The SCIENCE behind the Story

Determining Zebra Mussels' Impacts on Fish Communities

When zebra mussels appeared in the Great Lakes, people feared for sport fisheries and estimated that fish population declines could cost billions of dollars. The mussels would deplete the phytoplankton and zooplankton that fish depended on for food, people reasoned.

However, food webs are complicated systems, and disentangling them to infer the impacts of any one species is fraught with difficulty. Thus, even after 15 years, there was no solid evidence of widespread harm to fish populations.

So, aquatic ecologist David Strayer of the Institute of Ecosystem Studies in Millbrook, New York, joined Kathryn Hattala and Andrew Kahnle of New York State's Department of Environmental Conservation (DEC). They mined data sets on fish populations in the Hudson River, which zebra mussels had invaded in 1991.

Strayer and other scientists had been studying aspects of the community for years. Their data showed that after zebra mussels invaded the Hudson:

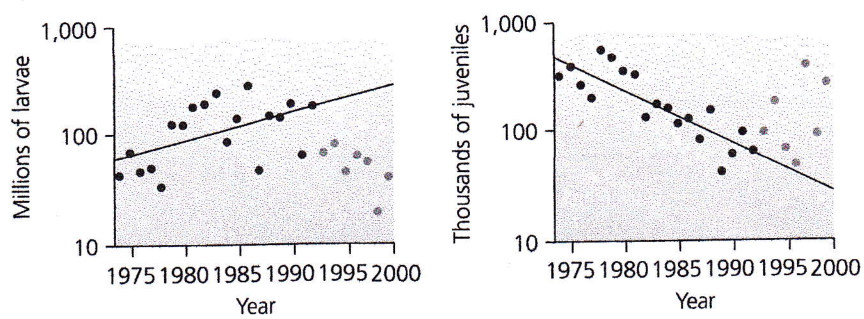
- Biomass of phytoplankton had fallen by 80%.
- Biomass of small zooplankton had fallen by 76%.
- Biomass of large zooplankton had fallen by 52%.

Dr. David Strayer, Institute of Ecosystem Studies, sampling aquatic invertebrates

Zebra mussels increased filter-feeding in the community 30-fold, depleting phytoplankton and small zooplankton and leaving larger zooplankton with less phytoplankton to eat. Overall, the zooplankton and invertebrate animals of the open water (which are eaten by open-water fish) declined by 70%.

However, Strayer had also found that *benthic*, or bottom-dwelling, invertebrates in shallow water (especially in the nearshore, or *littoral*, zone) had increased notably, because the mussels' shells provide habitat structure and their feces provide nutrients.

These contrasting trends in the benthic shallows and the open deep water led Strayer's team to hypothesize that zebra mussels would harm open-water fish that ate plankton but



(a) American shad **(b) Tessellated darter**

Larvae of American shad **(a)**, an open-water fish, had been increasing in abundance before zebra mussels invaded (red points and trend line). After zebra mussels invaded, shad larvae decreased (orange points). Juveniles of the tessellated darter **(b)**, a littoral fish, had been decreasing in abundance before zebra mussels invaded (red points and trend line). After zebra mussels invaded, they increased (orange points). SOURCE: Strayer, D., et al., 2004. Effects of an invasive bivalve (*Dreissena polymorpha*) on fish in the Hudson River estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 924–941. © 2004. Reprinted by permission of NRC Research Press.

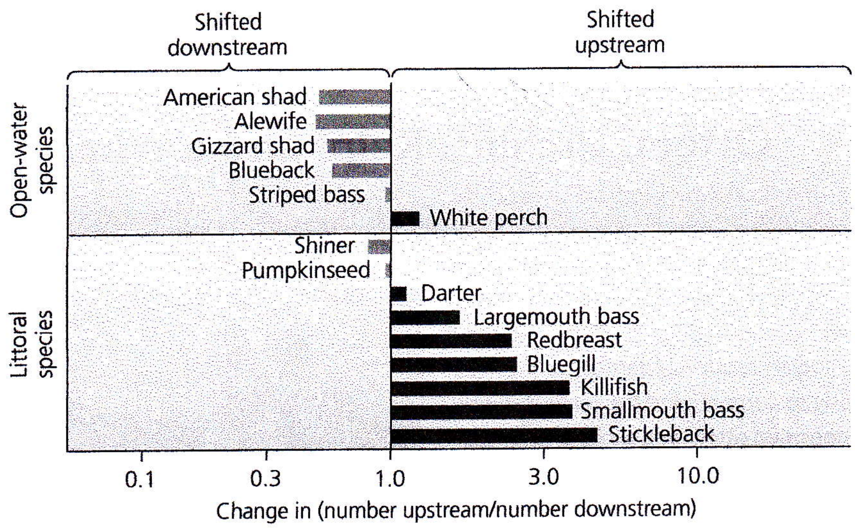
Animals at high trophic levels, such as wolves, sea stars, sharks, and sea otters (see Figure 4.13), are often viewed as keystone species that can trigger trophic cascades. However, other types of organisms also can exert strong community-wide effects. "Ecosystem engineers" physically modify the environment shared by community members. Beavers build dams and turn streams into ponds, flooding large areas of dry land and turning them to swamp. Prairie dogs dig burrows that aerate the soil and serve as homes for other animals. Ants disperse seeds, redistribute nutrients, and selectively protect or destroy different insects and plants within the radius of their colonies. And zebra and quagga mussels alter the communities they invade by filtering plankton out of the water.

Less conspicuous organisms and those toward the bottoms of food chains may exert still more impact. Remove the would help littoral-feeding fish. They predicted that following the zebra mussel invasion, larvae and juveniles of six common open-water fish species would decline in number, decline in growth rate, and shift downriver toward saltier water, where mussels are absent. Conversely, they predicted that larvae and juveniles of 10 littoral fish species would increase in number, increase in growth rate, and shift upriver to regions of greatest zebra mussel density.

To test their predictions, the researchers analyzed data from fish surveys carried out by DEC scientists and consultants over 26 years, spanning periods before and after the zebra mussel's arrival. Strayer's team compared data on abundance, growth, and distribution of young fish before and after 1991.

The results supported their predictions. Larvae and juveniles of open-water fish, such as American shad, blueback herring, and alewife, tended to decline in abundance in the years after zebra mussels were introduced **(see first figure, part (a))**. Those of littoral fish, such as tessellated darter, bluegill, and largemouth bass, tended to increase **(see first figure, part (b))**.

Growth rates showed the same trend: Open-water fish grew more slowly after zebra mussels invaded, whereas littoral fish grew more quickly. In terms of distribution in the 248-km (154-mi) stretch of river studied, open-water fish shifted downstream toward areas with fewer zebra mussels, whereas littoral fish shifted upstream toward areas with more zebra mussels (**see second figure**). Overall, the data



Young of open-water fish, such as American shad, blueback herring, and alewife, tended to shift downstream toward areas with fewer zebra mussels in the years following zebra mussel arrival. Young of littoral fish, such as killifish, bluegill, and largemouth bass, tended to shift upstream toward areas with more zebra mussels. SOURCE: Strayer, D., et al., 2004. Effects of an invasive bivalve (*Dreissena polymorpha*) on fish in the Hudson River estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 924–941. © 2004. Reprinted by permission of NRC Research Press.

supported the hypothesis that the fish community would respond to changes in food resources caused by zebra mussels. The results were published in 2004 in the *Canadian Journal of Fisheries and Aquatic Sciences*.

As Strayer continues his research, he and his colleagues learn more and more. In 2008 they published a broader analysis of the Hudson's food web showing that although littoral species benefited from zebra mussels, the fact that the mussels clarified the water made littoral species more susceptible to variation in clarity due to sediment input at times of high water flow.

Strayer and others also recently showed that populations of native mussels and clams in the Hudson had crashed after the zebra mussel invaded (likely as a result of competition for food), but that starting in 2000, these native bivalves, instead of going extinct, suddenly stabilized and persisted at about 4–22% of their pre-invasion population sizes. Strayer's team has not yet determined the reason for this turnaround, but they suggested that perhaps the native species could continue to play a role in the community.

Research such as this can help illuminate the often obscure impacts that particular species interactions have on communities as a whole. In this case, the research may also help fisheries biologists to manage commercially and recreationally important fish populations in the Hudson River and other areas invaded by zebra mussels. ■

fungi that decompose dead matter, or the insects that control plant growth, or the phytoplankton that are the base of the marine food chain, and a community may change very rapidly indeed. However, because there are usually more species at lower trophic levels, it is less likely that any single one of them alone has wide influence. Often if one species is removed, other species that remain may be able to perform many of its functions.

Identifying keystone species is no simple task, and there is no universally accepted definition of the term to help us. Community dynamics are complex, species interactions differ in their strength, and the strength of species interactions can vary in time and space. **THE SCIENCE BEHIND THE STORY** (pp. 90–91) gives an idea of the surprises that sometimes lie in store for ecologists studying these interactions.