Modeling invasive activity: Zebra mussels' infiltration of North American rivers

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The invasion of nonnative species has widespread and detrimental effects on both local and global ecosystems. These intruders often spread and multiply prolifically, overtake and displace native species, alter the intended interactions between flora and fauna, and damage the environment and economy. A particularly pesky invader is the zebra mussel (*Dreissena polymorpha*). Given its abundancy, fecundity, and heartiness, zebra mussels frequently outcompete native bivalves. Their dominance interrupts the natural cycle of nutrients and disrupts the structure and function of infested waterworks. These so-called "ecosystem engineers" generate substantial removal costs for individuals, corporations, and towns; estimates indicate that zebra mussels cause $1 billion in damages and control costs every year.

While some species can easily spread upstream in unidirectional river environments, not all invasive species are able to do so. In a paper publishing on Thursday, May 25th in the *SIAM Journal on Applied Mathematics*, Qihua Huang, Hao Wang, and Mark Lewis present a continuous-discrete hybrid population model that describes the invasive dynamics of zebra mussels in North American rivers. "We wanted to develop and apply a mathematical model to understand the interaction between population growth and dispersal, environmental conditions, and river flow in determining upstream invasion success of zebra mussels," Huang said.

Since its introduction to North America in 1986, the zebra mussel has invaded several large rivers, including the Mississippi, Hudson, Ohio, and St. Lawrence. "Rivers are key natural resources, and once zebra mussels invade the consequences can be disastrous," Lewis said. "Not only are the rivers themselves affected, they can spread the zebra mussels to new downstream locations." The mussels consume algae that is otherwise meant for native fish populations, and are considered unsafe for human consumption because they accumulate pollutants and toxins when filtering.

Three main phases—larvae, juveniles, and adults—characterize the mussel's life cycle. Larvae are planktonic, and drift through the water for a few days or weeks before setting on a surface and activating the juvenile stage. Upon sexual maturation in their second year of life, juveniles are considered adults and can reproduce once water temperatures are warm enough. "The larval life stage is relatively short compared to the zebra mussel lifespan," Huang said. "As a result, a model for the spread of zebra mussels in a river requires the introduction of different time scales." The authors chose to assume that settled larvae, juveniles, and adults all have the same survival rate.

Zebra mussels' survival in North American rivers is contingent upon a myriad of physical, biological, and chemical factors, including—but not limited to—water temperature, flow rates, salinity, turbidity, and pH levels. They are most heavily affected by unidirectional water flow, which shifts river sediment, sweeps mussel larvae downstream, and inhibits attachment to the benthos - the river bottom. "The dynamics of unidirectional water flow found in rivers can play an important role in determining invasion success," Huang said. "The alteration of hydrodynamic regimes associated with water management has direct effects on river ecosystem dynamics." As a result, it is difficult for zebra mussels to spread upstream in high flow rivers.

Because the zebra mussel has unusual dynamics, classical models do not suffice. Instead, the authors develop and employ a novel, impulsive, spatially-explicit population model. "In the model, the dynamics of the dispersing larvae stage are governed by an advection diffusion-reaction equation, while juvenile and adult growth are described by two difference equations that map the population density in the current year to the population density in the next year," Huang said. These equations combine the process-oriented population growth model with a hydrological model, based on available data about river flow dynamics.

Past researchers have proposed three measures of population persistence that reflect reproductive output of zebra mussels. The measures denote the fundamental niche of the population, the source-sink distribution, and the net reproductive rate (R_0)—the average number of adult mussels produced from a single adult throughout its lifetime. If $R_0>1$, a population will grow; if R_0