Twenty years of zebra mussels: lessons from the mollusk that made headlines

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In the 20 years since zebra mussels (*Dreissena polymorpha*) first appeared in North America, they have become one of our most widespread and abundant freshwater animals, and have fundamentally transformed freshwater food webs and biogeochemistry. Indeed, few human impacts on North American fresh waters have been greater or more far-reaching than the arrival of this single species. Nevertheless, ecological research has been uneven, and important research questions remain unanswered, especially concerning the long-term, large-scale effects of the invasion. Economic impacts have also been incompletely estimated, although they already exceed $100 million. We know little about the extent to which large outreach programs about zebra mussels have changed public knowledge, attitudes, or behaviors, and there are still substantial gaps in policies to curb the establishment, spread, and impacts of species like zebra mussels. Scientific, educational, and policy responses to the zebra mussel invasion highlight our successes and limitations concerning alien species in general.

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Since zebra mussels (*Dreissena polymorpha*) first appeared in North America in 1988 (Hebert *et al.* 1989; see Carlton [in press] for a precise chronology), the mollusk has become the iconic alien species. The appearance of zebra mussels, together with many other invaders, highlighted the absence of effective controls on alien species in North America, and helped to usher in an era of heightened awareness about alien species. Now that we have had two decades to observe zebra mussels in North America, this seems a good time to reflect on what we have learned from the invasion and how this illuminates advances and limitations in scientific understanding, management, and policy about alien species in general. Here, I will consider four important questions that were raised at the outset of the invasion (Roberts 1990): (1) How far would the species spread in North America? (2) What ecological and economic impacts would result? (3) Might this high-profile invader raise public concern about alien species? (4) Would we develop effective controls and policies to manage this and other alien species?

In a nutshell:

- Zebra mussels have spread widely across North America since they were first observed in 1988
- The ecological impacts of this highly invasive species are substantial and far-reaching
- The economic impacts of zebra mussels have not been fully estimated, but are far in excess of $100 million
- Research, public outreach, and policy responses have all failed to adequately address the problems caused by zebra mussels and other alien species

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Range and spread

Early predictions that the species would spread widely across North America (Strayer 1991) have been realized (Figure 1). This invasion has been well documented (USGS 2008); good information on the spread and current distribution of the species is readily available and widely used by the public and scientists alike. Similar databases are available for other high-profile invaders (NBII 2008; USGS 2008), but there are as yet no comprehensive databases on alien species in North America, and the distribution and spread of many alien species across the continent remain poorly documented.

The availability of good information on distribution has encouraged the development of models to predict the rate of spread and ultimate range of zebra mussels in North America. Gravity models have been especially useful in predicting the spread of zebra mussels (Bossenbroek *et al.* 2001, 2007; Leung *et al.* 2004). These models show that zebra mussels spread by both natural processes and human transport. Colonization of North America has proceeded through a combination of long-distance leaps (eg downstream through the Mississippi River basin, or overland into Lake Mead), medium-distance jumps (eg movement of mussels into inland lakes from the Great Lakes), and short hops (eg movement between the lakes within a regional lake district).

Spread has slowed in recent years as the most vulnerable bodies of water have been colonized (Johnson *et al.* 2006), but will presumably continue for many years, until the entire potential range is filled. This future expansion will extend range boundaries, but, more importantly, will fill in suitable habitats within these range boundaries. For instance, Johnson *et al.* (2006) estimated that < 5% of suitable inland lakes in the Great Lakes region were

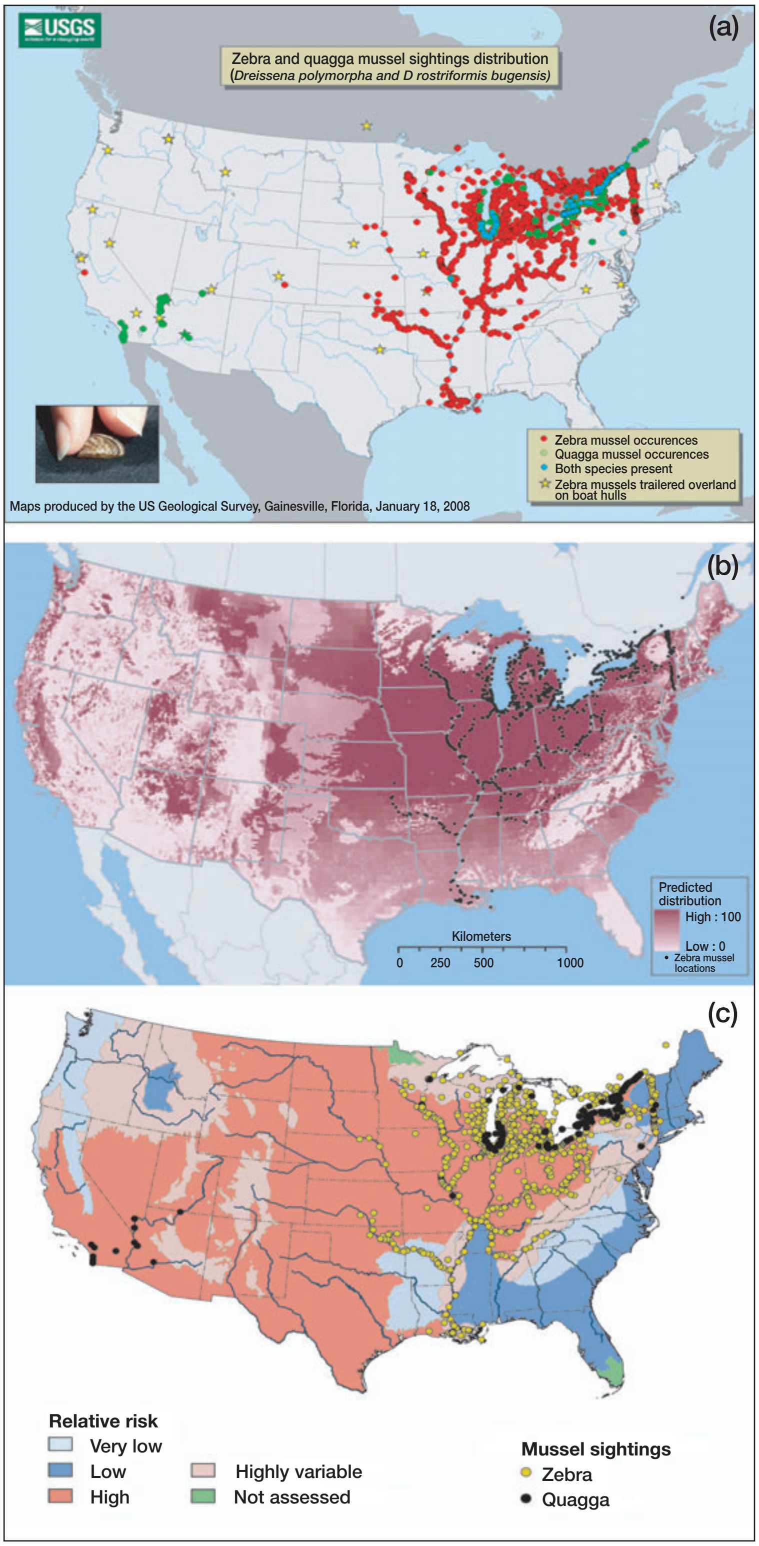

Figure 1. *(a) Distribution of the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*Dreissena bugensis*) in North America, as of January 2008 (USGS 2008; see Panel 1). (b) Potential distribution of* D polymorpha *in the US, based on climatic and geological variables (Drake and Bossenbroek 2004). Darker shades show higher likelihood of invasion, and dots show localities from which the species was known as of 2003. (c) Potential distribution of* Dreissena *spp in the US, based on dissolved calcium concentrations. Dots show sites where* Dreissena *spp had been observed as of October 2007. Reproduced from Whittier* et al. *(2008).*

invaded by zebra mussels by 2003. Human behavior will determine how quickly (or if) zebra mussels will spread to other lakes in the region.

Models of the potential range predict that zebra mussels will spread much further across North America (Strayer 1991; Drake and Bossenbroek 2004; Whittier *et al.* 2008), but, ultimately, they will be limited by extreme temperatures (both warm and cold) and inadequate calcium concentrations. The most recent models agree broadly in forecasting a wide range for zebra mussels in the East and Midwest, but disagree on how far the invasion will spread west of the Rockies (Figure 1). Despite these areas of disagreement, it seems likely that zebra mussels will not spread to calcium-poor waters (such as those found in most of New England and the Pacific Northwest), very cold waters (northern Canada), and very warm waters (much of the US Southwest). They will also probably not occur much in ponds and small streams (Strayer 1991; Bobeldyk *et al.* 2005).

These models are part of a great advance over the past 20 years in modeling the spread (Hastings *et al.* 2005; Lockwood *et al.* 2007) and ultimate ranges (Jeschke and Strayer 2008) of alien species. This progress has been supported by the increased availability of environmental databases and sophisticated statistical methods, and has provided much useful information to environmental managers and policy makers.

Ecological and economic impacts

The chief concern regarding the arrival of zebra mussels in North America was that they would have major economic and ecological impacts. Economic losses from the Great Lakes were forecast to be $4 billion in the first decade, and collapses of sport fisheries and native shellfish were predicted (Roberts 1990; Cooley 1991; Hebert *et al.* 1991). Recent scientific papers have confirmed that zebra mussels can have serious and far-reaching impacts. At the risk of oversimplifying, the arrival of zebra mussels caused planktonic food webs to wither and littoral food webs to flourish. Populations of phytoplankton and small zooplankton fell, often by > 50%, sometimes with subsequent irruptions of inedible or toxic phytoplankton (Vanderploeg *et al.* 2001; Effler *et al.* 2004; Raikow *et al.* 2004; Caraco *et al.* 2006). The loss of phytoplankton, in turn, substantially increased water clarity (Caraco *et al.* 1997; Effler *et al.* 2004; Zhu *et al.* 2006) and concentrations of soluble nitrogen and phosphorus (Caraco *et al.* 1997; Makarewicz *et al.* 2000; Effler *et al.* 2004), which, in some ecosystems, fueled increased production of rooted plants and attached algae (Caraco *et al.* 2000; Pillsbury *et al.* 2002; Zhu *et al.* 2006). Increases in littoral primary production led to increased populations of littoral animals (Strayer and Smith 2001; Strayer *et al.* 2004). Populations of consumers that depended on phytoplankton, such as benthic animals and large zooplankton, also fell sharply in many invaded ecosystems (MacIsaac *et al.* 1995; Pace *et al.* 1998; Lozano *et al.* 2001; Strayer and Smith 2001). In at least some ecosystems, populations of planktonic bacteria increased, perhaps in response to decreased grazing by zooplankton (Findlay *et al.* 1998). The shelter and food provided by dense zebra mussel beds fostered large local increases in benthic animal populations (Ward and Ricciardi 2007), whereas fouling and competition for food caused many populations of native bivalves to decline, sometimes to the point of local extinction (Ricciardi *et al.* 1998; Strayer and Malcom 2007).

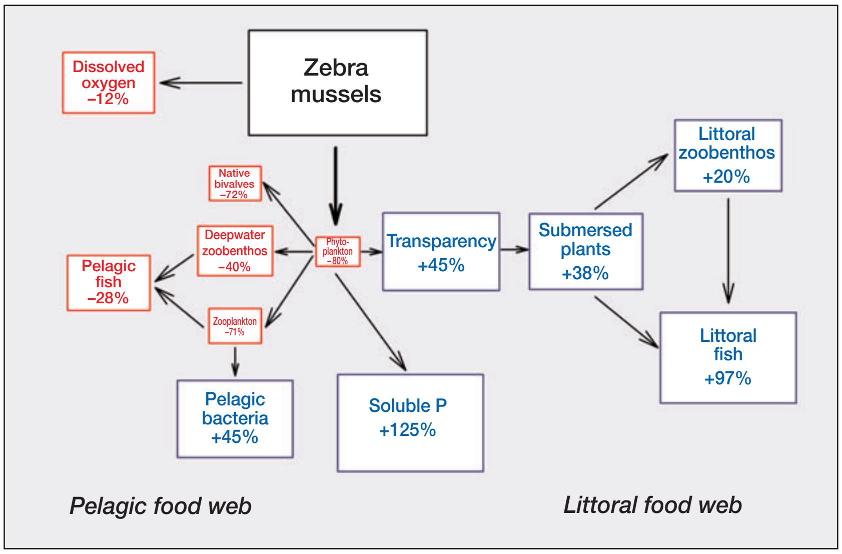

Figure 2. *Summary of the effects of the zebra mussel invasion on the Hudson River ecosystem. The area of each box is proportional to the change in each component that was associated with the zebra mussel invasion; blue boxes show increases, whereas red boxes indicate decreases. The response of submersed plants is based on net primary production, and the response of fishes is based on the median change in population size of young-of-year; responses of all other biotic components are based on biomass. Zoobenthos excludes bivalves. P = phosphorus. From Caraco* et al. *(1997, 2000); Findlay* et al. *(1998); Pace* et al. *(1998); Strayer and Smith (2001); Strayer* et al. *(2004).*

Zebra mussels also caused some important ecological effects that are perhaps less obvious than those discussed above. Remarkably, the respiration of some dense zebra mussel populations was great enough to substantially reduce dissolved oxygen in the water column (Caraco *et al.* 2000; Effler *et al.* 2004). Likewise, it appears that zebra mussels took up enough calcium (to build their shells) from the lower Great Lakes to reduce concentrations of calcium carbonate below the saturation concentration in the summer, thereby preventing episodes of calcite precipitation that reduced water clarity. This effect on water clarity was much larger than the effect of phytoplankton consumption by the mussels (Barbiero *et al.* 2006). Finally, changes in food web structure caused by invasion altered pathways of contaminant cycling as well (Morrison *et al.* 1998).

These changes were perhaps best documented in the Hudson River – a large, tidal river in eastern New York State – which was thoroughly transformed by the zebra mussel invasion (Figure 2). In the Hudson, and in many other North American lakes and rivers, the arrival of this single invader caused ecological changes that were as large and far-reaching as major human impacts such as eutrophication, acidification, altered hydrology, and habitat destruction.

Nevertheless, the ecological impacts of the zebra mussel invasion are incompletely understood, perhaps because ecologists have generally chosen to work on the most tractable questions, rather than the most important ones. In particular, research has focused chiefly on variables that respond quickly, can be studied at small spatial scales, and are easy to measure. This has led to important gaps in our knowledge. The responses of some important ecological variables take decades to play out. For instance, the transformation of sediments from mud or sand to shell-hash composed of zebra mussel shells, may profoundly affect the physical suitability of sediments as habitat for benthic animals, the stability of the sediment surface, and biogeochemical exchanges between lake water and sediments. Standing stocks of empty zebra mussel shells in the Hudson River are 34 g dry mass (DM) m^{-2}, with local aggregations as high as 2.7 kg DM m^{-2}

Panel 1. What's in a name?

Two similar species of *Dreissena* were introduced into North America in the 1980s. The zebra mussel (*Dreissena polymorpha*) is very widespread in North America (Figure 1) and Europe, and is by far the best known species of the genus. The quagga mussel (known variously as *Dreissena bugensis*, *Dreissena rostriformis*, or *Dreissena rostriformis bugensis*) currently has a more restricted distribution on both continents, and has so far established populations in North America only in the Great Lakes, the St Lawrence River, a rapidly spreading cluster of sites in the US Southwest, and a few quarries into which it was probably deliberately introduced (USGS 2008; Figure 1).

The two species are morphologically similar enough that they are difficult to distinguish, and are broadly similar ecologically. Nevertheless, there are differences between the species, the most important of which are the ability of the quagga mussel to thrive on soft sediments, in the deep water of lakes (eg Patterson *et al.* 2002), where it may have major ecological impacts, as well as its ability to displace the zebra mussel from such habitats.

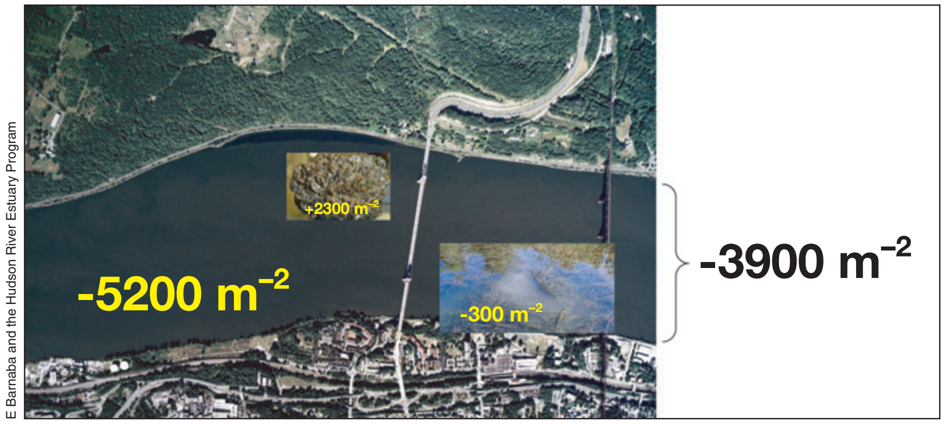

Figure 3. *Effects of the zebra mussel invasion on numbers of benthic invertebrates other than zebra mussels in three different habitats (beds of rooted vegetation, zebra mussel beds, and unvegetated sediments outside of zebra mussel beds) in the Hudson River (yellow numbers), and in the river as a whole (black number; Strayer and Smith 2001). The size of the picture of each habitat is proportional to its areal extent in the river. Although numbers of benthic invertebrates rose in zebra mussel beds, they fell in other habitats and in the river as a whole.*

(Strayer and Malcom 2006, and unpublished). Despite its potential importance, this process has not been addressed by ecologists.

Processes studied only at small spatial scales may give a misleading impression of the responses of larger systems. Many studies have shown that zebra mussels increase populations of benthic animals locally (Ward and Ricciardi 2007). However, the few studies performed at larger spatial scales show that the number of benthic invertebrates in the entire lake or river actually declines (Nalepa *et al.* 1998; Lozano *et al.* 2001; Strayer and Smith 2001), because declines in populations outside the zebra mussel beds outweigh any local increases within the beds (Figure 3).

Finally, some response variables have been avoided simply because they are difficult to measure or analyze, even though they are important. Perhaps the most striking example is the response of fish populations to the zebra mussel invasion, which was a central concern when zebra mussels were first discovered in North America (Roberts 1990; Cooley 1991), and was projected to consitute the largest part of estimated economic damages. Because the size, location, and condition (eg somatic growth rates, allometry) of fish populations are difficult to measure accurately, are highly variable, and are affected by factors other than zebra mussels, analyses of how the zebra mussel invasion has affected fish populations have been attempted only a few times. These analyses (reviewed by Strayer *et al.* 2004) suggest that zebra mussels have strong effects on fish populations in some ecosystems, but that the size and even direction of these effects vary across ecosystems and fish species, preventing any simple generalizations.

Surprisingly, the economic impacts of the zebra mussel invasion have also been poorly documented, although they are probably substantial and far-reaching. The cost to power plants and municipal drinking-water plants alone in North America during 1989–2004 was $267 million (Connelly *et al.* 2007b). The economic effects of the zebra mussel invasion on recreation, commercial fisheries, commercial shipping, and other activities seem not to have been studied at all. These effects have probably been large, and some (eg increased water clarity for recreation) may have been positive. Even more far-reaching economic impacts have occurred. For instance, city planners in Syracuse, New York, had hoped to rehabilitate the polluted Onondaga Lake by diverting sewage effluent from the lake into the Seneca River. However, the large population of zebra mussels that were established in the river consumed so much oxygen that the river became unsuitable as a site for sewage disposal, forcing city planners to consider other alternatives (Effler *et al.* 2004). In sum, we are far from having a full appreciation of the economic effects of the zebra mussel invasion, even though this was articulated as an important question at the very beginning of the invasion (Roberts 1990).

Although I have argued that scientific research on zebra mussels is far from perfect, the scientific response to the zebra mussel invasion (Figure 4) does show that rapid progress can be made when the attention of the scientific community is focused on a specific issue. This same conclusion applies to alien species research in general, where an enormous scientific literature (reviewed by Lockwood *et al.* 2007) developed over the past two decades has vastly improved both basic scientific understanding and management of alien species. This literature has shown that many alien species have had large, difficult-to-control ecological and economic impacts. Nevertheless, both the zebra mussel literature and the broader literature on alien species suffer from the same essential deficiencies. Questions that are important but difficult to answer have received inadequate attention; issues such as the broad economic impacts, or the long-term and large-scale impacts of invaders, have received very incomplete answers (Pimental *et al.* 2000; Strayer *et al.* 2006; Hawkes 2007). One might conclude that scientists and funders working on alien species have preferred to seek precise answers to small questions, rather than approximate answers to large questions.

Public understanding

Much effort has been expended on educating the public about zebra mussels and other invaders, via websites, brochures, wallet cards, lectures, newspaper articles, and other routes, in an attempt to slow the spread of these species. Consequently, zebra mussels probably have a higher public profile than any other freshwater invertebrate in North America. These educational campaigns must therefore be regarded as at least partially successful; for example, recreational users often provide the first reports of zebra mussels in newly invaded waters (Kraft 1993). Nevertheless, important challenges remain. Some members of the public still harbor naïve ideas about the benefits and dangers of moving zebra mussels and other alien species across the landscape. Recreational divers probably introduced zebra mussels into two lakes far outside their established range to improve water clarity for recreational diving. These new populations serve as nuclei for new infestations, far beyond the established range of the species, with consequent economic and ecological costs. However, a popular dive website still says "Zebra mussels are the best thing that ever happened to Dutch Springs" (one of these lakes; New Jersey Scuba Diver 2007), without any acknowledgment of the larger dangers of moving this species into uninfested regions. In addition, I frequently encounter recreational users (anglers, swimmers, boaters, birdwatchers, etc) who simply know nothing about zebra mussels and their impacts.

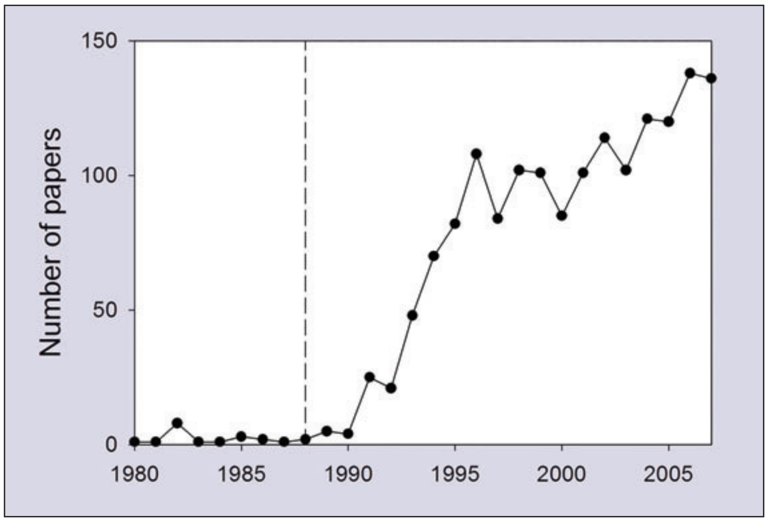

Figure 4. *Number of papers in* Web of Science *(search term* "Dreissena"*) as of January 24, 2008. The vertical dashed line represents 1988, when zebra mussels were first discovered in North America.*

Studies have confirmed that the public, policy makers, and even natural-resource managers may know little about even the highest-profile invaders (Connelly *et al.* 2007a). More disturbingly, we still have very little information about the extent to which various outreach tools have been successful in educating people about alien species, or motivating them to change their behavior. It is difficult to assess or improve the ultimate potential of outreach efforts in the absence of such vital information.

Finally, it is striking how often laypeople refer to the zebra mussel invasion as if it were an isolated and puzzling problem, rather than part of a broader environmental problem that has predictable causes, consequences, and cures. One hears about the "zebra mussel problem", the "snakehead problem", the "emerald ash borer problem", and so on. The public needs to understand that these are manifestations of a single problem – species invasions are an inevitable, predictable, and potentially controllable consequence of specific human actions and behaviors, not a long series of random, unconnected problems. Until such a time when the general public realizes this, it seems unlikely that they will contribute much to a general solution.

Controls and policy responses

Because zebra mussels foul water intakes and other infrastructure, there has been much interest in developing, testing, and applying various methods to control zebra mussels in contained settings around power plants, drinking water intakes, boats, and the like. Methods such as treatment with oxidants, flocculants, heat, dewatering, mechanical removal, and pipe coatings are now widely practiced (Crosier and Molloy 2002). Options for controlling zebra mussels in the more open settings of lakes and rivers are much more limited. Massive amounts (131 000 kg) of potassium chloride were applied to a small (5-ha), hydrologically isolated quarry in Virginia to eradicate a population of zebra mussels (Virginia Department of Game and Inland Fisheries 2008), but there are no prospects for eradicating or controlling this species in most open waters.

Public-policy response to the zebra mussel invasion has been substantial but ultimately inadequate. The alarming early predictions about zebra mussels led to a flurry of interest in implementing policies that would minimize the undesirable impacts of established invaders and prevent the arrival and establishment of new ones. Thus, the US government passed the Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 and its reauthorization as the National Invasive Species Act of 1996, and set up the Aquatic Nuisance Species Task Force (1990) and National Invasive Species Council (1999). These actions encouraged better management (eg ballast-water control), better interagency cooperation, and more research on alien species. In addition, zebra mussels were listed as "injurious" under the Lacey Act (whose shortcomings were addressed by Fowler *et al.* 2007), restricting interstate commerce in the species, even though this action was not taken until December 1991, after mussels had already established themselves in 10 US states and two Canadian provinces, and after options for meaningful control had already become limited. Despite the demonstration that ballast-water is an important pathway of introduction for the zebra mussel and many other freshwater and marine species (Ruiz and Carlton 2003), mandatory ballast-water controls were instituted for the US only in 2004, and allow for many

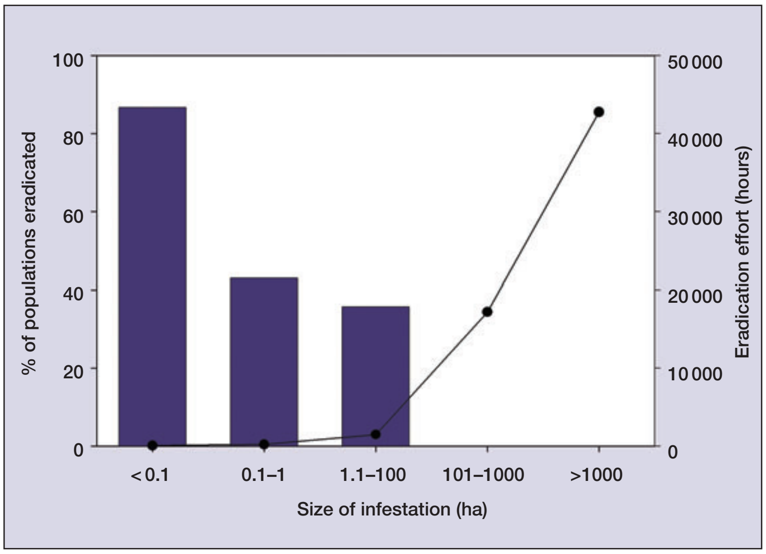

Figure 5. *Percentage of infestations of alien plant species in California that were successfully eradicated (vertical bars) and the amount of effort expended on eradication (black line), as a function of the area of the initial infestation. From data of Rejmánek* et al. *(2005).*

exceptions (Donohue 2007). Furthermore, recent research has shown that ships carrying only small amounts of ballast water ("no ballast on board" or NOBOB ships), now exempt from ballast controls, may nevertheless carry diverse communities of animals, algae, and microbes (Duggan *et al*. 2005). Current policies for ballast water in the US do not, therefore, protect our aquatic ecosystems from further invasions. We still do not have any coordinated system for the early detection and eradication of harmful invaders, despite evidence that control is often expensive and ineffective if we wait for the invader to become well established (Figure 5). More broadly, the current approach to alien species prevention and control in the US is still a patchwork of inadequate policies that are poorly coordinated; focused on species rather than vectors; slow; largely reactive rather than proactive; and does not meet the recommendations of experts on invasive species ecology and management (Lodge *et al*. 2006).

Conclusions

The zebra mussel lived up to early predictions that it would spread rapidly across North America, and thus has joined the long and growing list of alien species around the world with strong economic and environmental impacts. Its appearance in North America helped to give birth to the study of invasion ecology, now a major part of general ecology, and spurred public concern and policy on alien species. Nevertheless, the example of the zebra mussel suggests that invasion ecologists too often shy away from difficult but important research questions in favor of more tractable ones. Outreach has probably been effective in raising public awareness about zebra mussels and other alien species, although its ultimate effect on changing public behavior has not been well assessed. Alarm associated with the appearance of zebra mussels drove advances in control technologies and policies for better prevention and management of species invasions in the US, but much remains to be done before we have a coordinated and effective policy.

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