Marine Environmental Laboratory in Seattle, Washington, boarded the ship.

Nevitt says Bates "was just being nice" in chatting with the injured interloper he discovered in the team's quarters. But Bates says he found Nevitt's olfaction problem interesting. "I told her that if I had to put a bet on [an oceanic] compound that had an odor, it would be dimethyl sulfide (DMS)," a gas given off by phytoplankton, microscopic plants that live in surface waters. He gave Nevitt a map of a DMS plume over Antarctica's Drake Passage, which showed that the compound concentrates over zones of upwelling and mixing, where the phytoplankton concentrate. "It changed the way I thought about the problem," Nevitt recalls. "I realized the birds were navigating through an olfactory landscape," complete with low-concentration valleys and DMS-rich mountain peaks. The tiny crustaceans eaten by the seabirds can also elevate DMS levels when they chow down on phytoplankton, providing a potentially solid food clue for the birds.

Sniffing out the good. European starlings use smell to find beneficial nesting material, but appear to lose that ability when breeding is done.

Nevitt was eventually able to document that several kinds of petrels and prions, another type of seabird, home in on DMS-laced vegetable oil slicks more often than odorless control slicks. But the preliminary findings, published in *Nature* in 1995, raised new questions. How, for instance, do the birds follow the changing gradients of DMS in the often turbulent atmosphere, where odor plumes can become fragmented? One possibility, she says, is that the odor cue prompts the birds to execute a search pattern, such as a broad turn, just as some salmon automatically swim against the prevailing current upon encountering a desirable odor. Over the next year, Nevitt and ornithologist Henri Weimerskirch of France's CNRS research agency in Villiers will look for such response patterns as they use satellites to track snowy petrels and other antarctic seabirds on their foraging trips. They will also block some birds' sense of smell to see if that alters the foraging strategy.

While petrels may follow their noses to food, chickens apparently call on olfaction to help them avoid eating bad-tasting insects. Guilford and colleagues have shown that chicks presented with bright, contrasting colors typical of insects that produce noxious odors won't reject the offering unless they can sense both odor and color. Such "multimodal" responses are also being studied by Lesley Rogers and colleagues at the University of New England in Armidale, Australia, who are using combinations of odors and colored beads. Related studies that monitor where olfactory stimuli are processed in the brain have also produced hints that chicks can develop "lateralized" olfaction, in which the right and left nostrils feed separate signals to the brain. In a kind of multitasking, cells in "the left nostril might be on the lookout for noxious odors, while the right is involved in something else," she says.

Other scientists are studying how chicken farmers might benefit from imprinting chicks on certain odors while they are still in the egg. Preliminary studies have shown that chicks exposed to odors in the final days of development—when tissue plugs melt out of nostrils and the chick begins breathing air that seeps through the eggshell—are attracted to the same smells after hatching. If the findings hold up, adding familiar odors to food and coops could improve production by reducing the stress the birds experience when confronted with new settings and foods, notes poultry scientist Bryan Jones of the Roslin Institute in Midlothian, United Kingdom.

And Nevitt speculates that olfaction studies might eventually influence conservation strategy too, by helping breeders of endangered birds provide the olfactory cues needed to get the young birds off to a good start. Rogers and others caution, however, that progress could be slow, because lab and field studies involving odors "are hellishly difficult to set up and control." Toucan experts, for instance, say figuring out whether real toucans use fruit odors in foraging could take years. But Guilford is upbeat about the prospect of learning more about how birds use smell. "There is plenty of room for speculation," he says, "and plenty more for experiments." –DAVID MALAKOFF

NEWS

Salmon Follow Watery Odors Home

Researchers are beginning to understand how salmon form the critical olfactory memories that guide them home from the sea to the streambeds where they hatched years before

While the smell of fresh-baked bread may pull us irresistibly down unfamiliar streets until we stand at the bakery door, that's about as much as we humans ever rely on olfaction to guide our travels. But for some animals, olfactory homing is a matter of life and death. Recent work has shown that some birds depend heavily on their sense of smell to find food and to navigate (see page 704). And salmon sniff their way back from ocean or lake to the streambed where they hatched, guided by an odor signature derived from the unique mix of elements such as plants, animals, and soils in their home stream and imprinted on their memory years earlier.

Homeward bound. Migrating salmon like these follow olfactory cues.

The survival of a salmon population depends on the fish's ability to return to their birthplace to spawn, because many of their physical and behavioral traits have been selected over generations for the survival advantage they provide in that particular stream. Now neuroscientists and fisheries biologists are learning just how salmon form the olfactory memories that guide them home. They are uncovering the physiological changes that prepare young salmon for olfactory imprinting and are finding out when in the animals' life cycles those changes occur. They are also gleaning clues to the biochemical basis of imprinting.

This work should help the management of salmon and their close relatives, though not necessarily of all fish that use olfactory homing. Some, such as lamprey eels, find spawning sites by sniffing out pheromones, an achievement that appears to be instinctive rather than learned.

Nevertheless, salmon represent an important and frequently threatened species, and conservation managers are eager to put the

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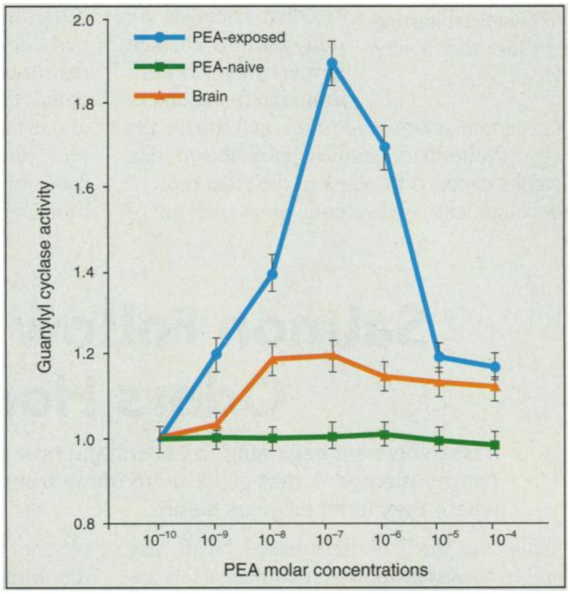
new information to use. "If the mechanism of olfactory imprinting could be clarified, this would definitely contribute to the [conservation] of valuable salmon resources," says fisheries biologist Hiroshi Ueda of Hokkaido University in Japan.

On the Pacific coast of the United States alone, salmon have been lost from 40% of their one-time range, and stocks are threatened or endangered in another 27%. To save endangered populations, conservation managers need to be sure that hatchery-raised fish imprint properly, to minimize their straying to other streams. "We need to get more mechanistic about it and figure out what is actually occurring during the development of these fish that causes them to home," says biologist Jeff Hard of the Northwest Fisheries Science Center in Seattle.



The makings of memory? The odor molecule PEA triggers much more cGMP production in olfactory neurons from salmon that were imprinted on PEA than in those from the "PEA-naive" fish that were not.

The first demonstration that salmon migrate based on odors learned in their youth came in the mid-1970s from Arthur Hasler's team at the University of Wisconsin, Madison. Graduate student Allan Scholz exposed hatchery-raised coho salmon to one of two odorant chemicals, morpholine or phenethyl alcohol (PEA), tagged the fish, and released them into Lake Michigan. Although the smells on which the fish imprint in nature are probably mixtures of odorants, Scholz's experiment proved one chemical was enough to guide them. Two years later, when it was time for the salmon to return to their native stream to spawn, Scholz spiked one stream near the release site with morpholine and another with PEA. Of the returning fish the researchers subsequently recovered, more than 90% were found in the stream spiked with the chemical to which they had been exposed.

The researchers then worked out when the fish were most susceptible to the imprinting. In the original experiments, Scholz had exposed the salmon to the odorant molecules when they were just over a year old, during a period known as smolting when the fish prepare to migrate and experience, among other things, a surge in thyroid hormone (TH). That surge proved crucial for imprinting. When Scholz gave younger fish a hormone to elevate their TH levels, those fish—which otherwise would not have been able to imprint—learned the odors.

That suggested that coho salmon find their way home based on olfactory memories formed at smolting time. But it didn't explain the behavior of another salmon species, the sockeye. Sockeye spawn in tributaries of lakes; a few months after hatching, the young fry swim to the lake, where they spend a year before smolting and heading to sea. When they return, they home in not just on the lake, but on the very tributary where they hatched—something they shouldn't be able to do if they imprinted only at smolting time. "That suggested there might be more than one period of imprinting," says Scholz, now at Eastern Washington University in Cheney.

In recent years, Scholz's group in Washington has identified that early period by working with a population of sockeye salmon in Washington's Columbia River system. The team found high TH levels in young fish shortly after hatching, and fish exposed to PEA or morpholine during that time chose to spawn in stream beds scented with the chemical to which they had been exposed.

While that work showed that TH primes the fish for imprinting, it left open the question of how a smell leaves its mark on the fish's olfactory system. In the late 1980s, Andrew Dittman and Gabrielle Nevitt, then graduate students at the University of Washington (UW) in Seattle, joined with behavioral ecologist Tom Quinn, also at UW, to seek the answer. Nevitt, working in the lab of UW electrophysiologist Bill Moody, recorded the electrical activity of olfactory receptor neurons from the noses of PEA-imprinted fish as well as from fish that hadn't been exposed to PEA. She found that, compared to controls, the noses of PEA-imprinted fish contained a higher fraction of PEA-responsive neurons, and those neurons had a heightened sensitivity to the compound.

In spite of the common view that all learning occurs in the brain, the discovery suggested that the fishes' olfactory memories consisted at least partly of changed neural responses in their noses. But, notes Nevitt, now at the University of California (UC), Davis, this form of learning does not seem to be unique to salmon: A team at the Monell Chemical Senses Center in Philadelphia found in 1993 that repeated exposure of mice to certain odorant chemicals increased the sensitivity of their sensory neurons to those odorants. And Robyn Hudson, a behavioral neuroscientist at the National University of Mexico, reported in 1995 that the olfactory neurons of baby rabbits have a heightened sensitivity to the odors of the foods their mothers ate while they were pregnant and nursing.

While Nevitt was doing her studies, Dittman, working in the lab of pharmacologist Daniel Storm at UW, found a clue to what might be making salmon olfactory neurons more sensitive to the smell of home. When he used PEA to stimulate neurons from imprinted fish, he found that the cells made more cyclic GMP (cGMP) than those from nonimprinted fish. cGMP is an intracellular messenger that helps transmit signals inside cells and might be influencing the responses of the olfactory neurons. But no one knows yet exactly how cGMP affects olfactory neurons, says Dittman, now a postdoc with John Ngai at UC Berkeley. To really understand the neural changes that underlie imprinting, Dittman wants to trace more completely how imprinting alters the signaling pathway by which an odorant binding to the olfactory receptor molecule causes the neuron to fire.

In Ngai's group, he plans to address that issue. David Speca, a graduate student with Ngai, recently developed a means to identify the olfactory receptor that responds to a particular odorant. "That now allows us to look functionally for a PEA receptor," says Dittman, "and then see how its expression or function is altered during imprinting."

If the approach works, it might yield information about the mechanism of imprinting that would provide a simple assay for telling when hatchery-raised fish have formed ample memories of their surroundings. That could be a big boon to those who manage salmon stocks and need to optimize the imprinting of hatchery fish so that they don't stray into the home beds of wild populations, threatening the wild gene pools. A gauge for imprinting would also help managers of captive breeding programs mounted as last-ditch efforts to save vanishing populations, by ensuring that the fish they release are properly imprinted. "Right now the only assay for imprinting is whether the fish come back 5 years later," says UW's Quinn. "If there were some assay to tell whether the fish have imprinted or not, that would be very useful." Indeed, for some endangered salmon populations it could be a matter of life and death. –MARCIA BARINAGA

SOURCE: A. DITTMAN *ET AL.*, *NEURON*