

Recent mass invasion of the North American Great Lakes by Ponto–Caspian species

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The human-aided spread of species beyond their natural range is a significant form of global change and a major threat to biodiversity¹. Although species distributions change naturally over geological time, human activities have greatly increased the rate and the spatial scale of these changes by accidentally or deliberately moving organisms across the world. Among the ecosystems most susceptible to invasion are lakes and estuaries^{2–5}. During the past century, the North American Great Lakes have received an increasing amount of biological pollution, particularly from the discharge of ballast water by transoceanic ships. A ballasted ocean freighter entering the Great Lakes typically carries three million liters of water, which is discharged before taking on cargo; in total, 800 million liters of ballast water are released into the system every year⁶. Because this water often contains various life stages of algae, invertebrates and fishes, transoceanic shipping has delivered hundreds of plant and animal taxa to North America, and is the major vector of aquatic invasions worldwide⁷. Nonindigenous species now dominate the food webs of the Great Lakes and have caused profound ecological and economic impacts^{2,3,8,9}. More invaders will inevitably arrive in the Great Lakes as expanding global trade creates new dispersal opportunities for aquatic flora and fauna.

Can we predict future invasions of the Great Lakes? Spatial and temporal patterns of invasion might be sufficiently pronounced to identify future threats and, thus, to guide management decisions regarding where to allocate resources for detection and for prevention¹⁰. In fact, changes in the type and the source of ship ballast over time have produced distinct phases in the invasion history of the Great Lakes. Before 1900, most ships visiting the Great Lakes used solid ballast, such as rocks, sand and mud, which was dumped at the destination port before the ships received cargo. Most of the nonindigenous species introduced during this period were plants transported as seeds². Subsequently, liquid ballast became widely used. Numerous species of nonindigenous algae and zooplankton became established when larger ships began to arrive following the opening of the St Lawrence Seaway in 1959. Arguably, the introduction of

The North American Great Lakes have been invaded and dramatically altered by more than 145 alien species. Many invasions have occurred during the past few decades because of the release of Eurasian ballast water from transoceanic ships. Current regulations require ships to exchange foreign ballast with highly saline water before entering the Great Lakes; this procedure should prevent colonization by strictly freshwater species, but species with broad salinity tolerance might survive transport in exchanged water. A recent series of invasions by euryhaline organisms from the Black and Caspian Seas region signals a new phase in the transformation of the Great Lakes – one that supports the concept of an ‘invasional meltdown’.

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the zebra mussel *Dreissena polymorpha*, one of the most dramatic invasions of modern times, was predictable based on a pattern of ballast-water introductions over the past three decades. About 75% of the flora and fauna introduced to the Great Lakes since 1970 is attributed to ballast-water release by Eurasian ships^{2,3}.

The recent invasion history of the Great Lakes reveals a more intriguing pattern: 70% of invading species discovered since 1985 are native to fresh and brackish waters of the Ponto–Caspian region (Black, Caspian and Azov Seas). In fact, seven of the eight species of invertebrates and fishes recently introduced by ships are Ponto–Caspian endemics (Table 1). These invasions have altered physical habitat, disrupted food webs and caused local extinctions of native species^{3,8,9,11,12}. In terms of population size and biomass, Ponto–Caspian animals have rapidly

become dominant members of benthic and pelagic communities throughout the Great Lakes and the St Lawrence River^{3,11–13}.

The recent influx of these species appears to be related to both their euryhalinity (broad salinity tolerance)^{14,15} and their increasing colonization of European ports. The Ponto–Caspian biota is diverse (e.g. greater than 950 metazoan species have been recorded in the Caspian Sea alone)^{15,16} and has evolved in basins with a tumultuous geological history of fluctuating water levels and salinities. Consequently, species of freshwater origin (i.e. those that reside in river deltas) generally tolerate salinities of up to approximately 13 ppt (Ref. 15). Dozens of these species have expanded their distributions across Europe during the past century, aided by the extensive construction of shipping canals and reservoirs, and by the intentional stocking of invertebrates as food to enhance fish production^{16–20}. For example, successive invasions of the Rhine River by Ponto–Caspian fauna occurred following the opening of the Rhine–Main–Danube Canal in 1992 (Refs 20–22), which links the Rhine and other waterbodies in western Europe with the Black Sea. Having dispersed through inland waterways, Ponto–Caspian fauna are now abundant at estuarine ports that are used extensively by ships destined for the Great Lakes^{20,23,24}.

Table 1. Non-native animals established in the Great Lakes–St Lawrence river drainage since the mid-1980s

Species	Common name	Year of discovery	Endemic region	Mode of transfer	Probable donor region	Refs
<i>Gymnocephalus cernuus</i>	Ruffe	1986	Ponto–Caspian ^a	Ballast water	Danube River	28
<i>Dreissena polymorpha</i>	Zebra mussel	1988	Ponto–Caspian	Ballast water	Baltic Sea	2
<i>Dreissena bugensis</i>	Quagga mussel	1989	Ponto–Caspian	Ballast water	Black Sea	2
<i>Scardinius erythrophthalmus</i>	Rudd	1989	Eurasia	Bait release	Eurasia	2
<i>Neogobius melanostomus</i>	Round goby	1990	Ponto–Caspian	Ballast water	Black Sea	11
<i>Proterorhinus marmoratus</i>	Tubenose goby	1990	Ponto–Caspian	Ballast water	Black Sea	11
<i>Potamopyrgus antipodarum</i>	New Zealand mudsnail	1991	New Zealand	Ballast water	Baltic Sea	3
<i>Alosa aestivalis</i>	Blueback herring	1995	Atlantic North America	Canal	Atlantic North America	3
<i>Echinogammarus ischnus</i>	Amphipod	1995	Ponto–Caspian	Ballast water	Baltic Sea	26
<i>Cercopagis pengoi</i>	Waterflea	1998	Ponto–Caspian	Ballast water	Baltic Sea	13

^aAlthough the ruffe is distributed across Eurasia, it is endemic to the Danube (western Black Sea) basin.

Can current ballast-water management stem the tide of invasions?

In response to the onslaught of ship-borne exotic species in the Great Lakes, in May 1993 the USA implemented a regulation that requires inbound vessels to exchange freshwater/estuarine ballast with highly saline oceanic water²⁵. Locke *et al.*⁶ report that approximately 90% of ships comply with this regulation. In theory, this procedure should greatly reduce the risk of invasion because freshwater organisms would be purged or killed by seawater, and would be replaced by marine organisms that would not survive if released into the freshwater Great Lakes. However, two Ponto–Caspian species, the amphipod *Echinogammarus ischnus*²⁶ and the waterflea *Cercopagis pengoi*¹³, were apparently introduced after implementation of ballast water regulations. *Echinogammarus* was present at only one site in the Detroit River in 1995, but has since spread throughout the lower Great Lakes and into the St Lawrence River¹². *Cercopagis* was found in Lake Ontario in 1998 and Lake Michigan in 1999. Another Ponto–Caspian crustacean, the amphipod *Corophium mucronatum*, was discovered in a benthic sample from Lake St Clair in 1997 but has not become established²⁷. Specimens of European flounder *Platichthys flesus* and Chinese mitten crab *Eriocheir sinensis* have also been reported since 1993, but these brackish-water species cannot reproduce in the Great Lakes (E.L. Mills, pers. commun.). Such introductions are a signal that current ballast water management might be insufficient to prevent nonindigenous aquatic organisms from reaching North American inland waters.

Ballast-water exchange often fails to achieve the oceanic salinities mandated by law because residual freshwater always remains in the tanks owing to the position of the pump intake. Up to 5% of the original ballast-water volume might remain, depending on the design of the tank (S. Gollasch, pers. commun.). Residual water in 'emptied' ballast tanks has been found to contain up to 30 million zooplankton⁶, which can be resuspended and mixed with new ballast water. Euryhaline Ponto–Caspian species are less likely to be killed by contact with seawater, particularly if they arrive as resistant resting stages (e.g. as cysts, ephippia and diapausing eggs). Ships entering the Great Lakes with no ballast on board might carry tank sediments containing resting stages of algae and invertebrates; these could be placed in suspension when the ship re-ballasts and released at another port if the ship takes on new cargo. Researchers have found up to 150 resting stages per cm³ of sediments from ships visiting German ports (S. Gollasch, pers. commun.). Therefore, without more effective ballast-

water controls, continued invasion and transformation of western European and North American inland waters by Ponto–Caspian species is highly probable.

Invasion corridors to the Great Lakes

The introductions of *Echinogammarus*²⁶, gobiid fishes¹¹, and the ruffe (*Gymnocephalus cernuus*)²⁸ demonstrate that organisms lacking both a planktonic stage and parthenogenetic reproduction (two traits thought to facilitate ballast-water transport and subsequent colonization)^{7,26} can still successfully invade via transoceanic shipping. In spite of ballast-water regulations, demographic requirements for population establishment and the stochastic vagaries of species introduction²⁹, the invasion corridors (Box 1) linking Eurasia with the North American Great Lakes appear to be delivering organisms at rates high enough to load the dice in favor of Ponto–Caspian colonization. The current influx of Ponto–Caspian crustaceans, mussels and fishes signals a new phase in the invasion history of the Great Lakes characterized by strong selection for euryhaline organisms.

Interestingly, this transfer has been strongly one-sided, because few freshwater species from the North American Great Lakes have invaded European inland waters^{20,23}. The comparatively large pool of euryhaline species immigrating from Ponto–Caspian basins is the simplest reason for this asymmetry, notwithstanding the possibility that Ponto–Caspian fauna are inherently better colonizers. Perhaps, more importantly, a relatively higher number of ships could be carrying ballast to the Great Lakes from Europe because of current trade patterns⁶.

Ship-borne organisms from Ponto–Caspian basins might have invaded the Great Lakes using at least three possible routes: (1) through the Mediterranean Sea directly from international ports (e.g. Kherson, Nikolayev and Melitopol) that fringe the Black and Azov seas; (2) through the Dnieper River and the Pripet–Bug canal system into the Vistula and Neman Rivers, and emerging in the Baltic Sea; and (3) through the Danube River and the Rhine–Main–Danube canal, and down the Rhine River to ports (e.g. Rotterdam and Antwerp) on the North Sea. The first route was used by the quagga mussel *D. bugensis*³⁰, and possibly by the ruffe²⁸, the round goby *Neogobius melanostomus*¹¹ and the tubenose goby *Proterorhinus marmoratus*¹¹. The second and third routes require western ports to act as secondary donor regions to the Great Lakes; either route might have been used by the amphipod *E. ischnus*^{17,31}. The ruffe, whose population in the Great Lakes is genetically similar to a population in the

Box 1. Invasion corridors

We define an invasion corridor as a transportation system and pathway that facilitates the long-distance dispersal of species towards particular regions. A terrestrial invasion corridor might consist of (for example) trucking routes, rail lines or aircraft flying between islands. The most important transportation system for aquatic invasions is ship traffic carrying ballast water laden with propagules of potential invaders; at any given moment, a few thousand species are in motion around the globe in ship ballast tanks⁷. Examples of aquatic invasion corridors include ship traffic between:

- The northwest Atlantic and coastal habitats of the UK; the northwest Atlantic has donated approximately 20% of the nonindigenous species found in British waters⁴³.
- East Asian ports (e.g. Tokyo Bay) and San Francisco Bay. The East Asian region is the origin of approximately 20% of the 234 nonindigenous estuarine species in the system⁴.

Species dispersal along invasion corridors is often highly asymmetric. The effects of invasion corridors change with intensity of vector traffic (e.g. changes in trade patterns) as well as with environmental conditions in the donor region (affecting the availability of propagules) and the recipient region (promoting or hindering the establishment of new species)⁴⁴.

Danube River²⁸, might also have used the third route. Other species continue to spread into central and western Europe through a variety of canal systems^{17,20}. At least 40 Ponto-Caspian species have expanded their ranges over the past few decades and most of these possess life stages that are easily transported in ship ballast water^{17-21,31,32}.

In spite of the possibility that the most aggressive and ecologically significant invaders have already arrived in the Great Lakes, several species warrant concern as potential future invaders^{3,10}. Among these is the Ponto-Caspian amphipod *C. curvispinum*, a suspension feeder that lives in mud tubes constructed on rocky substrata. From 1987 to 1991, *C. curvispinum* colonized hundreds of kilometers of the lower Rhine and achieved densities of 220 000 to 750 000 individuals m⁻². It has displaced populations of filter-feeding caddisflies and of zebra mussels (a previous invader) by smothering hard surfaces with muddy encrustations and by reducing suspended organic matter in the river through its filtration activity³². It is widely distributed in Europe and is present in high densities at Baltic Sea ports^{17,23}. The discovery of a living specimen of *C. mucronatum* in Lake St Clair²⁷ suggests that *Corophium* spp. will become established in the Great Lakes in the near future.

An invasional meltdown in the Great Lakes?

Ponto-Caspian species have successfully invaded a broad range of communities in the Great Lakes and adjacent waterways. For example, the planktonic crustacean *Cercopagis pengoi* first became established in Lake Ontario¹³, which has the highest degree of planktivory among the Great Lakes³³. The zebra mussel has spread throughout the Mississippi River system, which contains the world's richest endemic assemblage of freshwater mussels⁹. Similarly, the presence of an abundant competitor, the amphipod *Gammarus fasciatus*, did not prevent the rapid colonization of the lower Great Lakes by *Echinogammarus*¹². These examples suggest that aquatic invasions are mediated more by dispersal opportunity and favorability of abiotic conditions than by the composition of the recipient community, in contrast to the traditional view that diverse communities of competitors and predators resist invasion^{34,35}. Although cases exist where native assemblages repel invaders³⁶, even the most complex aquatic systems have been invaded multiple times, as demonstrated by plant and animal invasions of endemically rich communi-

ties in Lake Victoria³⁷ and the Caspian Sea. The Caspian Sea was rapidly invaded by numerous Mediterranean invertebrates following the opening of a major shipping canal between the Don and Volga Rivers^{15,16}. Thus, Moyle and Light³⁶ contend that all aquatic systems are invulnerable, an argument supported by Cornell and Lawton's assertion that ecological communities are rarely saturated with species³⁸.

Moreover, the success of some Ponto-Caspian invaders in the Great Lakes appears to have been enhanced by previous invasions – in contrast to the concept of biotic resistance, which predicts that communities become more resistant to invasion as they accumulate more species³⁵. Simberloff and Von Holle³⁹ have proposed an alternative model: as the cumulative number of attempted and successful introductions increases, each perturbing the system and possibly facilitating one another, the recipient community becomes more easily invaded over time. Chronic exposure to introduced species thus subjects a community to 'invasional meltdown' (an accelerated rate of invasion), particularly when there are facilitative interactions between coevolved invaders.

This phenomenon might be occurring in the Great Lakes with the reconstruction of Ponto-Caspian foodwebs. The establishment of large zebra mussel populations might have facilitated the rapid invasion of the round goby, a major predator of the mussel in the Caspian Sea basin¹¹. Furthermore, *Echinogammarus*, a deposit-feeder commonly associated with zebra mussels in Europe⁴⁰, has replaced other amphipods in zebra mussel beds in Lake Erie and Lake Ontario¹². In fact, food (biodeposits) and shelter provided by mussel beds have stimulated a 20-fold increase in *Echinogammarus* biomass in Lake Erie⁴¹. This probably had an additional positive impact on *Neogobius*, because *Echinogammarus* is an important prey item for immature round gobies⁴². Another example is the Ponto-Caspian hydroid *Cordylophora caspia*, which feeds on zebra mussel larvae and uses mussel shells as a substrate²³. Although it has been rather inconspicuous in the Great Lakes for decades, luxuriant growths of *Cordylophora* have been observed on newly formed mussel beds in Lake Michigan in recent years (T. Lauer, pers. commun.). In Lake St Clair, zebra mussel filtration has dramatically improved water quality conditions for exotic and native macrophytes, which, in turn, provide additional substrate for juvenile mussels⁸. These examples suggest that positive interactions among invading species are more common than has previously been assumed.

Future directions: calling for a new perspective on aquatic invasions

Mass invasions presently occurring in the Great Lakes and some North American estuaries^{4,5} do not fit into any classic ecological theory. Unfortunately, traditional invasion paradigms are derived exclusively from terrestrial studies and have not been formally tested for aquatic organisms. In particular, the widely cited view that species-rich communities are resistant to invasion or become increasingly resistant with each species addition³⁵, is apparently invalid for aquatic systems subject to frequent human vector activity. A new conceptual framework is needed to understand aquatic invasions, particularly when they are occurring in spasms or at an accelerated rate as in, for example, the Great Lakes², the Baltic Sea²³ and San Francisco Bay⁴. We must determine the factors that promote 'invasional meltdown'³⁹ in aquatic communities. Furthermore, we

need to identify invasion corridors linking donor and recipient regions (e.g. using genetic comparisons of invading and potential source populations^{28,30}), and incorporate them into predictive models. Mass invasions might be the predictable consequence of one or more invasion corridors exerting intense propagule pressure on a recipient system.

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