Epidemic this year? Check the lake's shape

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Baker Lake was one of the lakes featured in the survey of fungal epidemics in *Daphnia* populations. Credit: M.A. Duffy

Of all the things that might control the onset of disease epidemics in Michigan lakes, the shape of the lakes' bottoms might seem unlikely. But that is precisely the case, and a new *BioScience* report by scientists from Indiana University Bloomington and four other institutions explains why.

"In the paper, we go through several explanations for what is going on," said IU Bloomington biologist Spencer Hall, the report's lead author. "We are looking at the zooplankton that is infected, the fish and other creatures, the ecology, the limnology, and even the physics. Of all those explanations, the shape of the lake basins was the most powerful factor."

Also contributing to the report were scientists from the University of

Illinois at Urbana-Champaign, the National Science Foundation, the University of California at Santa Barbara, and the Georgia Institute of Technology.

"This paper is a synthesis of research on a model system for the study of disease ecology," said Alan Tessier, coauthor and program director in the NSF's Division of Environmental Biology. "It combines limnological, epidemiological, ecological and evolutionary perspectives to address a general question about the occurrence of epidemics in nature. It illustrates the value of interdisciplinary approaches to understanding the emergence of patterns in systems of complex biotic and abiotic interactions."

The disease in question is caused by a fungus that infects *Daphnia dentifera*, the water flea that plays a critical "grazer" role in many freshwater lakes of the American Midwest. Recent research by Illinois biologist Carla Cáceres, Hall and others shows the epidemics usually start in late summer or early fall.

The fungus slowly consumes the tiny crustacean's blood (hemolymph) and produces spores that fill all that remains. For the fungal spores to make it to the next potential host, the *Daphnia* host's exoskeleton must be opened -- and it must be opened in an area where the spores are exposed to living, uninfected *Daphnia* dentifera. Whether that happens effectively each year can be predicted by ascertaining whether the lake bottom is v-shaped, with gently sloping sides, or u-shaped, with walls that descend rapidly away from shore.

The topography of lake bottoms has profound consequences for the lakes' ecology and movement of water that is driven by surface and subsurface temperatures.

"Gravity currents," which are induced by changes in water temperature, are almost completely invisible to the naked eye. Introducing dyes (orange) can illustrate motion. Cold-induced gravity currents typically move downward from a lake's near-shore waters. When the currents reach water of equal temperature, they move inward toward a lake's center (rightward in the image). Credit: A. Parsons-Field

U-shaped lakes have less near-shore nursery areas, and likely as a result, bluegill fish populations tend to be lower. Bluegill are a major *Daphnia dentifera* predator.

With fewer bluegill in u-shaped lakes, *Daphnia* tend to be larger, and larger *Daphnia* have a higher chance of eating spores and becoming infected. Fewer bluegill also means more *Chaoborus*, an invertebrate that is also eaten by bluegill -- and that also eats *Daphnia dentifera*.

Unlike bluegill, which tends to eat *Daphnia dentifera* cleanly and excrete a heavy spoor that quickly sinks to the lake bottom (and probably out of the ecological picture), *Chaoborus* are "messy" eaters that chew up *Daphnia* and spit quite a bit of the exoskeleton -- and spores contained in it -- back out. This invertebrate predator, then, spreads spores of the parasite and catalyzes epidemics.

With the scene set, all that's needed, Hall said, is a beginning.

"Physics gets the epidemic going," Hall said. "*Chaoborus* keeps it going."

As evening air and/or late summer storms cools the near-shore waters of u-shaped lake basins, the water sinks until it reaches water of similar temperature, at which point the waters move away from shore. This creates a water flow, bringing nutrients (and latent spores) from shore out to the middle of the lake, where more *Daphnia dentifera* and *Chaoborus* live.

Daphnia dentifera filter feed, ingesting some spores. *Chaoborus* eats the water fleas, breaking some husks and spewing spores into near-surface waters. Some of the spores may sink to the lake bottom and out of the picture, but during the day, the warmth of summer and fall air keeps the near-surface waters turbulent and that creates a churning effect. Some spores are pulled upward and remain available for *Daphnia dentifera* to eat. Spore-containing waste produced by *Chaoborus* and bluegill near shore can re-feed the system in subsequent evening, as cool air drives shore waters back to the lakes' centers.

"We hypothesize that spores are pulled out to the water column by these flows, called 'gravity currents,'" Hall said. "Several physical factors inhibit gravity currents in v-shaped lakes."

This image shows two *Daphnia dentifera* that are infected with the fungus *Metschnikowia bicuspidata* (from the top, first and third), and two that are uninfected (second and fourth). The darker areas of infected *Daphnia* (body and head) are where fungal spores have collected. Credit: A.J. Tessier

Hall and his coauthors argue that fungal disease epidemics infrequently occur in v-shaped lakes because dense bluegill populations prey intensely on both infected *Daphnia dentifera* and *Chaoborus*. High predation intensity inhibits production and spread of infectious spores, thereby damping spread of epidemics.

"The system is really interesting, but this research also gets at a bigger issue -- how do the basic features of habitats drive major biological phenomena?" Hall said. "Understanding the relationship between the spatial aspects of a habitat and what happens within them will be a major focus of future study."

The scientists also considered six other basic mechanisms behind fungal disease. These included links between phosphorus and host density, nutrition of algal resources for hosts, and genotype differences between the hosts of u- and v-shaped lakes. All of these were rejected based on the evidence. Selective predation by bluegill, sloppy predation by *Chaoborus*, *Daphnia* body size, and gravity currents were supported, and all four of these mechanisms were influenced -- or controlled -- by lake basin shape. The scientists also found a possible relationship between epidemic likelihood and the density of another *Daphnia* species, D. pulicaria, but confirmation requires more study.

More information: "Why are Daphnia in Some Lakes Sicker? Disease Ecology, Habitat Structure, and the Plankton," BioScience, v. 60 no. 5, by Spencer R. Hall et al

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