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Changes in global economies and trade: the potential spread of exotic freshwater bivalves

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Abstract The globalization of economies and trade have facilitated the spread of exotic species including the five most important freshwater suspension feeding invaders *Dreissena polymorpha*, *D. bugensis*, *Corbicula fluminea*, *C. flumi-nalis*, and *Limnoperna fortunei*. We suggest that the spread of these exotic species has not been a continuous process, but rather punctuated by periods of rapid long distance spread (jump), during which species greatly expanded their geographic ranges. Each jump has been associated with changes in the tempo of some human activity, such as the construction of shipping canals for trade, building of reservoirs for water storage and power production, political boundary changes or changes in political systems, which affected the position or permeability of national borders, human migration, changes in the mode and volume of international trade, or recent industrial practices and environmental laws. We hypothesize that the rate of spread of exotic species depends on the spatial scale of spread and may be accelerated or slowed by various human activities. In general, aquatic exotic species may quickly spread along connected waterways in a new continent they invade and soon reach their maximum range (continental scale). However, it will take much longer to colonize all isolated regions (regional scale) and longer still to spread to all isolated lakes and river systems (local scale). The difference in the rate of colonization across scales may be several orders of magnitude.

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Introduction

Historically, most European and American freshwaters lacked powerful benthic suspension feeders that attain high densities, have high growth rates, rapid recruitment, significantly alter the substrate (ecosystem engineers), and provide a direct link between benthic and pelagic components of an ecosystem. However, such species did exist in Asia, Africa, and small regions of south-eastern Europe, including the invasive *Dreissena polymorpha*, *D. bugensis*, *Corbicula fluminea*, *C. fluminalis*, and *Limnoperna fortunei*.

Due to human activities, especially international trade and the globalization of economies, these species have spread far beyond their native ranges, crossed oceans and colonized large regions within Europe, the Americas, and Asia. Increasingly, two or sometimes three species of exotic bivalves are found together, such as *Dreissena* and *Corbicula*, which have never overlapped in the past. In the future many freshwater regions around the globe may host up to five (or even more) non-native species that have large ecological and economic impacts (reviewed in Karatayev et al. 1997, 2002, 2005a; Ricciardi 1998; McMahon 1999).

The introduction of exotic species, including bivalve suspension feeders, has a long history, dating back at least to the Middle Ages. For example, the soft-shelled estuarine clam, *Mya arenaria*, most likely was introduced to Northern Europe from North America by Vikings in the 13th century (Strasser 1999). With an increase in international trade over the 19th and especially the 20th centuries, many more species have been introduced into different parts of the world (Mills et al. 1993a; Fofonoff et al. 2003). We contend that the spread of exotic species has not been a continuous process, but rather punctuated by periods of intense activity during which some species greatly expanded their geographic range (jump, Reid 1899). For five important freshwater invaders, *Dreissena polymorpha*, *D. bugensis*, *Corbicula fluminea*, *C. fluminalis*, and *Limnoperna fortunei*, each jump was associated with changes in the tempo of some human activity, such as the construction of shipping canals for trade, building of reservoirs for water storage and power production, political boundary changes and changes in political systems, which affected the position or permeability of national borders, human migrations, changes in the mode and volume of international trade, and recent industrial practices and environmental laws (Table 1).

The goal of this paper is to: summarize the principal factors that have facilitated the large-scale spread of exotic freshwater bivalves, summarize the potential or realized impacts of these invaders on freshwater ecosystems, compare their physiological or environmental limits, and predict their potential distribution and spread on a global and regional scale.

History of spread

Dreissena polymorpha (zebra mussel) is native to the fresh and brackish waters of the Caspian and Black Sea drainage basins (Mordukhai-Boltovskoi 1960; Starobogatov and Andreeva 1994). In the late 1700s to early 1800s, *D. polymorpha* spread through canals built for commerce to connect the rivers of the Black and Baltic Sea basins (reviewed in Starobogatov and Andreeva 1994; Karatayev et al. 2003a). After these canals were built, international trade increased considerably, and in 1824, *D. polymorpha* was found in London (Kerney and Morton 1970). By the first half of the 19th century there was intense ship traffic among all major European ports, and within a few decades *D. polymorpha* had spread to many western European countries, including the Netherlands (1826), Germany (1830), Belgium (1833), France (1838), and Denmark (1840) (Kerney and Morton 1970; Kinzelbach 1992; Starobogatov and Andreeva 1994). The zebra mussel invasion across Europe was rapid, and it was found as far as London within ~20 years. In 1986 *D. polymorpha* was discovered in the Laurentian Great Lakes in North America (Hebert et al. 1989). Once introduced, it spread rapidly throughout the Great Lakes and connected waterways including major rivers, and eventually invaded many inland lakes in both Canada and the United States (reviewed in McMahon and Bogan 2001). Although the initial spread of zebra mussels throughout most of Europe including

England occurred in the 1800s, *D. polymorpha* was not discovered in Ireland until 1997 (although it likely arrived in 1993/94; Minchin 2000) and Spain in 2001 (bij de Vaate et al. 2002).

A related species, *Dreissena bugensis* (quagga mussel), has a smaller natal distribution, limited to the Dnieper-Bug Liman (large coastal lake, connected to the Black Sea), and the lower reaches of the South Bug and Ingulets rivers, flowing into the liman (Andrusov 1897). Although *D. bugensis* colonized North America at the same time as *D. polymorpha*, in the mid 1980s (Mills et al. 1993b), *D. bugensis* did not follow the colonization of Europe by *D. polymorpha*. Although there was extensive ship traffic between areas inhabited by *D. bugensis* and other regions of eastern and western Europe through the middle of the 20th century, *D. bugensis* remained restricted to the Dnieper-Bug Liman and the lower reaches of the Southern Bug River. Only by the 1940s *D. bugensis* had spread throughout the Dnieper River and its tributaries and eventually colonized the Dniester River. By the 1980s it occurred in the River Don system (Russia) (Zhulidov et al. 2004), and subsequently in the early 1990s colonized reservoirs along the River Volga from its upper reaches to the Caspian Sea (Antonov and Kozlovsky 2001; Orlova and Shcherbina 2001). Finally, in 2002, adult *D. bugensis* were found in the Uchinskoe Reservoir, which provides drinking water for Moscow, and the following year in the Moscow River within the city of Moscow (Lvova 2004).

Corbicula fluminea (Asian clam) is native to southern and eastern Asia (eastern Russia, Thailand, Philippines, China, Taiwan, Korea, and Japan), Australia, and Africa, whereas *C. fluminalis* is native to Central Asia. In 1938 *C. fluminea* was found in the Columbia River, Washington (USA) and it subsequently spread throughout 36 continental states, Hawaii, and northern and central Mexico (reviewed in McMahon 1999). In the late 1970s both *C. fluminea* and *C. fluminalis* were introduced to Europe, and *C. fluminea* spread across France, Portugal, Spain, Germany, Belgium, the Netherlands (reviewed in McMahon 1999), and Hungary (Csanyi 1998–1999). In 1998 *C. fluminea* was found in Britain for the first time (Howlett and Baker 1999). The current distribution of *C. flumi-*

nalis includes France, Portugal, Spain (Araujo et al. 1993), the Netherlands (bij de Vaate and Greijdanus-Klaas 1990), Germany (Haesloop 1992), Belgium (Swinnen et al. 1998), Hungary (Csanyi 1998–1999) and Ukraine (Voloshkevich and Son 2002). In South America *C. fluminea* was reported simultaneously from Argentina (Ituarte 1981) and Brazil in the early 1980s (Veitenheimer-Mendes 1981), and in both cases the initial invasion was estimated to be around 1970. At present its range extends from northern Patagonia, around 39°S, to Uruguay and southern Brazil. It is very likely to be present in Perú and Bolivia as well (Darrigran 2002).

Limnoperna fortunei (golden mussel) occurs naturally in fresh and brackish waters of southern Asia, including China, Thailand, Korea, Laos, Cambodia, Vietnam, and Indonesia (reviewed in Ricciardi 1998). In 1965 *L. fortunei* colonized Hong Kong (Morton 1975), and in the late 1980s Japan (Magara et al. 2001). In the early 1990s it spread to South America (Pastorino et al. 1993), and is presently found in Argentina, Uruguay, Paraguay, Bolivia and Brazil (Darrigran 2002).

In addition to the species listed above, there are at least two other suspension feeding bivalves, the dreissenid *Mytilopsis sallei* and the mytilid *Modiolus striatulus*, that also have the potential to colonize freshwater systems (Morton 1979), and therefore could pose future threats as invaders around the globe.

Factors that facilitate the large-scale spread of exotic freshwater bivalves

Construction of shipping canals and reservoirs

For thousands of years, since the last glaciation, the geographic range of *D. polymorpha* was limited to the Black and Caspian Sea basins. In the 18th century the demand for Russian fire wood and other goods grew considerably in Western Europe. As a consequence, canals were built between the Dnieper and Zapadnyi Bug Rivers (1775), the Dnieper and Neman Rivers (1804) and Dnieper and Zapadnaya Dvina Rivers (1805), in Russia (what is now Belarus) to connect

Table 1 Factors that have facilitated the geographic spread of freshwater exotic bivalves *Dreissena polymorpha*, *D. bugensis*, *Corbicula fluminea*, *C. fluminalis* and *Limnoperna fortunei*

| Period	Factor	Result
Industrial revolution, 18–19th centuries	Construction of channels in Russia for trade with Northern Europe	Spread of *D. polymorpha* across Europe
Beginning of the 20th century (North America)	Extensive human immigration	*C. fluminea* brought into North America
20th century (Europe). Political borders erected between Eastern and Western Europe	Restricted trade between Eastern and Western Europe and changes to water quality	Restricted spread of exotic species between socialist and capitalist countries
20th century (Eastern Europe)	Controlled and subsidized economies	Commercial fishery spread *D. polymorpha* Construction of reservoirs allowed *D. polymorpha* to increase its densities *D. bugensis* colonized reservoirs in Ukraine and Russia
20th century (Western Europe)	Market economy	Expansion of recreational activity spread *D. polymorpha* (*D. polymorpha* found in isolated lakes in the Alps in the 1960s)
End of the 20th century (Europe). Collapse of the Soviet Union	Political borders much less restrictive to trade and commerce Increase in recreational activity in Eastern Europe	Increase in exchange of exotic species between Eastern and Western Europe Further spread of *D. polymorpha* to isolated lakes and river systems
End of the 20th century (Global Scale)	Increased international trade	*D. polymorpha* and *D. bugensis* established in North America *C. fluminea* and *L. fortunei* spread to South America *C. fluminea* and *C. fluminalis* established in Europe

shipping routes between the Black Sea and Baltic Sea basins (Zhadin 1946; Kinzelbach 1992; bij de Vaate et al. 2002; Karatayev et al. 2003a). *Dreissena polymorpha* followed the transport of goods by inland waterways during the beginnings of the Industrial Revolution (Kinzelbach 1992; Table 1). Although the spread of *D. polymorpha* to waterbodies connected through shipping canals was rapid, subsequent spread to isolated waterbodies was slower and affected by different factors, including political borders, economic systems (socialism vs. capitalism), recreation, and commercial activities (Karatayev et al. 2003a).

By the beginning of the 20th century, most of the countries in Eurasia with extensive trade and habitats suitable for colonization by *D. polymorpha* were invaded, thus further range expansion essentially ground to a halt. The assumption that trade-related transport was involved in the range expansion of *D. polymorpha* is supported by the fact that some commercially less active countries,

like Ireland, remained free of this invader until very recently. Increases in the leisure-craft industry, increases in the value of the Irish pound and removal of value-added tax in the 1990s probably provided the opportunity for zebra mussels to invade Ireland on used craft imported from Britain by truck and ferry (Pollux et al. 2003). Similarly, new trade routes, such as the Main-Danube canal, which opened for shipping in 1992, now provide important routes for other Ponto-Caspian species to migrate west (bij de Vaate et al. 2002).

There is a similar association between commercial ship traffic and the geographic range expansion of *L. fortunei* in South America. *L. fortunei* was first found in the Río de la Plata Estuary in 1991 (Pastorino et al. 1993). The Paraná River and its two major tributaries the Paraguay River and the Paranaíba River have intensive year-round boat traffic. *L. fortunei* spread rapidly in these rivers, around 250 km year^{-1}, traveling over
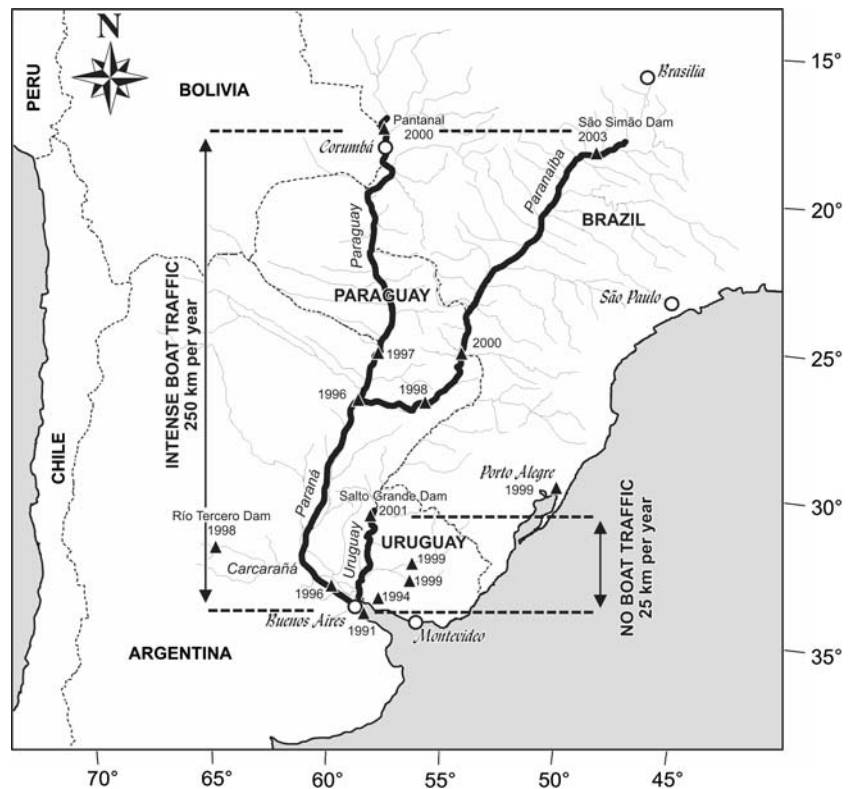
3,000 km in the 10 years since its initial invasion
(Fig. 1; Darrigan 2002). In contrast, along the
Uruguay River, which also feeds into the Río de la
Plata, but has very restricted boat traffic, the up-
stream colonization has been almost an order of
magnitude slower (Fig. 1).

While human built interbasin canals were
instrumental for the swift dispersal of *D. poly-
morpha*, the construction of reservoirs may have
led to the range expansion and invasion by
D. bugensis. Greater tolerance to siltation, low
oxygen conditions, and low temperatures allowed
D. bugensis to flourish in the newly constructed
reservoirs in the Ukraine, where it replaced
D. polymorpha as the dominant species in the
second half of the 20th century (Zhuravel 1967;
Lubyanov and Zolotareva 1976; Pligin 1979).
Similar patterns were observed in reservoirs in
the Volga River basin (Antonov and Kozlovsky
2001; Orlova and Shcherbina 2001) and in the
Laurentian Great Lakes, where *D. bugensis* col-
onized cold, deep areas of lakes and outnumbered
D. polymorpha (Dermott and Munawar 1993;
Mills et al. 1993b; Roe and MacIsaac 1997).

Dams can facilitate the dispersal of invasive
species not only through the creation of different,
more favorable, environmental conditions, but
also through the enhancement of recreational
activities, which are usually associated with river
damming projects. Around 2000 *L. fortunei* was
found in Argentina in the Río Tercero Reservoir
(D. Boltovskoy, pers. observation), which drains
into the Paraná River through the Tercero-Car-
carañá rivers, neither of which is navigable. This
reservoir is a popular tourist destination for
boating and fishing. It is quite probable that
L. fortunei was introduced by trailered boats
moved overland from the Paraná or Uruguay
rivers, paralleling the transport of *D. polymorpha*
into inland lakes in North America by recrea-
tional boaters (Padilla et al. 1996; Buchan and
Padilla 1999).

Human migrations and freshwater bivalves as
food

In North America, the first live *C. fluminea* were
found in 1938 in the Columbia River, Washington

(Burch 1944). *C. fluminea* is cultivated for food in Taiwan and Japan, and appears in Asian food markets. Thus, it is speculated that Asian immigrants brought this species to North America as a food source (reviewed in Britton and Morton 1979; Table 1). *Corbicula* continues to be shipped around the world for food, and the shipping of live *C. fluminea* from China has been suggested as one of the possible routes for the introduction of *L. fortunei* to Japan (Magara et al. 2001).

Political borders

The establishment of a socialist political system in Eastern Europe restricted trade with Western Europe, and led to the development of very different socio-economic regimes. As a result, different vectors were responsible for the spread of *D. polymorpha* in these two parts of Europe (Table 1). For example, what is now Belarus was divided between the USSR and Poland from 1922 to 1939, and the range expansion of *D. polymorpha* across this border was slow relative to the expansion that progressed once that border was removed (Karatayev et al. 2003a). Also, different transport mechanisms were responsible for the spread of *Dreissena* in Eastern and Western Europe, which had contrasting economies and social structures. In Western Europe leisure boat traffic was the major vector for the spread of zebra mussels to isolated lakes (Kinzelbach 1992), while in the Soviet Union commercial fishing spread *D. polymorpha* to isolated lakes (Deksbakh 1935; Karatayev et al. 2003a). In the Soviet Union fisheries were subsidized by the government, promoting increased fisheries activity, likely more so than in the west, which had no such subsidies. When the Soviet Union dissolved, the commercial fisheries subsidies stopped, and, as a consequence, commercial fishing activity declined rapidly. In the 1970s the commercial fishing industry included 230 Belarusian lakes, whereas in the 1990s only 119 lakes were exploited (Karatayev et al. 1999). Subsequently, recreational activities have become much more common and are now responsible for the spread of *D. polymorpha*, resulting in the colonization of many isolated lakes and lake systems that are used only for recreation (A. Karatayev and L. Burlakova, pers. observation). In the former Soviet Union *D. polymorpha* was also deliberately stocked into several waterbodies to improve the food supply for fishes and water quality (Karpevich and Lokshina 1965), or was accidentally introduced with other transplanted species (Sergeeva 1968, reviewed in Grigorovich et al. 2002). Some western European scientists also proposed using zebra mussel for water quality management (Reeders and bij de Vaate 1990; Reeders et al. 1993), and they were introduced into at least two small eutrophic ponds (Reeders et al. 1993).

Increased international trade in the 20th century

Increases in the wheat trade between North America and the former Soviet Union probably facilitated the introduction of *D. polymorpha* and *D. bugensis* into North America in the 1980s (Table 1). The Soviet Union suffered poor wheat harvests in the late 1970s, and became dependent upon foreign sources of grain. The United States initiated a grain embargo in 1980 to penalize the Soviet Union for its invasion of Afghanistan. During this embargo, although US trade dropped sharply, Canadian wheat trade with the Soviet Union increased dramatically, completely offsetting the US embargo (Webb et al. 1989). After 16 months and a change in American administrations, the grain embargo was lifted and wheat trade between the US and Canada and the Soviet Union increased (Webb et al. 1989). This dramatic increase in wheat shipments to the Soviet Union corresponds with the introduction of dreissenids into the Great Lakes. In addition, increased water quality in the Great Lakes in the 1980s made them suitable for zebra mussel colonization (Mills et al. 2003). Increased trade in the last quarter of the 20th century also accelerated the spread of other exotic bivalves: South America was colonized by *C. fluminea* and *L. fortunei*, and Europe was invaded by *C. fluminea* and *C. fluminalis*. Globalization of trade is now considered the primary driver of biological invasions in aquatic systems in general (reviewed in Ruiz and Carlton 2003b).

Recent industrial practices and environmental laws

Successful invasion depends upon the size of invader populations at their source as well as the ability of individuals to survive and successfully reproduce at their new destinations. Anthropogenic modification of habitats can increase or decrease both the likelihood that a potential invader is transported from a source area as well as the success of that invader once it is moved to a new region. For example, pollution can reduce abundances of or eliminate native species, allowing more tolerant invasive species to colonize (Den Hartog et al. 1992). Alternatively, improvement in water quality can facilitate invasion by improving environmental conditions for all life stages of the invader. Following their initial spread, zebra mussels were common through much of Eastern and Western Europe, however, as industrialization developed, pollution increased and some waters became unsuitable for *Dreissena*. Recently, environmental laws across Europe have restricted the dumping of pollutants and required the cleanup of major rivers. As a result of improved water quality, zebra mussels have reinvaded these rivers (bij de Vaate et al. 1992; Jantz and Neumann 1992; Burlakova 1998). Further improvements in water quality are expected with implementation of the European Union's Water Framework Directive, and we may therefore see continued recolonization of European waters by zebra mussels. Similarly, in North America many of the rivers and lakes currently invaded by zebra mussels previously would have been unsuitable. In the late 1960s and early 1970s the water quality of Lake Ontario was so degraded that many doubted it would be possible to restore this ecosystem (Mills et al. 2003). However, implementation of strict environmental measures resulted in rapid improvements in water quality. The subsequent improvement in water quality in all of the Laurentian Great Lakes and associated rivers has been correlated with a dramatic increase in the number of successful invasions by a wide range of taxa, including dreissenids, which are now important ecological factors driving dramatic changes in these systems, preventing restoration of the native communities (Mills et al. 2003).

Similar patterns may be seen throughout the world. Decreases in water quality are often associated with industrialization and dense human populations. These impacts on water quality may close the door to either the introduction of species or the donation of prospective invaders to other areas. Alternatively, strict environmental laws and improvements in water quality open the door to both donation and successful introduction of species. Recent political and economic changes in China have resulted in rapid industrialization and dramatically increased international trade. Simultaneously, water quality degradation and pollution have substantially increased (Morton 1988, 1989; Liu and Hills 1998). Although Chinese ports served as a source of invaders in the 1980s, as water quality decreases they are unlikely continue as sources of new invaders to other parts of the world. In the future, if there are environmental improvements that restore water quality, we may once again see increased invasion of species from China.

Ecological effects

The spread of exotic bivalves has the potential to alter freshwater ecosystems world wide. All five species discussed above are not only extremely aggressive invaders, often dominate water bodies they invade. They are very effective ecosystem engineers, altering both ecosystem structure and function (Phelps 1994; Karatayev et al. 1997, 2002, 2005a; McMahon 1999; Darrigran 2002; Sylvester et al. 2005). As suspension feeders, they may have similar effects on the ecosystems they invade (Figs. 2, 3). However, *D. polymorpha*, *D. bugensis*, and *L. fortunei* are exclusively suspension feeders and are byssate, requiring hard substrate for their attachment, while both species of *Corbicula* are infaunal and can either feed on suspended particles or remove organic matter from the sediments by pedal feeding. Thus, their overall ecosystem effects are likely to be different. Although more information is available for *D. polymorpha* (Fig. 2) than *D. bugensis* or *L. fortunei*, their impacts on freshwater ecosystems are likely to be similar. Ecosystem impacts are better known for *C. fluminea* (Fig. 3) than for
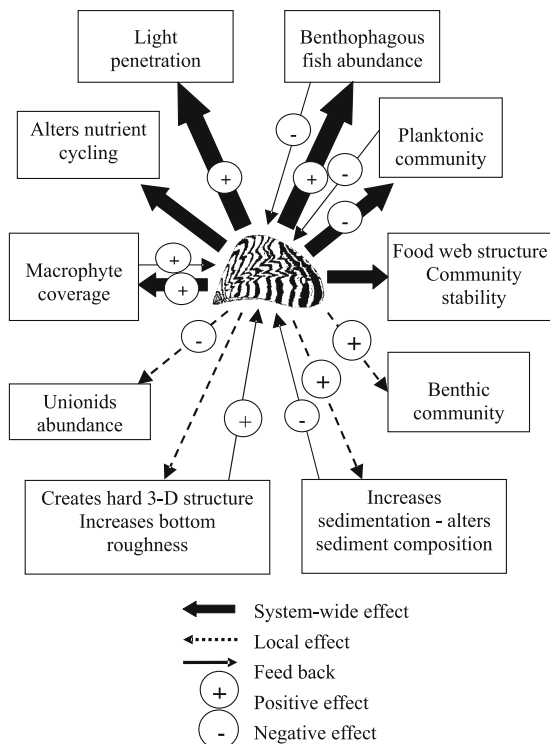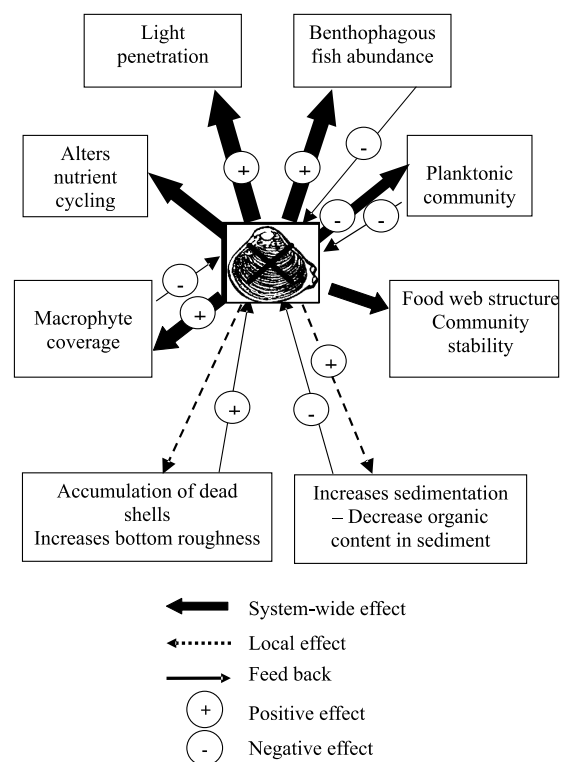
Fig. 2 Ecosystem impacts of *Dreissena polymorpha*

Fig. 3 Ecosystem impacts of *Corbicula fluminea*

C. fluminalis; because these two species are ecologically similar in most respects, their effects on ecosystems are also expected to be similar. In all cases, the impacts of these invaders will be most apparent locally and will depend on abundance. Although these bivalves are benthic, as suspension feeders they will impact planktonic communities, increase benthic–pelagic coupling, improve water clarity and compete with zooplankton for food. As ecosystem engineers they will have various impacts on habitat structure, biomineralization, oxygenation, and benthic and planktonic community structure (Morton 1997; Karatayev et al. 1997, 2002, 2005a; Darrigran 2002; Mayer et al. 2002; Vanderploeg et al. 2002; Mills et al. 2003; Burlakova et al. 2005).

Habitat requirements

Dreissena polymorpha

Subspecies of *D. polymorpha* have different salinity tolerances that range from totally fresh-

water to 18‰. The subspecies *D. p. polymorpha* that invaded Western Europe and North America, tolerates salinities <6‰ (reviewed in Karatayev et al. 1998). It tolerates temperatures from 0°C to 33°C, but does not grow or reproduce until waters reach 10–11°C (Table 2). *D. polymorpha* is restricted to waters with neutral or alkaline pH > 7.3 and calcium content >25 mg l^{-1} (Ramcharan et al. 1992; Burlakova 1999); also, it is sensitive to pollution. Extreme eutrophication has resulted in the extirpation of populations (Stanczykowska and Lewandowski 1993; Karatayev et al. 2003a). *Dreissena polymorpha* is intolerant of even moderate hypoxia and, although it may colonize the deep oxygenated areas of some lakes, it is usually restricted to the littoral and sublittoral zones (reviewed in Karatayev et al. 1998; McMahon 1999). Substrate availability affects the distribution and abundance of *D. polymorpha* within a waterbody (Zhadin 1946; Lyakhnovich et al. 1994; Karatayev et al. 1998). Although druses of *D. polymorpha* can be found on mud and silt when attached to shell fragments or other hard substrata (Berkman et al. 1998;

Table 2 Habitat characteristics and environmental limits of invasive freshwater bivalves

Parameter	Dreissena polymorpha	Dreissena bugensis	Corbicula fluminea	Corbicula fluminalis	Limnoperna fortunei
Upper salinity limit (‰)	6 (reviewed in Karatayev et al. 1998)	3.5 (reviewed in Lyakhnovich et al. 1994)	14–17 (Evans et al. 1979; McMahon 1999)	24 (Morton 1986)	15 (reviewed in Boltovskoy et al. 2006)
Lower temperature limit (°C)	0 (Luferov 1965)	0[a] (Orlova 1987)	0–2 (Mattice 1979; Rodgers et al. 1979; Janech and Hunter 1995)	0[b] (Volkova 1962)	0 (Choi and Shin 1985; Choi and Kim 1985)
Upper temperature limit (°C)	33 (reviewed in Karatayev et al. 1998)	31 (review in Karatayev et al. 1998)	36–37 (Dreier and Tranquilli 1981; Britton and Morton 1982)	No data	35 (reviewed in Ricciardi 1998)
Minimal temperature for reproduction (°C)	12–15°C (reviewed in Lvova et al. 1994)	5–7°C (Roe and MacIsaac 1997)	15°C (McMahon 1999; Rajagopal et al. 2000)	6°C (Rajagopal et al. 2000)	17°C (Morton 1977; Boltovskoy and Cataldo 1999)
Lower pH limit	7.3–7.5 (Ramcharan et al. 1992; Burlakova 1999)	No data	5.6 (Kat 1982)	No data	5.5 (Boltovskoy et al. 2006)
Lower calcium limit (mg l⁻¹)	25–28 (Burlakova 1999; Ramcharan et al. 1992)	No data	3 (Boltovskoi, D., unpubl.)	No data	3 (Boltovskoy et al. 2006)
Lower oxygen limit at 20°C (mg l⁻¹)	1.8–2.4 (Spiridonov 1972; Shkorbatov et al. 1994)	1.5 (Shkorbatov et al. 1994)	1–3 (Belanger 1991, at 25–30°C)	No data	0.5 (Boltovskoy et al. 2006)

[a] Found in the upper River Volga, which freezes in winter

[b] Reported from the Irtysh River, which freezes in winter

Karatayev et al. 1998), densities are usually highest on hard surfaces including rocks, sand, shells, and macrophytes.

Dreissena bugensis

Dreissena bugensis has a lower salinity tolerance than *D. p. polymorpha* (< 4‰) (Table 2). Its current distribution suggests a lower temperature limit similar to *D. polymorpha* (0°C). However, *D. bugensis* appears to be less tolerant of high temperatures than *D. polymorpha* (Dyga and Zolotareva 1976; Antonov and Shkorbatov 1990; Domm et al. 1993; Mills et al. 1996). In the Zaporozhskoe Reservoir (a cooling reservoir for a power plant in the Ukraine), quagga mussels can survive in waters ≤30.5°C (Dyga and Zolotareva 1976) while zebra mussels tolerate waters ≤33°C. *D. bugensis* also appears to grow and reproduce at lower temperatures than *D. polymorpha* (Dermott and Munawar 1993; Mills et al. 1993b; Roe and MacIsaac 1997). *D. bugensis* is more tolerant of low oxygen concentrations than the zebra mussel (Shkorbatov et al. 1994), which may be related to its lower respiration rate (Stoeckmann 2003). Also, quagga mussels may be much more successful colonizing soft sediments (reviewed in Mills et al. 1996). To our knowledge, there are no published data on pH or calcium limits for *D. bugensis*. Zhulidov et al. (2004) found higher densities of *D. bugensis* than *D. polymorpha* in waters with higher mineral and calcium content in Russian rivers, and suggested that this may indicate a difference in their calcium or mineral requirements.

Corbicula

Although more is known about the environmental requirements of *C. fluminea* than *C. fluminalis*, these two species differ in their tolerance and preference for certain physical characteristics of freshwaters (Table 2). *C. fluminalis* is more salinity tolerant than *C. fluminea* (Zhadin 1952), and can tolerate salinities ≤25‰ (reviewed in Morton 1986). The lower temperature limit for *C. fluminea* is 2°C (Graney et al. 1980; French and Schloesser 1996; Table 2), however they can be found in colder regions where they find refuge in waters heated by thermal power plants.

C. fluminea populations may expand out of these heated refugia as waters warm seasonally (Graney et al. 1980; French and Schloesser 1996). Janech and Hunter (1995) found a population of *C. fluminea* surviving temperatures as low as 0°C in the Clinton River, Michigan, suggesting a lower thermal limit for this species. Although there are no data on the lower temperature limit for *C. fluminalis*, this species is found in Siberian rivers, including the Irtysh River, which freeze over in winter, indicating that it can survive temperatures down to 0°C (Volkova 1962). *C. fluminea* can tolerate temperatures ≤36–37°C, and will grow and reproduce in waters warmer than 10–11°C. Although, there are no similar data for *C. fluminalis* (Table 2), it may grow and reproduce at lower temperatures. In the River Rhine *C. fluminea* released larvae from May to September at temperatures >15°C. In contrast, *C. fluminalis* reproduced during October–December and March–April, when water temperatures range from 6 to 15°C (Rajagopal et al. 2000). There are no published data on the pH limits for either *C. fluminea* or *C. fluminalis*, however, there is some evidence that *C. fluminea* is more tolerant of lower pH waters than *D. polymorpha*. *Corbicula fluminea* is found in Mosquito Creek (Florida, USA) where the pH is 5.6, which results in shell dissolution and may be a major source of mortality for clams over 3 years old (Kat 1982). *Corbicula fluminea* are intolerant of even moderate hypoxia (reviewed McMahon 1999) and therefore are usually restricted to the well-oxygenated littoral and sublittoral zones. As opposed to *Dreissena*, *Corbicula* is infaunal and does not attach to hard substrata. Therefore, sediments like sand, sometimes mixed with silt or clay, are best for *C. fluminea* (Belanger et al. 1985; Leff et al. 1990); they are much less abundant on rocks and in pure silt, especially where oxygen concentrations are low (Leff et al. 1990; Karatayev et al. 2003b). *Corbicula fluminea* is rarely found in sediments beneath submerged macrophytes (Karatayev et al. 2003b).

Limnoperna fortunei

In the Rio de la Plata estuary *L. fortunei* has been found at a maximum (bottom) salinity of 13.7‰

(at the time of sampling; D. Giberto, pers. communication) in an area where salinities can vary from 5 to 15‰ within a matter of hours (Guerrero et al. 1997; Boltovskoy et al. 2003). In the lower Paraná River and Río de la Plata Estuary, where population densities reach over 200,000 m^{-2}, surface water temperatures vary seasonally between 10 and 29°C (Boltovskoy and Cataldo 1999; Cataldo and Boltovskoy 2000), while in the upper Paraná River *L. fortunei* experience temperatures as high as 32–33°C. In Japan this species survives winter water temperatures of 5–6°C (Magara et al. 2001), and in Korea reproducing populations have been found in the Paldang Reservoir, which has winter surface water temperatures as low as 0°C (Choi and Kim 1985; Choi and Shin 1985). Thus, the lower thermal limit of *L. fortunei* appears to be similar to *C. fluminea* and *D. polymorpha*.

Unlike *Dreissena*, *L. fortunei* is tolerant of mildly acidic waters, and in contrast to both *Corbicula* and *Dreissena* it is tolerant of very low oxygen concentrations (Table 2). In addition, *L. fortunei* can withstand high organic loads and industrial pollution. In urbanized stretches of the Río de la Plata high densities of *L. fortunei* occur in areas polluted with raw sewage and runoff from storm water outlets (Boltovskoy et al. 2006). Near urban centers along the lower Paraná delta where *Limnoperna* thrives, waters and sediments contain many pollutants (e.g., Zn, Cr, Cu, benzo(a)pyrene, PCBs) at concentrations several times above those considered hazardous for aquatic life (Topalian et al. 1990; Villar et al. 1998; Cataldo et al. 2001a). Bioassays with juvenile *C. fluminea* indicate that these waters, pore waters and sediments are unsuitable for the survival of this bivalve (≥75% mortality in 144 h of exposure; Cataldo et al. 2001a, b).

Similar to *Dreissena*, *L. fortunei* requires hard substrata for attachment, and can attach to the roots of reeds and other aquatic plants. It can also be found on soft substrata, especially when bottom mud is compacted and covered by a thin hardened crust (Boltovskoy et al. 2006).

Potential for future spread

Predictions of the potential distribution (spatial extent or range) of exotic species can be made at different spatial scales of resolution. For example, on a global scale, the area of potential spread of freshwater bivalve invaders can be predicted based on habitat requirements and environmental limits set by climate factors such as temperature tolerance (minimum and maximum water temperatures for survival, reproduction, growth and larval development). On a local scale, other habitat parameters such as salinity, pH, and calcium content will determine whether a particular waterbody is suitable for colonization. Other factors such as oxygen content and substrate type govern the distribution of species within waterbodies. The hierarchy of spatial scales we consider here are:

- global scale—the whole potential range world wide
- continental scale—colonizable areas within a given continent
- regional scale—large drainage basins or countries (or states as in the USA)
- local scale—smaller units (districts, counties, local lake systems)
- waterbody scale—each colonizable waterbody
- habitat scale—each colonizable area within a waterbody.

Although the bivalves considered here differ somewhat in their temperature tolerances, there is considerable overlap among them, and all have wide temperature tolerances (Table 2). Based on thermal tolerance alone, all of these species have the potential to invade all continents except Antarctica, but none except *C. fluminea* has fully reached this potential. *Corbicula fluminea* can now be found across Eastern and Western Europe, North and South America, as well as its native continents of Asia, Africa and Australia. *Dreissena* is found across Eastern and Western Europe and North America, but has not yet invaded Asia, Africa, South America or Australia. *Limnoperna* is native to Asia and now also occurs in South America.

Even within continents where these species are native, there are large regions where they can be considered invaders, i.e., the entire continent cannot be considered their native range. Thus, they can be considered invaders when transported to these regions outside of their native range.
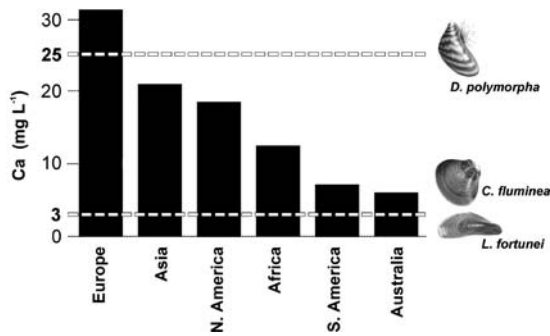
Fig. 4 Mean calcium concentrations in rivers on different continents (Wetzel 1975) and minimum calcium requirements for *Dreissena polymorpha*, *Corbicula fluminea*, and *Limnoperna fortunei*

Within different regions of continents where these species have invaded, they have rarely fully invaded all potentially habitable areas, and within regions, at the local and waterbody scale, most inland lakes and many small rivers are yet to be colonized. For example, *D. polymorpha* colonized Belarus in the beginning of the 19th century, but currently only ~17% of 553 lakes surveyed have been invaded (Karatayev et al. 2003a). In Ireland only ~60 of over 4,000 lakes are known to be colonized as of 2005 (D. Minchin, pers. observation). Similarly, although *C. fluminea* is currently found in 87% of the counties that have abundant surface waters in Texas, USA, it has colonized only 23% of all reservoirs with a surface area >0.1 km^2 (Karatayev et al. 2005b). In most cases, these species are far from colonizing all of their potential range or habitat.

Colonization of Asia and Africa by *Dreissena* has been expected (e.g., Starobogatov and Andreeva 1994), but high calcium requirements for establishing sustainable populations may curtail its spread (Ramcharan et al. 1992; Fig. 4). Most Australian and South American fresh waters have low concentrations of calcium, averaging 4 and 7 mg l^{-1}, respectively (Wetzel 1975). In contrast, many North American and most European freshwaters have calcium concentrations that normally exceed 20–30 mg l^{-1} (Wetzel 1975; Payne 1986; Fig. 4).

Limnoperna fortunei may colonize areas unfit for *D. polymorpha* due to their low calcium content. *Limnoperna fortunei* can be found in high densities in waters with calcium concentrations as low as 3–4 mg l^{-1}, such as the middle Paraná River (Maglianesi 1973; Table 2, Fig. 4). Thus, it is possible that in the near future *L. fortunei* will colonize North America, Europe, Africa, and Australia, and expand its range in South America and Asia.

On a global scale all of these species have the potential to overlap. However, within the same region, local area, or waterbody, each may be present where the others are less abundant or absent, thus avoiding competition. Where they overlap, species with similar habitat use will be expected to compete, such as waterbodies where both *Dreissena* and *Limnoperna* were to invade. As suspension feeders, under conditions of food limitation all of these bivalves have the potential to compete for food. Under some circumstances they may also compete for space, in particular species of *Dreissena* and *Limnoperna*, which attach to hard substrata. The extent to which competition will govern the coexistence of these exotic bivalves is currently unknown.

Several studies have predicted that *D. bugensis* may out compete *D. polymorpha* in Lakes Erie and Ontario (Mills et al. 1999; Baldwin et al. 2002). However, in Lake Erie, even in areas dominated by *D. bugensis*, *D. polymorpha* remains the dominant species attached to macrophytes, reflecting a habitat partitioning between these two species (Diggins et al. 2004). In several North American waterbodies *C. fluminea* coexists with *D. polymorpha* and *D. bugensis* (e. g., Lake Erie, A. Karatayev, pers. observation), although dreissenid mussels may have some negative impact on *C. fluminea*, whose valves serve as an attachment site for *Dreissena* (Lake Wawasee, Indiana, Lake Erie, A. Karatayev, pers. observation).

In Western Europe *C. fluminea* and *C. fluminalis* coexist with *D. polymorpha* (van der Velde et al. 1994; Rajagopal et al. 2000) and in South America *C. fluminea* is found with *L. fortunei* (e.g., Rio De La Plata; Villar et al. 1999). The coexistence of the two species of *Corbicula* in the River Rhine has been attributed to differences in reproductive strategies, reproductive periods, and possibly food preferences (Rajagopal et al. 2000).

Although *L. fortunei* can attach to and overgrow individual *Corbicula*, they typically colonize

1%–2% of the population (Boltovskoy et al. 1997; Cataldo and Boltovskoy 1998). In the Rio de la Plata, where *C. fluminea* and *L. fortunei* have both been present since the early 1990s, concentrations of suspended particulate organic matter are thought to largely exceed the needs of *L. fortunei* (Sylvester et al. 2005), but may be limiting for *C. fluminea* (Boltovskoy et al. 1995). However, as *C. fluminea* can also pedal feed from the sediment (Aldridge and McMahon 1978; McMahon 1999), the effects of competition for food with *L. fortunei* may be relatively small.

At present all five of the species considered here do not co-occur therefore it is difficult to predict if they will all compete, and if they do, under what conditions which species will be the superior competitor. Theoretically all of these could coexist in the same waterbody, each occupying a slightly different niche. For example, in a hypothetical lake with a wide warm littoral zone, a deep cold profundal zone, and high local organic enrichment, *D. polymorpha* could dominate the littoral zone (especially attached to macrophytes), *D. bugensis* could colonize the cold, silty profundal zone, *L. fortunei* could flourish in areas with high organic pollution and periodic hypoxia, and *C. fluminea* could colonize unconsolidated sediment in well oxygenated littoral and sublittoral zones.

We suggest that the rate of spread of the exotic species considered here as well as others depends upon the spatial resolution of the scale of spread, and may be accelerated or slowed by various human activities (Fig. 5). In general, aquatic exotic species quickly spread along connected waterways within a recently invaded continent, and soon reach their maximum range (continental scale). However, it takes much longer to colonize all regions within a continent and much longer again to spread to isolated lake and river systems (local scale). This difference in the rate of colonization across different spatial scales may be several orders of magnitude. For example, it took less than 40 years for *D. polymorpha* to spread across the European continent (what was then north-western Russia, including present day Belarus, Poland, and the Baltic states, Great Britain, the Netherlands, Germany, Belgium, France) through canal systems. However, at the regional
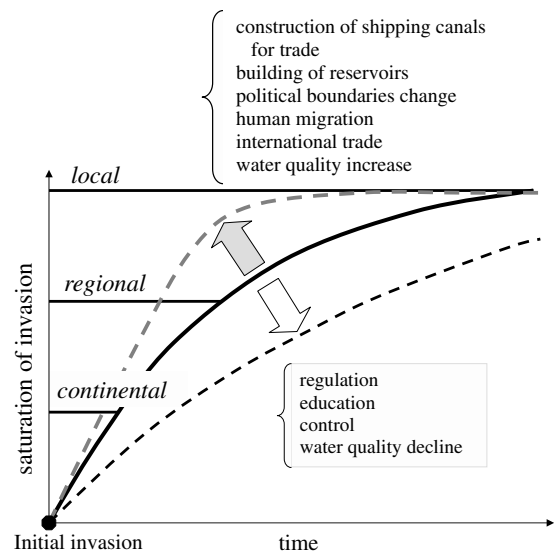
Fig. 5 Model of the timing of spread of exotic species across different spatial scales. The rate of spread can be either increased or decreased by changes in political boundaries, economics, trade, environmental regulations or education

scale it took 150 years for *D. polymorpha* to spread across geographical barriers into the Alpine region in Central Europe (Kinzelbach 1992) and almost 200 years to reach Ireland (Minchin 2000) and Spain (bij de Vaate et al. 2002). At the local scale, the spread of zebra mussels in Europe is still far from complete. For example, in Belarus most lakes remain free of zebra mussels (Karatayev et al. 2003a). Zebra mussels continue to invade new lakes in Lithuania (S. Olenin, pers. communication), Belarus (A. Karatayev, and L. Burlakova, pers. observation), Britain and Ireland (D. Minchin, pers. observation).

The same pattern has been found in North America. In less than 10 years after zebra mussels were first found in the Laurentian Great Lakes, they spread throughout most of the major connected river systems east of the continental divide. However on a regional scale this spread has been much slower, and at a local scale, the spread to isolated lake systems, and even further to the waterbody scale, has been even slower (Padilla 2005). Of the >15,000 inland Wisconsin lakes, only 6 were colonized by 1998 (Buchan and Padilla 1999), and by 2005 less than 1% of these lakes were colonized (Padilla 2005). Kraft and

Johnson (2000) found that the annual rate of colonization of inland lakes was from 0% to 12% per year, far slower than the initial rate expansion throughout North American connected navigable waterways (Johnson and Padilla 1996).

The rate of spread at different spatial scales can be affected by various types of human activities as well as the biology of the invasive species (Fig. 5). The construction of shipping canals or reservoirs, changing political boundaries, human migrations, the volume and direction of international trade, and changes in water quality can create different opportunities for the spread and establishment of exotic species. In contrast, environmental and trade regulations, education and deterioration of water quality may reduce rates of spread and close some opportunities for introduction (Fig. 5). Therefore, the realized rates of spread of exotic species can be affected by changes in political borders, levels of industrialization and environment conditions and regulations, and modified by education and direct action that enhance or reduce spread. Dove and Wallis (1981) found that direct educational programs greatly reduced the rate of spread of another aquatic invader, Eurasian watermilfoil, in Canada.

Recently, risk assessment has been an approach used to evaluate the potential mechanisms of spread and introduction of invaders for a variety of systems and types of species (reviewed in Ruiz and Carlton 2003a; Anderson et al. 2004). Risk assessment characterizes the likelihood and severity of potential adverse effects of exposure to hazardous agents or activities (i.e., stressors), and includes assigning probabilities to particular behaviors or links in behavior that will affect a particular outcome, in this case, the introduction or spread of an invader (Orr 2003; Anderson et al. 2004). Assessing the likely transmission mechanisms and vectors capable of spreading a species is a part of a risk assessment that management may be used to reduce spread (Ruiz and Carlton 2003b).

For any risk assessment of the spread of an invasive species, the first task is identifying all potential vectors responsible for spread, the time periods when these might operate, the spatial scales at which each will be important, and the probability of the relative contributions of each to realized spread. For aquatic invaders there are a number of well-recognized vectors that will spread introduced species, each operating at different spatial and temporal scales (Table 3; Carlton 1993; Buchan and Padilla 1999, 2000; Ruiz and Carlton 2003a, b). Spread at the largest spatial scales is affected by the least number of vectors. At smaller scales the number of possible vectors for transmission, for example among regions and to local areas, increases considerably (Table 3). Although the number of individuals that must be transmitted to actually establish a new invasion remains unknown, it is generally agreed that the greater the number of individuals transmitted, and the greater the frequency of movement, the greater the probability, and therefore risk, of a successful invasion (Schneider et al. 1998; Buchan and Padilla 2000; reviewed in Ruiz and Carlton 2003b). These numbers and probabilities are likely to be species specific and dependent upon factors like life history, growth and reproductive characteristics.

The relative risks associated with different transport mechanisms will also be affected by many of the factors discussed above, including the establishment or removal of political boundaries, changes in political or economic systems, especially as they alter trade, and environmental regulations. The timing of the introduction of different invaders is also similarly affected. For example, Corbicula colonized North America much earlier than Dreissena, most likely because C. fluminea was deliberately introduced as a food item. Dreissena has never been used as food for humans and, therefore, this vector has not spread the zebra mussel.

Overall, as globalization increases, we can expect to see an increased risk of invasion. However, recognizing these risks allows us to take measures that will minimize or mitigate risk, reduce spread and transmission of unwanted invaders, and minimize the unwanted environmental and economic costs and consequences of the introductions of new species. International cooperation, acceptance and adherence to agreements such as the IMO Conventions on hull fouling and ballast water and ICES Code of Practice are the first steps towards slowing or stopping the spread of invaders.

Table 3 Potential vectors that spread freshwater invaders. Each vector will affect different spatial scales, and different species. The relative risk of transmission by each of these vectors will be affected by social, economic and political factors including political boundaries, canals, environmental regulations, trade agreements and education

Vector	Species	Scale of spread
International shipping	*Dreissena polymorpha*	Continental
	Dreissena bugensis	Regional (within continent trade)
	Limnoperna fortunei	
	Corbicula fluminea	
	Corbicula fluminalis	
Transport for food/aquaculture	*Corbicula fluminea*	Continental
	Corbicula fluminalis	Regional
		Local
Domestic shipping, Barge transport	*Dreissena polymorpha*	Regional
	Dreissena bugensis	
	Limnoperna fortunei	
	Corbicula fluminea	
	Corbicula fluminalis	
Leisure craft	*Dreissena polymorpha*	Regional
	Dreissena bugensis	Local
	Limnoperna fortunei	
Commercial fishing gear	*Dreissena polymorpha*	Local
	Dreissena bugensis	
	Limnoperna fortunei	
	Corbicula fluminea	
	Corbicula fluminalis	
Trailered boats, Snagged plants	*Dreissena polymorpha*	Regional
	Dreissena bugensis	Local
	Limnoperna fortunei	
Stocking fish	*Dreissena polymorpha*	Regional
	Dreissena bugensis	Local
	Limnoperna fortunei	
	Corbicula fluminea	
	Corbicula fluminalis	
Sport fishing	*Dreissena polymorpha*	Local
	Dreissena bugensis	
	Limnoperna fortunei	
	Corbicula fluminea	
	Corbicula fluminalis	
Deliberate introduction	*Dreissena polymorpha*	Local
	Dreissena bugensis	
	Limnoperna fortunei	
	Corbicula fluminea	
	Corbicula fluminalis	

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