Invasive mussels regulate nutrient cycling in the largest freshwater ecosystem on Earth

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Biogeochemical cycles involve the fluxes of chemical elements within and among ecosystems. These cycles are complex, potentially involving interactions among hundreds of species as well as numerous physical processes. Organisms and physical processes can both move elements, such as nutrients, among different ecosystems and across habitats within an ecosystem. Lakes and oceans often have distinct, vertically distributed habitats, which are connected by biogeochemical fluxes. The open water (pelagic) habitat overlies the benthic (bottom) habitat, and chemicals such as C, N, and P are cycled within and between the two habitats by a multitude of processes. In addition, because they reside at low elevations in the landscape, aquatic ecosystems often receive considerable amounts of water and chemicals from their surrounding landscapes (their watersheds). The Laurentian Great Lakes of North America (hereafter, Great Lakes) collectively represent the largest freshwater ecosystem in the world, containing over 20% of Earth's surface freshwater. In PNAS, Li et al. (1) show that nonnative species of mollusks can regulate the P cycle of these socioecologically important ecosystems. Strikingly, these benthic animals, which reside in a narrow zone at the sediment–water interface, can regulate P cycling throughout the entire water columns of these enormous ecosystems.

Historically, biogeochemical cycles have been considered to be controlled by microbes as well as physical processes such as runoff, wind, and currents. Direct effects of animals on biogeochemical fluxes have been viewed as unimportant, compared to fluxes mediated by microbes, except in unusual circumstances (2, 3). However, many recent studies show that animals can be important in modulating biogeochemical cycles in a myriad of ecosystem types and at multiple spatial and temporal scales (4–6). Yet, the importance of "zoogeochemical" effects is quite variable among ecosystems. Within aquatic ecosystems, this paper by Li et al. (1) reveals the importance of animals, in this case a single genus of mussels, in regulating biogeochemical cycles at a spatial scale that is by far larger than any other study.

The zebra mussel, a species of bivalve in the family Dreissenidae, invaded the Great Lakes from Eurasia in the late 1980s and subsequently spread to many lakes and rivers across North America (7). Several years after the zebra mussel invasion, many ecosystems were subsequently invaded by the quagga mussel, a species in the same genus (*Dreissena*) as zebra mussels. Populations of dreissenid mussels can reach tremendously high levels, sometimes exceeding 10,000 individuals per square meter of lake or river bottom (7). These mussels reside on the lake or river bottom and filter overlying water, thereby trapping particles that they consume. In most ecosystems, the majority of particles filtered by dreissenids are phytoplankton, that is, algae suspended in the water column.

Some of the particles filtered by mussels are deposited onto the lake or river bottom as pseudofeces (particles that are filtered from the water but not ingested) or feces (Fig. 1). Mussels assimilate energy and nutrients from ingested particles, which they use for growth and reproduction. However, some of the nutrients they assimilate, such as N and P, are subsequently released as excretion (urine) rather than used for growth. Excreted nutrients are released in dissolved inorganic forms (e.g., N as ammonium and P as phosphate) that are directly available to phytoplankton. When abundant, dreissenids can greatly alter the fluxes of nutrients; in particular, they greatly increase the flux of nutrients from pelagic to benthic habitats (8).

Using ecosystem-level simulation models, calibrated with an abundance of lake-specific data, Li et al. (1) demonstrate the remarkable effect dreissenid mussels (hereafter, mussels) have on P cycling in the Great Lakes. These effects are striking and result from the high population densities achieved by these invaders. Mussels affect P cycling in two main ways: Their populations sequester massive amounts of P in their biomass, and they mediate a large flux of P between pelagic and benthic habitats. The biomass of

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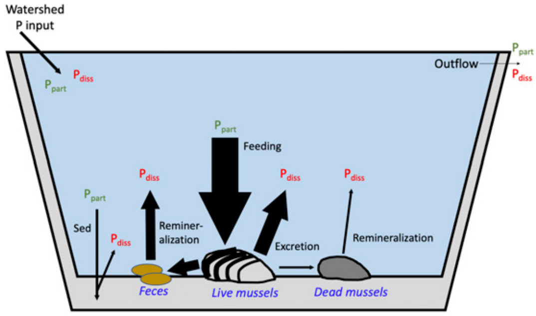

Fig. 1. Diagram illustrating the impacts of dreissenid mussels on P fluxes in the Laurentian Great Lakes, exemplified using fluxes from Lake Michigan as depicted in figure 4 of ref. 1. The widths of the arrows correspond to the magnitudes of annual P fluxes; for perspective, feeding represents the largest flux (36 Gg·y^{-1}) and the outflow (to Lake Huron) is the smallest flux (0.2 Gg·y^{-1}). P_{diss} = dissolved inorganic P, which is readily taken up by phytoplankton; P_{part} = particulate P, most of which is in phytoplankton cells; Sed = sedimentation of particulate P independent of mussels; some of the sedimented P is returned to the water column in dissolved form. "Feces" also includes pseudofeces. Mineralization of dead mussels includes dissolution of shells as well as decomposition of dead soft tissue.

zebra and quagga mussels now represents >90% of benthic animal biomass in four of the Great Lakes (all but Lake Superior), and while several native animals have declined since the invasion, dreissenid biomass greatly exceeds that of preinvasion native benthic animals. Perhaps even more impressive, within each lake these mussel populations contain in their bodies about as much P as the entire water column above them (1). This is truly remarkable when one considers that the mussels live in a thin zone about 10 to 20 cm thick on the lake bottom, whereas in both Lakes Huron and Michigan the mean lake water depth is >80 m.

Dreissenids also greatly alter biogeochemical cycling rates, in particular fluxes of nutrients between the water column and the benthos. In Lake Michigan, feeding by mussels represents a flux of P from the water to the lake bottom that exceeds natural sedimentation of particles by ~10-fold (Fig. 1). A little more than one-third of the P filtered by mussels is shunted to the sediments as feces and pseudofeces, and an even larger fraction is returned to the water column via excretion. Much of the P in feces is mineralized by microbes and subsequently released into the water column in dissolved form. The release of P by mussels into the water exceeds the preinvasion sediment-to-water P flux by about 10-fold and also exceeds P input from the entire lake's watershed by about eightfold. Thus, the fluxes of P into and out of mussel populations now dominate the P cycle of these lakes. Some of the P in mussel bodies is also returned to the water column after mussels die and decompose (Fig. 1).

Overall, dreissenid populations represent a net benthic sink for P, that is, they mediate a net P flux from the water to the benthos, especially when their populations are expanding, that is, after invasion. As a consequence, the steady-state mass of P in the water column is much lower in Lakes Michigan, Huron, and Ontario, where mussel populations are still expanding, than it would be in the absence of these invaders. Furthermore, because mussels now dominate P cycling in these lakes, the water column P mass is relatively insensitive to P inputs from the lakes' watersheds. These are very important findings, both for understanding lake ecology as well as ecosystem management. P inputs to these lakes from their watersheds have been declining, in part because of management efforts to improve water quality. The model of Li et al. (1) predicts that the mass of P in the water column will continue to decline in these lakes and reach an equilibrium much lower than that expected in the absence of mussels, even if watershed P inputs do not decline further. This is important because this P supports phytoplankton, zooplankton, and several fish species of economic importance.

In Lake Erie, which is warmer and more productive than the other lakes, and where mussels invaded earlier, the situation is more complex. Here, mussels attained very high biomass and sequestered a mass of P comparable to that in the entire water column, as is currently the case in the other lakes. However, the mussel population has declined in Erie over the past 10 to 15 y. Thus, the steady-state P mass in the water column is not so different from that expected in the absence of mussels. This raises the question of what we might expect in the future in the other Great Lakes. If mussel populations decline in these lakes, as they have in Lake Erie, the equilibrium P mass in the water column may not differ much from that in a mussel-free ecosystem. However, even if this is the case, it will take decades for the mussel-free P mass equilibrium to be restored; such a long transient period is relevant for lake management because it is longer than the generation times of aquatic organisms, including many economically important fish species. The unknown future dynamics of mussel population growth introduces a great deal of uncertainty for fisheries management strategies. Indeed, Li et al. (1) argue that the mussel-induced changes in P dynamics point to the need for a new paradigm of water management, one that explicitly incorporates mussel ecology.

Lake ecologists and managers have somewhat of a love–hate relationship with nutrients, including P. On the one hand, the production of economically important fish species depends on an adequate supply of nutrients to fuel algal primary production and energy flow up the food chain. On the other hand, excess nutrients cause harmful algal blooms, some of which can produce toxins that severely degrade water quality and are detrimental to human health. The Great Lakes face both ends of this issue: For example, the western basin of Lake Erie has blooms of toxic cyanobacteria every summer that are the result of P inputs from its highly agricultural watershed (9), while Lakes Michigan and Huron are experiencing declining algal productivity that may reduce fisheries' yields (10). Finding the optimal level of productivity, and hence nutrient supply, to maximize fisheries' production while maintaining water quality is a challenge under any condition. Adding on the effects of invasive mussels only complicates this endeavor and again points to the need for new management paradigms that not only account for "bottom-up" processes (effects of nutrients on algae and trophic levels that rely on them) and "top-down" processes (effects of predators such as lake trout or walleye on lower trophic levels) but also the complex ways by which animals such as invasive mussels regulate nutrient cycling.

Zoogeochemistry, that is, the modulation of elemental cycles by animals, is an emerging area in ecology, as more and more studies reveal the importance of animals. Yet, animals have not been satisfactorily incorporated into biogeochemical models or paradigms (2–5). The effects of animals on biogeochemical cycles may be most easily revealed by invasive species, because these species often become very abundant and play unique roles, facilitating the detection of animal-mediated effects (11). The extent to which native and nonnative invasive animal species differ in how they regulate biogeochemical cycles is an area that needs attention. Benthic animals, whether native or nonnative, can often have large effects on water column processes (12), but one would assume these effects to be greatest in small, shallow ecosystems because the volume of water is small relative to benthic area. Li et al. (1) show that benthic animals can regulate the P cycles of the largest lakes on earth. Whether or not these effects in large ecosystems are confined to invasive species or can be mediated by native species remains to be seen, but Li et al. (1) provide an excellent template for examining such effects, combining a rich dataset with robust models. Future studies would be wise to follow this approach.

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