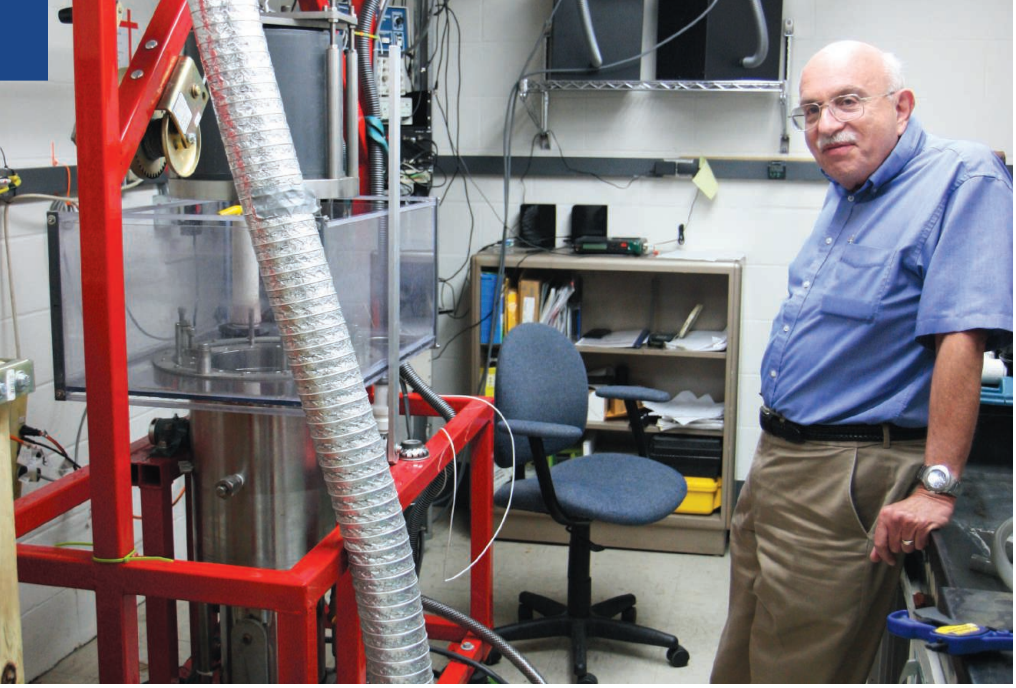

The godfather. Bioacoustician Arthur Popper (with the HICI-FT) used to test the effects of sounds produced by pile drivers on fish.

BIOACOUSTICS

The Sound in the Silence: Discovering a Fish's Soundscape

Bioacoustics pioneer Arthur Popper is getting ready to retire, but his work on how fish perceive sound isn't fading away

As an undergraduate more than 40 years ago, Arthur Popper took a detour on his way to a class on New York University's campus in the Bronx that set him on a course to become the godfather of fish hearing. Popper decided to visit a new pet shop, where he spied a fish without eyes. He began thinking about how it lived guided by its other senses. The encounter eventually led Popper, now a bioacoustician at the University of Maryland, College Park, to become one of the world's pioneers in understanding how fish perceive and respond to sound. "If I hadn't walked by that shop that day," he says, "I'd have a different life."

Today, Popper's professional life is defined by sound. Among bioacoustics researchers, he's widely known for the classic drawings of fish ear anatomy he produced as a young scientist and for co-editing a series of influential books that colleagues say has helped shape the growing field. Popper has also conducted innovative studies that have documented the effects of human-generated sound on fish and raised questions about the science underpinning government regulations designed to protect sea life from industrial noise. "I knew he was going to be successful as a scientist," says sensory biologist William Tavolga of the Mote Marine Laboratory in Sarasota, Florida, who oversaw Popper's doctoral work. "But there was no predicting the huge amount of work he's done and the quality of work."

And now that the irrepressible 69-year-old researcher is preparing for retirement, colleagues are wondering if anyone can take Popper's place—and whether he'll actually slow down. "I'm amazed at the energy of the guy," says marine biologist Robert Gisiner of the U.S. Navy's Energy and Environmental Readiness Division in Washington, D.C. "He could just run me into the ground and I'm 10 years younger."

An unanswered question

When Popper was growing up in New York City in the 1950s, many people still shared the notion of a silent ocean, popularized by the explorer Jacques Cousteau. That view has profoundly changed. We now know that many marine animals use sound to find food, avoid predators, and communicate. And humans have added their own cacophony: the thrum of ship screws, the blast of seismic air guns for oil exploration, and the concussive force of pile drivers used to build docks and bridges. Popper was one of the first to make the scientific community aware that humanmade noise could affect the behavior and health of animals other than marine mammals, says neuroethologist Darlene Ketten, who holds a joint appointment with the Woods Hole Oceanographic Institution and Harvard Medical School, both in Massachusetts.

As a graduate student at the City University of New York in the late 1960s, Popper initially wanted to focus on how blind fish determined where sound came from. "[It's] called sound-source localization," and the ability is considered to be one of the most powerful forces driving the evolution of hearing, Popper says. "Because if you just hear a sound and don't know where it's coming from, it's not worth hearing."

But sound bounced around in the fish tanks available to Popper at the time, making experiments impossible and forcing him to abandon his localization project. Even today, the question is hard to study, he says. "We know [fish] can localize sound, but how well and how they do it is still a mystery." Instead, Popper moved on to studying the hearing capabilities of Mexican blind cavefish (*Astyanax jordani*) and its eyed ancestor (*Astyanax mexicanus*). He discovered that these species had the widest hearing range yet measured in fish, and that blind cavefish didn't necessarily sense pressure stimuli better than their eyed relatives. After earning his doctorate, Popper ultimately landed jobs at the University of Hawaii, Manoa, and then at the Georgetown University School of Medicine in Washington, D.C., where he taught neuroanatomy.

In 1975, Popper learned scanning electron microscopy during a sabbatical, opening a new window into fish hearing. He used the skill to delve into the form and function of a fish's inner ear, mapping the orientation of hair cells and showing that fish can actually regenerate damaged ones.

"One of Art's biggest contributions was the anatomy he did on fish hearing," says longtime collaborator Anthony Hawkins, a bioacoustician and former head of fisheries research for Scotland. Researchers still use some of Popper's elegant, detailed drawings, he says: "We still don't know how it all works. But we have a lot of information on their anatomy."

Then, in the early 1990s, Popper began co-editing a series of books—called the Springer Handbook of Auditory Research (SHAR)—with his longtime friend and collaborator, fish-hearing specialist Richard Fay. There are now 45 volumes, and each is meant to aid investigators in understanding an area of hearing research they aren't necessarily experts in. Popper and Fay enlist

CREDIT: JANE J. LEE

Published by AAAS

specialists to cover topics as diverse as hearing in bats and music perception. "Hearing research has been changed by [the SHAR] series," Ketten says.

A hissy fit

In the last few decades, Popper has become known for figuring out how to conduct difficult experiments that examine how fish respond to sound both in the field and in the laboratory. One focus is understanding how the noise produced by pile drivers—widely used machines that pound supports for bridges and docks into bottom sediments—affect fish and other aquatic creatures that are protected by environmental regulations.

"When people do experiments with very loud sounds, [they] usually have to do it in the field because you can't simulate loud sounds in the laboratory," Popper says. That's because the volume is just too intense: For pile drivers, the sound can be louder than turning on a jet engine in a room.

But field experiments aren't easy. Piggybacking on construction projects while the crew tries to stay on schedule, for example, is less than ideal. And workers are not going to stop and wait while you get your fish into place, Popper says. As a result, past field trials had been "very weakly done, poorly controlled, by people who really don't understand how to evaluate the results of these experiments," he laments.

In 2004, he decided to see if he could bring the studies into a controlled lab setting after a frustrating consulting experience trying to determine safe noise thresholds for fish during pile-driving operations on the San Francisco–Oakland Bay Bridge in California. The trick was finding a device that produced the needed racket without deafening researchers.

The solution came from a colleague, mechanical engineer Peter Rogers of the Georgia Institute of Technology in Atlanta. As part of a Navy study of the possible health effects of loud underwater noise on divers, Rogers had built a machine that allowed scientists to study how high-intensity sounds affected the lungs of submerged rats outfitted with a kind of rodent scuba gear. Rogers modified the machine for use with fish, producing what Popper affectionately refers to as the "hissy fit," short for high intensity controlled impedance fluid-filled wave tube (HICI-FT).

It took about 2 years for Popper's lab to work out the kinks, but the machine now presides over a small room at the University of Maryland. A red metal frame supports a steel cylinder with 8.9-centimeter-thick walls, centered between two large shakers that vibrate, generating pressure waves akin to those produced by a pile driver. Tubes surrounding the HICI-FT draw away the enormous amount of heat generated by the shakers, and it perches on vibration isolation mounts to prevent it from shaking the entire building. Fish placed inside the chamber are exposed to sound levels they would experience if they were swimming up to 18 meters away from a pile-driving operation.

Several years ago, Popper and colleagues at the University of Maryland and the Pacific Northwest National Laboratory in Richland, Washington, started by giving juvenile Chinook salmon (*Oncorhynchus tshawytscha*) a hissy fit; regulators were interested in the experiments because the fish is an endangered species. They've since repeated the process with other species, including striped bass (*Morone saxatilis*) and lake sturgeon (*Acipenser fulvescens*).

Hearing capabilities. Fish hearing specialist Arthur Popper is not afraid to get dirty while trying to elucidate hearing sensitivity in walleye pollock.

CREDIT: DAVID MANN

The HICI-FT results, parts of which were published online June 2012 in *PLoS ONE*, show that the physiological effects experienced by the fish depend on the sound intensity and accumulated exposure. At lower sound levels, the pressure shifts caused by pile driving might cause minor blood vessels in fins to break and leak. Fish exposed to higher intensity sounds, however, could experience lethal and deafening injuries such as hemorrhaging of the heart and deflated or ruptured swim bladders. In some species, swim bladders both help fish regulate their buoyancy and conduct sound into the ear. Damaging the swim bladder could essentially renders species such as catfish hard of hearing. Popper and his colleagues also found that the sound thresholds needed to induce such trauma were higher than what people had previously thought. The take-home message, he says, is that the sound levels that regulatory agencies have been using as safety limits for fish are lower than necessary.

A working retirement

Although Popper would love to test other anthropogenic sounds fish encounter using the HICI-FT, it is headed back to the Transportation Research Board of the U.S. National Academies, which funded the device. It's just one loose end he's tying up as he prepares to retire in June 2013.

But even after taking his leave, Popper will have projects bubbling. This past June, for instance, he flew out to California to check on work he's started with tuna researcher Barbara Block of Stanford University in Palo Alto. Popper is helping train bluefin tuna (*Thunnus thynnus*) to respond to different sound levels in a bid to elucidate what the marine predators can hear. "It's the old operant-conditioning paradigm where the animal works for a food reward," he explains. The sleek animals have taken to the task, Popper hints, although he is cagey about the details since it's a work in progress. He's also helping plan a third international conference on the effects of noise on aquatic life, set for Budapest in August 2013. (He helped kick off the meetings in 2007.)

First, however, many of Popper's students and colleagues will gather in Florida next year to honor the researcher some call the "godfather" of their field. "Art is an amazing person all around and an excellent role model for anyone in science," Ketten says. Former students say that although Popper expected members of his lab to work hard, he also knew how to have fun, teasing lab members and colleagues. A few turn the tables: "Every now and then I threaten to take his Ph.D. away from him," says Tavolga, who was Popper's dissertation adviser. "But he says I can't do that because there's a statute of limitations."

–JANE J. LEE

Jane J. Lee is a writer in Washington, D.C.