Schaum, University of Edinburgh.

Somero, of Stanford University's Hopkins Marine lab, suggests that "increasing acidity is something you don't see, you don't taste, you don't feel," adding that the pH scale is difficult to grasp, even for students of science. "pH is just a darn hard thing to measure, compared with something like temperature," he states. Somero is optimistic that better instrumentation will be available soon, especially with a new X Prize now challenging inventors to design improved pH monitors. The Intergovernmental Oceanographic Commission of the United Nations Educational, Scientific, and Cultural Organization is sponsoring research and monitoring and has cofounded the Ocean Acidification Network to provide a central source of information for ocean scientists.

The ocean is now nearly 30 percent more acidic than it was at the beginning of the industrial era. Finding a comparable acidification event requires setting our time machine in reverse, going back 55 million years. Even then, that past shift was an order of magnitude slower, explained University of Bristol paleobiologist Daniela Schmidt, at the September 2012 Symposium on the Ocean in a High-CO_2 World in Monterey, California. With one eye on the past and one on the future, science is beginning to unravel patterns and processes linked to the seemingly inevitable shift to more acidic oceans, suggesting which organisms will be winners or losers in Earth's uncontrolled ocean acidification "experiment." And if the past is any indication, there will be surprises.

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