RIPPLE EFFECTS

How Lake Dwellers Control the Temperature and Clarity of Their Habitat

by ASIT MAZUMDER

IT WILL COME AS NO SURPRISE to anyone acquainted with nineteenth-century American literature that Henry David Thoreau had a fondness for lakes. In *Walden* he described one lake as the "earth's eye; looking into which the beholder measures the depth of his own nature." Thoreau's ocular metaphor was inspired by Walden Pond, near Concord, Massachusetts, where he began his well-publicized retreat in July 1845. He was quite taken with the pond, "remarkable," he wrote, "for its depth and purity." It also displayed a kaleidoscope of colors, "blue at one time and green at another, even from the same point of view." Nevertheless, "a single glass of its water held up to the light is as colorless as an equal quantity of air.... The bottom can easily be discerned at the depth of twenty-five or thirty feet."

Writing a century before the flowering of ecology, Thoreau could not have known that there was more to Walden Pond than met even his assiduous eye: ponds and lakes are complex communities of interacting living things—freshwater ecosystems—to which the clarity of the water, so vividly detailed in *Walden*, is of the utmost environmental importance.

To thrive freshwater ecosystems depend both on sunlight and on algae, microscopic plants that often live suspended in the water. Through photosynthesis algae convert light, carbon dioxide and water into oxygen and energy, which makes the plants invaluable to zooplankton and fish. Water-borne algae, however, process little of the available radiant energy; the remainder is scattered back into the atmosphere or is absorbed and stored as heat by the water itself. That heat storage profoundly influences the distribution of heat, or thermal structure, of a lake.

In this century investigators have learned a great deal about what shapes thermal structure. Most of their work has been focused on effects imposed by the external environment and on such so-called morphometric parameters of lakes as depth, volume and fetch, the distance over which wind blows across open water, creating friction and waves. But what has been virtually ignored in those studies is the feature that so impressed Thoreau at Walden: the clarity of the water, which goes a long way toward determining how deeply heat and light from the sun can penetrate the lake. And Thoreau's metaphor of a lake as the earth's eye has taken on a new, unexpected connotation.

In recent years much attention has been paid to the idea originated by the English atmospheric scientist James Lovelock according to which the earth is a kind of superorganism—the sum of its smaller, interdependent life-forms, which by competing for resources and habitats keep one another's populations in large-scale dynamic equilibrium. Life-forms on the earth have always, in Lovelock's view, modified the environment of the planet in profound ways. The fossil record, for instance, suggests that the oxygen concentration in the atmosphere has increased dramatically in the past three billion years as a result of photosynthesis by descendants of ancient cyanobacteria, or blue-green algae. Thus the physical circumstance in which life exists is to be seen as dictated not entirely by external factors to which life must simply adapt but also by opportunities and constraints of its own making.

Yet robust evidence for what has become known as Lovelock's Gaia hypothesis (after the Greek goddess of the earth) has been meager at best. Indeed, the Gaia hypothesis is so sweeping that some have called it unscientific: incapable of refutation or confirmation, an idea laced with more than a touch of the supernatural. What cannot yet be confirmed for the earth as a whole, however, can now be demonstrated in microcosm: through the earth's eye, so to speak. In field experiments in southern Ontario several colleagues and I have shown that the clarity and thermal structure of some small lakes are controlled not only by morphometric and other physical factors but also by the fish and plankton that inhabit those waters. Furthermore, within this restricted but nonartificial environment we were able to explore the complex feedback loops that occur between a community of organisms and the physical parameters of their surroundings. Although our studies certainly constitute no endorsement of the Gaia hypothesis, they are among the first to back up at least one of Lovelock's fundamental tenets: that nonhuman organisms actively shape their physical environment.

THE IDEA of thermal structure is well illustrated by lakes in southern Canada, where the sharp seasonal changes in temperature give rise to a diversity of thermal structures. In winter, of course, the waters are at their coldest. Come spring the ice cover melts and the water warms a bit; for a time, the water temperature remains the same from surface to bottom, usually holding at about forty degrees Fahrenheit. As spring gives way to summer, the uniform temperature gives way to rigid stratification, and the lakes separate into three layers: a warm, freely circulating upper layer called the epilimnion; the hypolimnion, a cooler, relatively stagnant zone near the bottom; and an intermediate layer of rapidly declining temperature known as the metalimnion, which, to a degree determined by its density, acts as a barrier between the top and bottom layers.

The thermal structure of a lake exerts a powerful influence over biological, chemical and physical processes throughout the ecosystem. To cite just one example, the diffusion of nutrients from the hypolimnion to the epilimnion can be reduced by thermal stratification—chiefly because of the density barrier at the metalimnion—resulting in a shortage of nutrients available for algal growth.

As sunlight passes through water, the light is attenuated by a combination of suspended particles, dissolved materials and the water itself. In colored lakes—those with high concentrations of dissolved organic matter, which tints the water—incident light can be largely absorbed. In contrast, algae in noncolored lakes either scatter light or absorb the photons into the chlorophyll, the green pigment responsible for photosynthesis. How much sunlight is absorbed by algae depends on the size and concentration of the algal cells. Small cells harvest light more efficiently than large ones because small cells have more surface area available for each unit amount of pigment, a phenomenon known as the package effect.

Water clarity can vary sharply from lake to lake, depending on the size and concentration of the algae. Lakes with dense populations of small algae tend to be eutrophic: they are murkier than lakes harboring large algal cells in similar concentrations. And lakes having few algae tend to be clear. Water clarity can be quantified by measuring the Secchi depth, named for the nineteenth-century Italian astronomer Angelo Secchi. A white disk, eight inches in diameter (a Secchi disk) is submerged in water; when the disk disappears from view, the Secchi depth has been reached. In lakes with high concentrations of small algae, the disk may become invisible at a mere three feet. Lakes with sparse or negligible algal populations may have Secchi depths of more than 130 feet.

ALGAL CONCENTRATIONS, and their consequences for water clarity, are largely a result of predator–prey relations, known as trophic dynamics or trophic-level interactions. The role of those relations in determining the clarity of ponds and small lakes was proved in the late 1950s, in studies conducted by the limnologist Jaroslav Hrbáček of the Czechoslovak Academy of Science. Hrbáček's experiments demonstrated that the clarity of water in a small lake can be altered by the changing patterns of fish predation.

As Hrbáček's work showed, organisms in aquatic systems can be usefully divided into four basic trophic levels, or functional groups. The first level is made up of photosynthetic algae, which capture sunlight and release oxygen, on which the other trophic levels ultimately rely for energy. The overall growth of algae depends on the supply of nutrients such as phosphorus. The second trophic level is the zooplankton—invertebrates, usually no more than one-tenth of an inch long, many of which feed and graze on the smaller algae. At the third level are small zooplanktivorous, or zooplankton-eating, fish such as yellow perch and sunfish. Finally, at the fourth level are the piscivorous, or fish-eating, fish including pike, walleye and bass, which prey on the zooplanktivores.

Traditional theories of trophic dynamics suggest that predators control the abundance of their prey. As piscivores increase in number, the population of their zooplanktivorous prey can be expected to decline. At the same time the reduction of zooplanktivores considerably improves the prospects for *their* prey, the zooplankton. And in the end a booming population of zooplankton will drain the lake of small algae. The reduction of the algal biomass can be mitigated if there is a particularly large supply of nutrients. But in most cases growing ranks of zooplankton—especially large zooplankton, which are

Max Ernst, The Frog Pond, *1956*

the most efficient grazers—will thin out the concentration of algae and so enhance the clarity of the lake.

People can be severely disruptive links in the aquatic food chain. Overfishing can bring about a dramatic increase in the concentration of algae and, thus, a sharp reduction in water clarity—thereby forcing tremendous perturbations in the ecosystem. The removal of piscivorous fish can foster an increase in the number of zooplanktivores, which eat up the large zooplankton. The depleted zooplankton are then dominated by the remaining small-bodied forms, which are poor grazers and cannot control the algal biomass. The algal population grows larger and denser. The overall effect is eutrophication of the lake, which people can exacerbate by adding algal nutrients such as phosphorus or nitrogen from domestic, industrial or municipal sources.

ONLY RECENTLY have studies shown that the size of individual algae, as well as the density of algal communities, exerts a powerful influence over the clarity of lake waters. In a 1980 article in the journal *Limnology and Oceanography* the limnologist W. Thomas Edmondson of the University of Washington in Seattle described a simple example to illustrate the relation. In a classroom demonstration Edmondson had displayed a flask of clear tap water, inside which was a small piece of chalk. When that chalk was ground into powder and added to the same quantity of water, the water turned turbid. Thus, although the mass of the chalk did not change, a rearrangement of the chalk particles from one large mass to many free-floating small masses made a striking difference in the amount of light that penetrated the water in the flask.

To demonstrate the same effect in nature I conducted experiments at Lake Saint George, a small lake outside Toronto, in late spring and summer of 1986 and 1987. My colleagues and I enclosed eight sections of the lake with polyvinyl walls, each twenty-six feet in diameter and fifty feet deep. We then removed all the zooplanktivorous fish from some of the enclosures and left the others alone. The removal of zooplanktivores—an act that mimicked excessive predation by piscivorous fish—allowed the large zooplankton to increase. In short order the thriving populations of zooplankton decimated the concentration of algae, especially the smaller algae. And with the decline of small algae came a marked improvement in the clarity of the water within the enclosures: at one point the Secchi depths of the enclosures without zooplanktivores were more than twenty feet—more than twice the Secchi depths of the enclosures with fish.

By clearing up the water we allowed more solar radiation to penetrate deeper into the lake, which raised temperatures sharply even at the top of the hypolimnion. As summer progressed, samples taken at different depths of the metalimnion—from thirteen feet to twenty-six feet—showed that the water temperature was from six to fourteen degrees Fahrenheit warmer in the enclosures without fish. And in due course both the heat content of the water and the depth of the epilimnion increased. By August, the final month of each four-month trial, the average heat content in the clearer enclosures was more than 25 percent higher than it was in the others. The epilimnion depth, meanwhile, was roughly fourteen feet in the enclosures without fish, compared with ten feet in the enclosures that still contained zooplanktivores.

LIMNOLOGISTS have long assumed that most of the heat in a lake, particularly at the lower depths, is transported there by wind-generated currents and turbulence. Decades of studies concurred that there is a high correlation between fetch, heat content and the depth of the epilimnion. As a result it was believed that the longer the fetch of a lake—meaning the more surface subject to the influence of the wind—the greater its heat content and the deeper its epilimnion. But in our studies each enclosure was the same size and was exposed to the same wind, sunlight and other climatic conditions. Hence the changes we observed in thermal structure could have been caused only by one variable: the extent to which, by manipulating the population of zooplanktivores, we altered the clarity of the water in the selected enclosures.

To further test this hypothesis we compared the clarity and thermal structures of two entire lakes, Saint George and Haynes, less than a mile apart. The two lakes are similar in appearance, but as ecosystems they contrast sharply, particularly in their relative numbers of zooplanktivorous fish. In Lake Saint George planktivores average 5,500 individuals a hectare, whereas in Haynes Lake the density is only about 100 individuals a hectare because of heavier predation by piscivores.

The numbers supported our results from the enclosure experiments. Water temperatures in the metalimnion were between eleven and twenty-three degrees higher in Haynes Lake; Secchi depths there averaged more than fourteen feet, compared with five feet in Lake Saint George; the heat content was as much as 40 percent higher in Haynes than in Saint George; and the depth of the epilimnion, about sixteen feet in Haynes Lake, was more than four feet greater than in Lake Saint George.

Those results contradict the traditional correlation between fetch, heat content and epilimnion depth. If wind-induced transport of heat associated with fetch were the principal force in regulating those factors in the two lakes, Saint George should have had a deeper epilimnion and higher heat content than Haynes because its fetch is twice as long. Precisely the opposite was observed.

In lakes, then, a change in the population of large predatory fish can alter the character of the entire freshwater ecosystem. For example, a boost to the stock of piscivores—which we simulated in our enclosure experiments—drains the lake of zooplanktivores, providing a boon to the large zooplankton that feed on the small, light-hoarding algae. When large zooplankton dominate, they tend to remove algae faster than the algae can reproduce—thus creating, through overconsumption, a potentially disastrous food shortage.

But there is a feedback mechanism: by reducing the biomass of algae near the surface of a lake, abundant large zooplankton improve water clarity. When a lake is clear, the sunlight can penetrate more deeply, which raises the water temperature and deepens the epilimnion. A deeper, warmer top layer opens up a new habitat, with plenty of light and a temperature high enough for algae to bloom at greater depths than they could when their numbers on the surface were high. So, although zooplankton can reduce their food supply in the upper waters, they can mold their environment in a way that stimulates algal growth elsewhere in the system, compensating, in many instances, for the loss of algae near the surface.

WHAT DOES the observation that organisms can influence their physical environment in this fashion imply for the understanding of ecosystems? Our experiments show that ecosystems are capable of homeostasis—the term coined in the 1930s by the American physiologist Walter Bradford Cannon to denote the tendency of living things to sustain a dynamic equilibrium with their changing environments. Homeostasis, which Cannon called the "wisdom of the body," pervades organ systems and cells. A familiar example is the sequence of responses of a mammal to cold: the temperature receptors in the skin are stimulated, causing peripheral blood vessels to constrict and body hair to become erect; further chilling activates the hypothalamus in the brain, which signals muscle tissue to start shivering and causes increased metabolism. Thus the body first increases its natural insulation, then produces more heat.

If, as our results indicate, freshwater ecosystems are endowed with a "wisdom of the body," the wider implications are hard to resist. Proponents of the Gaia hypothesis insist that the life-forms on the earth are to it as the cells and organs are to the body and that, like the body, the world practices self-regulation. Leaving aside the more dubious mysticism of Lovelock's theory, our evidence seems to be the first clear example, in microcosm, of those dynamics at work in a natural system.

The balance of organisms, of course, may be tenuous. When a lake becomes eutrophic, either because of changes in the distribution of fish or because of nutrient loading from outside sources, less heat is absorbed by the water. Consequently, more heat is lost to the atmosphere immediately above the surface of the lake. Much larger scale implications may follow from the fact that 71 percent of the surface of the earth is covered with water. It seems all too possible that widespread eutrophication could accelerate the already apparent trend toward global warming: more of the solar radiation impinging on the water surface will be scattered back to the lower atmosphere than will be absorbed. In a small Canadian lake life also seems subject to runaway circumstances in which the feedbacks no longer restore the system to its initial condition. Whether the larger world can sustain a precarious homeostatic stability, or is also subject to catastrophic runaway change, remains to be seen. ●

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