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

Anthony Ricciardi and Hugh J. MacIsaac

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’.

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 habitats, disrupted food webs and caused local extinctions of native species. The recent influx of these species appears to be related to both their euryhalinity (broad salinity tolerance) 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) 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. 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 23–25), 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. The zebra mussel Dreissena polymorpha, one of the most dramatic invaders 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.

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 habitats, disrupted food webs and caused local extinctions of native species. The recent influx of these species appears to be related to both their euryhalinity (broad salinity tolerance) 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) 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. 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 23–25), 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.
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 fresh-water/estuarine ballast with highly saline oceanic water. Locke et al. 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 freshwaters of Great Lakes. However, two Ponto-Caspian species, the amphipod Echinogammarus ischnus and the waterflea Cercopagis pengoi, 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 River. Cercopagis was found in Lake Ontario in 1998 and Lake Michigan in 1999. Another Ponto-Caspian crustacean, the amphipod Corophium marounum, was discovered in a benthic sample from Lake St Clair in 1997 but has not become established. Specimens of European flatfish 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 (B.E. 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 fresh-water 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 zooplankton, 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 arrous as resistant resting stages (e.g. as cysts, ephipnia and diapauing eggs). Ships entering the Great Lakes with so 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 cm² 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 ischnus and the waterflea (Gymnocephalus cernuus) demonstrate that organisms lacking both a planktonic stage and parthenogenetic reproduction (two traits thought to facilitate ballast-water transport and subsequent colonization) can still successfully invade via transoceanic shipping. In spite of ballast-water regulations, demographic requirements for population establishment and the stochastic vagaries of species introduction can lead to invasion of eastern European and North American inland waters by 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 patterns. 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. Kheros, Nikolayev and Melitopol) that fringe the Black and Azov seas; (2) through the Dnieper River and the Pripyat-Ilug canal system into the Vistula and Neman Rivers, and emerging in the Baltic Sea; and (3) through the Danube River and the Rhine-Man-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, and possibly by the ruffe G. cernuus, the round goby Neogobius melanostomus, and the tubenose goby <i>Pteroniphys marmoratus</i>. 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 <i>E. ischnus</i>. The ruffe, whose population in the Great Lakes is genetically similar to a population in the Danube (western Black Sea) basin.

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
<th>Year of discovery</th>
<th>Endemic region</th>
<th>Mode of transfer</th>
<th>Probable donor region</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gymnocephalus cernuus</td>
<td>Ruffe</td>
<td>1996</td>
<td>Porto-Caspian</td>
<td>Ballast water</td>
<td>Danube River</td>
<td>28</td>
</tr>
<tr>
<td>Dreissena polymorpha</td>
<td>Zebra mussel</td>
<td>1988</td>
<td>Porto-Caspian</td>
<td>Ballast water</td>
<td>Baltic Sea</td>
<td>2</td>
</tr>
<tr>
<td>Dreissena bugensis</td>
<td>Rugosa mussel</td>
<td>1989</td>
<td>Porto-Caspian</td>
<td>Ballast water</td>
<td>Black Sea</td>
<td>2</td>
</tr>
<tr>
<td>Scalaris oxyrhophthalus</td>
<td>Rudd</td>
<td>1989</td>
<td>Eurasia</td>
<td>Ball release</td>
<td>Eurasia</td>
<td>2</td>
</tr>
<tr>
<td>Neogobius melanostomus</td>
<td>Round goby</td>
<td>1990</td>
<td>Porto-Caspian</td>
<td>Ballast water</td>
<td>Black Sea</td>
<td>11</td>
</tr>
<tr>
<td>Proterorhinus marmoratus</td>
<td>Tubenose goby</td>
<td>1990</td>
<td>Porto-Caspian</td>
<td>Ballast water</td>
<td>Black Sea</td>
<td>11</td>
</tr>
<tr>
<td>Potamogeton antipodion</td>
<td>New Zealand water</td>
<td>1991</td>
<td>New Zealand</td>
<td>Ballast water</td>
<td>Baltic Sea</td>
<td>3</td>
</tr>
<tr>
<td>Alona schelkini</td>
<td>Blankealing</td>
<td>1995</td>
<td>Atlantic North</td>
<td>Baltic Sea</td>
<td>North America</td>
<td>3</td>
</tr>
<tr>
<td>Echinogammarus ischnus</td>
<td>Amphipod</td>
<td>1995</td>
<td>Porto-Caspian</td>
<td>Ballast water</td>
<td>Baltic Sea</td>
<td>26</td>
</tr>
<tr>
<td>Cercopagis pengoi</td>
<td>Waterflea</td>
<td>1998</td>
<td>Porto-Caspian</td>
<td>Ballast water</td>
<td>Baltic Sea</td>
<td>13</td>
</tr>
</tbody>
</table>

*Although the ruffe is distributed across Eurasia, it is endemic to the Danube (western Black Sea) basin.
Box 1. Invasion corridors

We define an invasion corridor as a transportation system and pathway that facilitates the long-distance dispersal of species to 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 tanks5. 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 waters4.
- 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)5.

Danube River9, might also have used the third route. Other species continue to spread into central and western Europe through a variety of canal systems10,11. 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 water11–13,15,16.

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 invaders14,15. Among these is the Ponto–Caspian amphipod Corophium, a suspension feeder that lives in mud tubes constructed on rocky substrata. From 1987 to 1991, C. vannutum 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 activity16. It is widely distributed in Europe, is present in high densities at Baltic Sea ports17,18. The discovery of a living specimen of C. maritimum in Lake St Clair19 suggests that Corophium spp. will become established in the Great Lakes in the near future.

An invasion 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 Cerco- pagus peregrinus first became established in Lake Ontario20, which has the highest degree of planktivory among the Great Lakes21. The zebra mussel has spread throughout the Mississippi River system, which contains the world’s richest endemic assemblage of freshwater mussels22. Similarly, the presence of an abundant competitor, the amphipod Gammarus fasciatus, did not prevent the rapid colonization of the lower Great Lakes by Echinogammarus21. 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 invasion2,22,25,26, although cases exist where native assemblages repel invaders24, even the most complex aquatic systems have been invaded multiple times, as demonstrated by plant and animal invasions of endemically rich communites in Lake Victoria27 and the Caspian Sea. The Caspian Sea was rapidly invaded by numerous Mediterranean inverteb-rates following the opening of a major shipping canal between the Don and Volga Rivers11,13,19. Thus, Myole and Light28 contend that all aquatic systems are invasible, an argument supported by Connell and Lawton’s assertion that ecological communities are rarely saturated with species29.

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 species30. Simberloff and Von Holle31 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 resistant over time. Chronic exposure to introduced species thus subjects a community to ‘invasion 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 basin32. Furthermore, Echinogammarus, a deposit-feeder commonly associated with zebra mussels in Europe33, has replaced other amphipods in zebra mussel beds in Lake Erie and Lake Ontario34. In fact, food (bioderposits) and shelter provided by mussel beds have stimulated a 20-fold increase in Echinogammarus biomass in Lake Erie35. This probably had an additional positive impact on Neogobius, because Echinogammarus is an important prey item for immature round gobies36. Another example is the Ponto–Caspian hydroid Cordyliphora cupea, which feeds on zebra mussel larvae and uses mussel shells as a substrate37. Although it has been rather inconspicuous in the Great Lakes for decades, luxuriant growths of Cordyli- phora have been observed on newly formed mussel beds in Lake Michigan in recent years (T. Lauer, pers. com- mun.). In Lake St Clair, zebra mussel filtration has dramati- cally improved water quality conditions for exotic and native macrophytes, which, in turn, provide additional substrate for juvenile mussels38. 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 estuaries39 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 addition, 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 sparsns or at an accelerated rate as in, for example, the Great Lakes3, that is, the Caspian Sea.

We must determine the factors that promote ‘invasion meltdown’ in aquatic communities. Furthermore, we
need to identify invasion corridors linking donor and recipient regions (e.g. using genetic comparisons of invading and potentially suitable populations, geographic range mapping), 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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