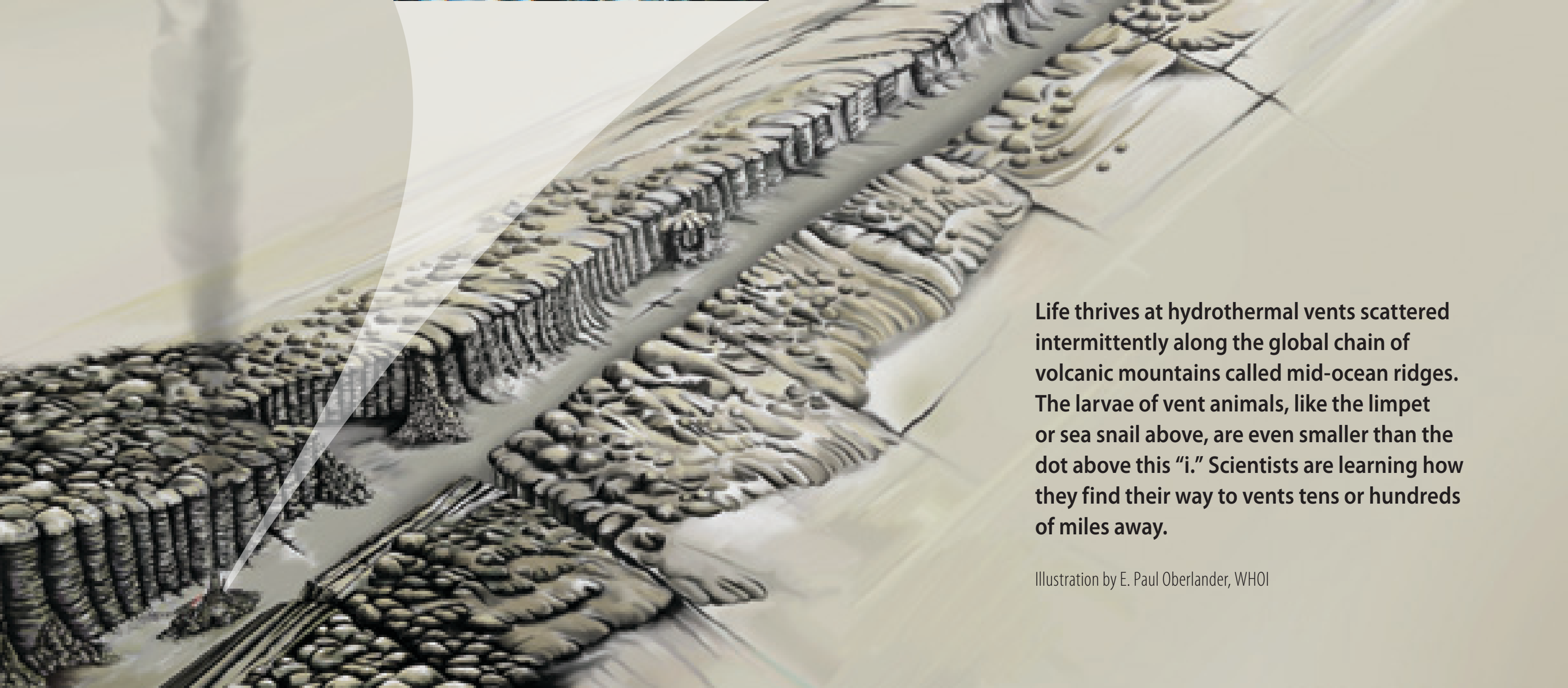
The mysterious movements of deep-sea larvae

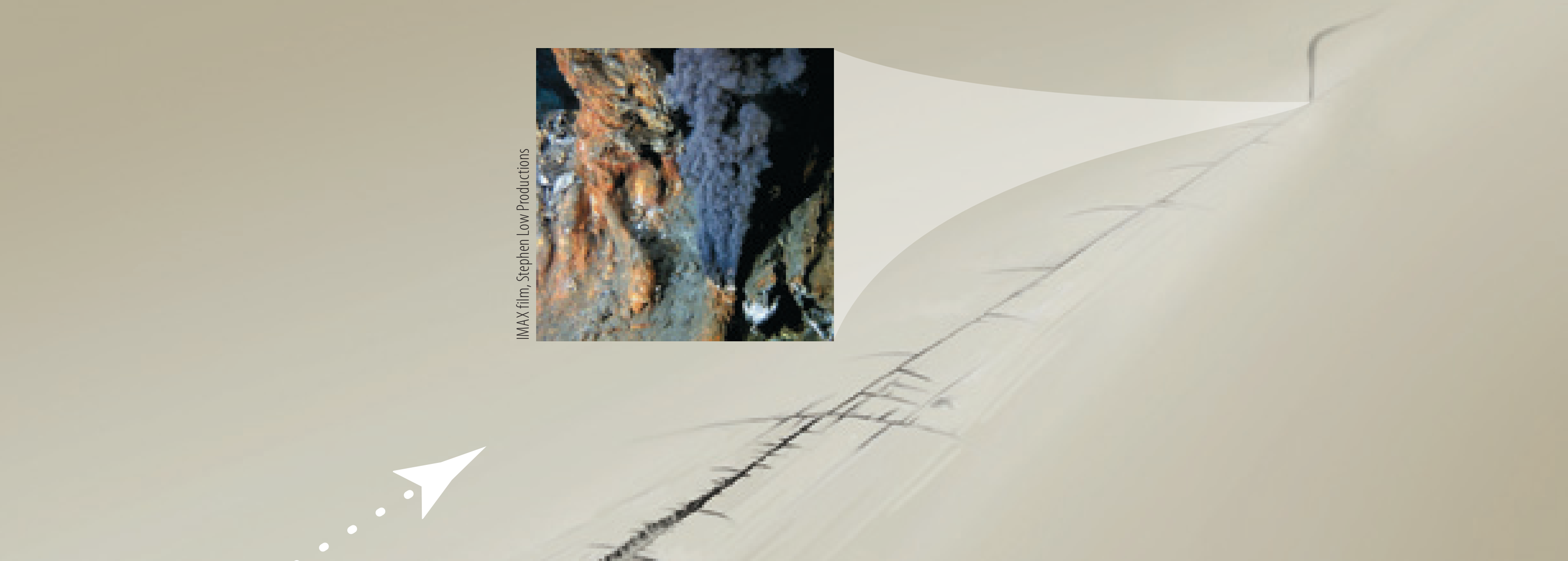
How do the tiny progeny of seafloor animals disperse through the ocean?

Courtesy of Lauren Mullineaux, WHOI



Life thrives at hydrothermal vents scattered intermittently along the global chain of volcanic mountains called mid-ocean ridges. The larvae of vent animals, like the limpet or sea snail above, are even smaller than the dot above this "i." Scientists are learning how they find their way to vents tens or hundreds of miles away.

Illustration by E. Paul Oberlander, WHOI



IMAX film, Stephen Low Productions

The marvelous migrations of fish and whales through the deep sea have been hard enough for us humans to follow. But what about tiny organisms—many smaller than the dot beneath this question mark? How they move from one spot to another in the depths has long remained beyond our grasp.

The enigma deepened in 1977, when scientists discovered spectacular and strange communities of animals clustered near vents on the seafloor. These so-called hydrothermal vents spew chemical-rich fluids that sustain clams, mussels, tubeworms, snails, and other species. Like shellfish in shallow waters, most of these relatively sedentary deep-sea animals reproduce by releasing eggs and sperm into the water. These develop into tiny floating larvae—the aquatic animal equivalent of seeds—that disperse, settle at vent sites, and grow.

Here's the catch: The vents are distributed intermittently along mid-ocean ridges—the long volcanic mountain chains that bisect the seafloor throughout the globe. These vents "turn on" and "turn off," fueled by the ebbs and flows of hot magma beneath the seafloor.

So how do the larvae, tinier than specks of dust, maintain their populations in such a patchy, transient environment? How do they get transported from one active vent site to another that might be tens of miles or more away?

These questions are keys to understanding how life has evolved on the seafloor and how it survives. Answering them requires a blend of biology, oceanographic physics, geology, and chemistry. So in 2006, scientists from Woods Hole Oceanographic Institution led a collaboration of researchers from different disciplines who investigated the broad range of factors that could influence larval movement, focusing on one particular mid-ocean ridge called the East Pacific Rise.

"There's so much happening down there that we simply needed to take an interdisciplinary approach," said WHOI biologist Lauren Mullineaux, "and I think everyone is glad we did."

The research project, dubbed LADDER (LArval Dispersal on the Deep East pacific Rise), is prompting scientists to rethink much of what they suspected about how deep-sea larvae disperse.

The seafloor repaved

In the late 1990s, Mullineaux and colleagues from Pennsylvania State University and University of North Carolina launched a project that began to make inroads into the lives of larvae. They developed high-pressure systems to culture deep-sea larvae in the lab and study the larval stages and life cycles of several species. During multiple visits over a few years to vent sites on the East Pacific Rise, the scientists used the submersible *Alvin* to place and later retrieve experimental blocks of rock around seafloor vents to collect larvae and learn how they settle.

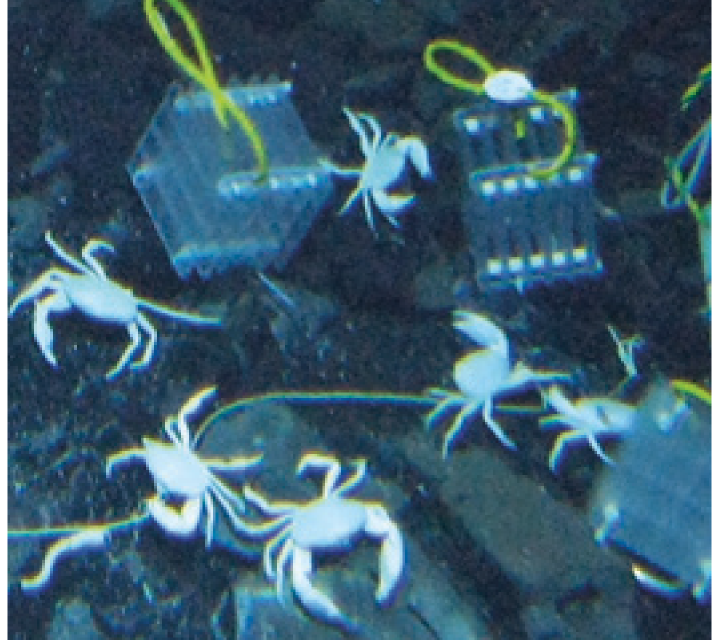
The researchers discovered that the larvae of one tubeworm species contain enough stored energy, in the form of lipids, to survive for 30 to 40 days. Some larvae had hairlike cilia for swimming, but those wouldn't take the tiny larvae very far. They needed to get swept into big ocean flows or currents. But what kind of flows and how far could they carry the larvae?

"We thought we had a pretty good sense of how the larvae got into the flows," Mullineaux said, "but we weren't sure what happened once the larvae were in the flows."

Then, in 2006, an unanticipated event gave researchers a rare opportunity. A series of excursions with *Alvin* showed that seafloor eruptions over several months on the East Pacific Rise had wiped out well-studied vent communities of organisms at 9°50'N, south of Mexico.

Until then, it had been hard for scientists to distinguish whether oceanic flows were bringing in larvae *to* 9°50'N from distant sites, or taking larvae *from* 9°50'N to other distant sites, or preventing larvae from leaving 9°50'N and forcing them to settle near their birthplace. Any of those were possible. New vents formed in the area, but the eruptions that paved over previous communities with lava presented the researchers with a clean slate and a chance to observe from its beginning how larvae colonize an area.

Biologist Carly Strasser prepares stacked plastic plates, nicknamed "sandwiches," to be used as artificial substrates on which larvae of vent animals can settle and grow.



Using the submersible *Alvin*, scientists placed the sandwiches on the seafloor. *Alvin* would return many weeks later to retrieve them.

What would larvae do?

Mullineaux jumped into action, teaming with Jim Ledwell and Dennis McGillicuddy from WHOI, Andreas Thurnherr from the Lamont-Doherty Earth Observatory at Columbia University, and Bill Lavelle from the National Oceanic and Atmospheric Administration. They conducted a series of seafloor experiments to capture as much information as possible about where new animals colonizing the clean-slate site came from and how they got there.

The experiments produced surprising findings. In the April 12, 2010, issue of *Proceedings of the National Academy of Sciences*, Mullineaux, WHOI biologists Susan Mills and Stace Beaulieu, and former WHOI/MIT graduate student Diane Adams reported that the vents were not colonized by species living at nearby vents but by two species of sea snails, or limpets, that hadn't lived there before. And the closest known populations of one of these, *Ctenopelta porifera*, were more than 200 miles (320 kilometers) north. How could they have traveled so far?

The researchers' next goal was to learn more about the oceanic flows that transport larvae. But it isn't easy to track larvae at the bottom of the sea. They are too small to affix with acoustic tags, too small to follow around in a submarine, and too diffuse to sample. So, the team embraced a tripartite plan to: 1) measure deep-sea currents, 2) use computer models that would simulate larval transport in oceanic flows, and 3) re-enact larval dispersal in the field with the help of a special dye-like tracer.

The process began with data collected by Thurnherr, who deployed current meters on the ridge to record how currents fluctuate. These data formed the basis of a computer model that Lavelle developed to simulate hydrodynamics on and around the ridges.

Next, McGillicuddy, a scientist in the WHOI Applied Ocean Physics and Engineering Department, used Lavelle's hydrodynamic model to (virtually) "release" particles representing larvae. He ran a series of computer simulations to see where the larvae would end up.

"The fundamental issue is that the interactions between the physical circulation and biological processes are so complex that it's hard to take a pencil and paper out and work out exactly what's going to happen," McGillicuddy said. "We use numerical models as a way to simulate the environment and explore how organisms may respond to physical forcing of various types."

Stay down and go far

McGillicuddy embedded in his models a certain degree of what he termed "sensitivity analysis" to account for larval physiology and behavior that Mullineaux and other biologists still don't fully understand. McGillicuddy can opt to change different interconnected variables every time he runs the model to analyze how various factors affect how larvae are transported.

Even with these variables, the models produced some surprising results. One of the early hypotheses was that larval movements could be influenced by plumes of fluids emanating from the vents. The hot plumes rise into cold seawater until they cool down and achieve what is called neutral buoyancy. Then they turn and drift horizontally, much the way smoke from a smokestack does.

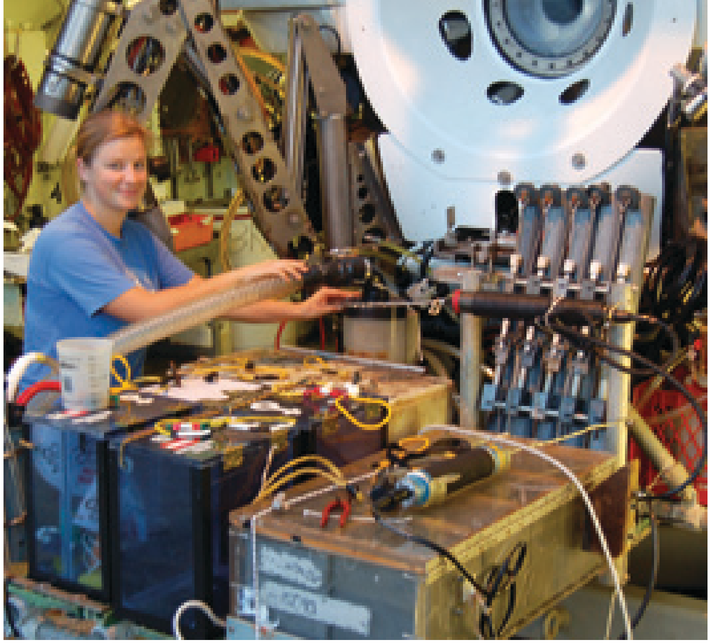
If this hypothesis held, larvae that manage to swim a few hundred meters off the ocean floor would be the ones dispersing long distances. The research by Thurnherr, Lavelle, and McGillicuddy, however, suggest that precisely the opposite may be true. They found evidence of ocean-bottom "jets"—fast currents traveling just under a quarter-mile per hour (10 centimeters per second) along the flanks of the ridge crest.

But even these jets could not quite transport the emigrating *Ctenopelta* larvae to new homes 200 miles away within their 30-day lifespan, Mullineaux said. "Either the larvae are using some other transport, or they are living longer than we thought," she said.

Follow the currents

Guided by these surprising findings, WHOI researchers launched the third phase of the LADDER plan: to test the model results in the field with the help of sulfur hexafluoride, or SF_6, a harmless compound that scientists can track as it goes with the flows, as larvae do.

For this experiment, the team turned to Jim Ledwell, another scientist in the Applied Ocean Physics and Engineering Department at WHOI and an expert on tracers. After studying McGillicuddy's



MIT/WHOI Joint Program graduate student Skylar Bayer checks *Alvin's* basket to find sandwiches retrieved from the seafloor.

Photos by Lauren Mullineaux, WHOI

Young tubeworms and other vent animals have settled and begun to grow on this sandwich.

model results, Ledwell went aboard WHOI's research vessel *Atlantis* to apply his expertise in the laboratory of the real world.

On Nov. 12, 2006, *Alvin* dove down into what's known as the "axial trough" on the East Pacific Rise—a 100-meter-wide chasm on the ridge's summit with steep cliffs tens of meters high on each side. It extends for kilometers along the spine of the ridge. In the first experiment of its kind, a specially designed injector system on *Alvin* released 6.6 pounds (3 kilograms) of the SF_6 along a ¾-mile (1,200-meter) section of the ridge 20 miles (32 kilometers) south of the vent site at 9°30'N.

Would the summit trough confine the flow of water and larvae and act as a conduit between habitable vent sites? Are some larvae swept up and away from the ridge, never to find a suitable vent to settle? What other factors determine the trajectories and distances larvae can disperse from their natal vents to remote vents?

Thirty-two days after the dye was released, Ledwell and company began methodically collecting water samples to find the tracer, using a sampling device called a CTD rosette, which is lowered on a wire from *Atlantis*. Over the next 20 days (bracketing the average 40-day larval lifespan), they sampled within the axial trough north and south of the release point. In results reported in the January 2010 issue of *Deep-Sea Research I*, they found the tracer at the 9°50'N site, demonstrating that larvae could make the 20-mile trip along the ridge axis within a larval lifespan.

Most of the tracer, however, was found in a patch about 30 miles (50 kilometers) west of the ridge. Currents appeared to move the tracer westward, away from the ridge crest where vents form. But then, about 25 days after release, the currents swung the tracer back toward the same ridge it came from.

The finding lent credence to another transport factor suggested earlier by Adams: eddies, or swirling currents, that may have carried the tracer or larvae away from the ridge at first, but then transported them back to the ridge.

"As these eddies come by, they make the tracer go one way for a while, and the other way for a while," Ledwell said. "It's just like the weather systems that come across in the atmosphere—the wind blows from the north for a while, and then a storm comes through and blows from the south."

Whatever explains why the tracer did what it did, results of the test surprised Mullineaux, who for years suspected that mixing processes in the water would prevent larvae from getting back on the ridge once they veered too far off. Now, she says, the data suggest that it's at least feasible for larvae to travel along previously unsuspected ocean pathways to colonize new sites farther along the ridge.

Ledwell agrees. "They might take circuitous routes," he said, "but the larvae certainly can use the currents for resettlement and getting where they need to go."

Beyond the LADDER project

As is usually the case, successful experiments provide answers—and even more questions, which LADDER project scientists are looking to follow up on. One factor they plan to closely examine is how seafloor topography influences current flows. In this case, a range of undersea mountains (or "seamounts") northwest of the site where the eruptions occurred and where the tracer was injected may have played a role in steering current patterns. The seamounts may redirect larvae back to their native ridge or trap larvae drifting through from other places and steer them to vent sites on the ridge.

For his part, McGillicuddy has more questions about how larvae behave. So he will continue to incorporate a greater number of realistic larval attributes into his model to see how they influence how and where the larvae are transported.

And Mullineaux would like to further investigate how the newly established vent communities evolve. Are the limpet species that colonized the areas depopulated by seafloor eruptions "pioneers that researchers hadn't been early enough to catch previously"? she asked. Or do they represent a "regime shift," in which new species take over sites previously dominated by different species?

"These are the kinds of questions we hope to be able to answer," she said.

—Matt Villano

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