Invasion essay

Reassessment of species invasions concepts: the Great Lakes basin as a model

Hugh J. MacIsaac[1,*], Igor A. Grigorovich[1] & Anthony Ricciardi[2]
[1]*Great Lakes Institute for Environmental Research, University of Windsor, Windsor, Ontario, Canada N9B 3P4;* [2]*Redpath Museum and McGill School of the Environment, McGill University, Montreal, Quebec, Canada H3A 2K6; *Author for correspondence (e-mail: hughm@uwindsor.ca)*

Abstract

The Laurentian Great Lakes have an extensive history of species introductions, many of which occurred as a result of ballast water discharge by trans-oceanic ships. Most nonindigenous species (NIS) of animals and protozoans that established in the Great Lakes since 1985 are native to the Black, Azov and Caspian Seas or other regions of Eurasia. Analysis of vector strength from global port regions indicates that these NIS, which include amphipods, crustacean zooplankton, mussels and fishes, have been transported principally along dominant shipping routes from native or introduced habitats in northern and western Europe to the Great Lakes. A large group of additional taxa, many of which have extensive invasion histories, is available for transfer to the Great Lakes from key European ports. Thus, joint consideration of invasion corridors and the NIS species established in key donor ports provides an indication of taxa that may colonize the Great Lakes in future. Recent studies indicate that risk assessment may be extended even further for inland lakes subject to NIS invasion from the Great Lakes in cases where invasion vectors can be identified and quantified. Identification of invasion corridors and quantification of vector pathways, using lakes as model systems, provide a promising opportunity for the evolution of invasion biology from a largely descriptive science into a more predictive and quantitative discipline.

Introduction

Natural species distributions are influenced by many factors including evolved dispersal mechanisms, distance from colonizing sources, presence of geographic barriers, and chance. Large-scale geological structures, including major mountain ranges and oceans, have historically posed nearly insurmountable barriers to dispersal of most taxa. These barriers have resulted in the evolution of distinctive regional biotas, which were characterized by Wallace and others (Brown and Lomolino 1998).

Paleoecological studies have revealed that natural distributions of species change slowly over the course of geologic time, often in association with climate changes (Graumlich and Davis 1993). Dispersal mechanisms and capabilities differ widely among taxa; thus the scale and even existence of geographic barriers is highly species-specific. Nevertheless, nonvolant terrestrial taxa are generally constrained by large water bodies, while strictly aquatic taxa are likewise limited by land. Despite these obvious generalities, rare events may facilitate dispersal of taxa to suitable habitats that were previously beyond the species' natural dispersal capabilities. These events are typically associated with intense storms or other unusual climatic conditions. For example, following a hurricane in the Caribbean Sea in 1995, the green iguana *Iguana iguana* colonized Anguilla after rafting 150 km on vegetative matter from a more southern Antilles island source (Censky et al. 1998). These events are believed to occur so infrequently that geographic barriers can be viewed as

essentially impermeable to penetration by most taxa in ecological time.

Aquatic species distributions may be likewise constrained by barriers. Distributions of many species today reflect, in part, historic ephemeral connections. For example, the natural distribution of the opposum shrimp *Mysis relicta* is thought to reflect dispersal opportunities in proglacial waters along the margin of retreating glacial ice sheets (Väinölä et al. 1994). Mysid vulnerability to planktivorous fish apparently limits its geographic distribution to deep lakes and its diurnal distribution to the deepest waters therein. However, human activities have greatly increased the temporal and spatial scales of species dispersal, and now constitute one of the most pressing conservation problems of freshwater ecosystems (Richter et al. 1997; Ricciardi et al. 1998; Sala et al. 2000). Introductions affect biodiversity in two different ways. First, widespread introductions of nonindigenous species (NIS) are causing global homogenization of what were once distinctive regional biotas (Lodge et al. 1998; Rahel 2000). Second, native biodiversity in aquatic communities may be profoundly and adversely affected by invasions of nonindigenous plants, fish, molluscs and crustaceans (e.g. Lodge et al. 1998; Ricciardi et al. 1998). Aquatic taxa including *Mysis relicta* have been intentionally stocked into lakes in Eurasia and North America to improve fisheries (Mordukhai-Boltovskoi 1964). These introductions, including those involving *Mysis relicta*, have often unfolded with serious unintended ecological consequences.

Rates of NIS introduction appear to be particularly high for lakes and coastal marine ecosystems (Carlton and Geller 1993; Cohen and Carlton 1998; Ruiz et al. 2000; Ricciardi 2001). Hebert and Cristescu (2002) estimated that human-mediated dispersal of crustacean zooplankton might exceed the natural rate by up to 50,000 fold. Doubtless these patterns are related to the intensity with which humans utilize these ecosystems for recreation, food sources and commerce, notably via commercial shipping (Cohen and Carlton 1998; Rahel 2000; Ruiz et al. 2000; Ricciardi 2001). The frequency of species invasion problems in aquatic and coastal ecosystems will likely continue to grow commensurate with enhanced global commerce and human exploitation of these communities. This problem may be exacerbated by 'natural' changes to species ranges owing to global climate change (Dukes and Mooney 1999; Carlton 2000). Predicting how and where NIS will invade will require a thorough understanding of the invasion process, including both concepts and models. In this paper we examine some of these concepts and models, and argue that much can be learned from examination of invasions of the Great Lakes and of inland lakes within the Great Lakes basin.

Elton's invasion concepts

Species invasions have been studied for most of the last century, though it was not until publication of Charles Elton's (1958) seminal volume The Ecology of Invasions by Animals and Plants that ecologists recognized the global scale of the problem and its threat to conservation of 'ecological variety'. Elton developed two streams of invasion concepts, one pertaining to characteristics of invading species, the other to features of invaded habitats. Quantitative descriptions of invading species may include, but are not limited to, the following: presence of r-selected traits, high dispersal rate, genetic variability and/or phenotypic plasticity, polyphagy and human commensalism (Lodge 1993). Features of invaded habitats may include climatic similarity to native habitat, early successional stages, low diversity of native predators, and a history of habitat disturbance (Lodge 1993). Elton's work clearly identified that successful invasions require an appropriate combination of species- and community-based factors. Many workers continue to explore the importance of species- and community-based concepts in their studies of invasions (e.g. Stohlgren et al. 1999; Stachowicz et al. 1999; Shurin 2000). In a note of caution, however, Lodge (1993; Box 2) reported that while many of these concepts were intuitively appealing, and, in some cases, supported by theoretical or empirical studies, exceptions to the patterns were numerous, and that many of the generalizations had not been tested statistically.

Interest in species- and community-based determinants of invasion success has not abated in recent years. One concept that has garnered particular interest has been that biological resistance by native species retards invasion by NIS (see Levine and D'Antonio 1999). Some recent studies have provided supportive evidence for this hypothesis (Stachowicz et al. 1999; Shurin 2000; Lyons and Schwartz 2001), although others have demonstrated that NIS establish in the same habitats that support communities rich with native species (e.g. Stohlgren et al. 1999; Lonsdale 1999; Levine 2000; Stadler et al. 2000). Moyle and Light (1996) noted

that the astonishing number and variety of aquatic ecosystems around the world that have been invaded by NIS indicates that most or all aquatic ecosystems are invasible, irrespective of native species diversity. In some cases, native species or established NIS appear to facilitate establishment of later-arriving NIS, a pattern opposite that predicted by the biotic resistance hypothesis (Simberloff and von Holle 1999; Ricciardi 2001).

Inability to isolate effects of specific independent factors, each of which have been speculated to affect invasion success, has hampered progress in invasion biology. For example, Levine and D'Antonio (1999) reported that covariation between native diversity and environmental factors including resource availability or disturbance can obscure underlying factors that affect invasion success. Davis et al. (2000) proposed that resource availability, defined as the difference between gross supply and uptake, could itself explain invasibility of plant communities.

Many of the concepts advanced to predict invasion success, including disturbance, native diversity, species invasiveness and the availability of colonizing propagules, are often confounded, thereby limiting definitive conclusions (Lonsdale 1999). A further problem exists in clearly defining the nature of disturbance. Because virtually every ecosystem on earth has been modified by human activity to some extent, tests of the disturbance hypothesis will require carefully controlled and replicated field experiments. Moreover, introduction of NIS itself constitutes a disturbance. Also troubling is the bias that pervades the frequency with which successful and unsuccessful invasions are reported. Successful invasions are probably far more likely to be reported because ecologists become aware of the invader's presence, usually owing to profound ecological or economic effects. Unsuccessful invasions are only reported when they involve easy-to-detect species. Invasions initiated by relatively small populations may remain undetected for an extended period of time and become discovered only after populations have grown large. Thus, it can be very difficult to adequately test invasion concepts if data are available only for invasions that have succeeded. As far as we are aware, no information exists on the ratio of successful to unsuccessful invasions for any freshwater ecosystem (but see Ruiz et al. 2000).

A number of recent studies have suggested that the number of propagules present in an inoculating population is positively correlated with invasion success (Lonsdale 1999; Levine 2000; Ruiz et al. 2000; Kolar and Lodge 2001; Mack and Lonsdale 2001; Ricciardi 2001). The importance of propagule pressure was clearly illustrated by Grevstad (1999), who noted that invasion success of colonizing beetles was positively correlated with the number of individuals released. This concept can be explored with models in which temporal and spatial spread of an established NIS are related to the probability distribution of propagule dispersal (i.e. redistribution kernel; Kot et al. 1996; Lewis 1997). While these models (see below) were developed principally for cases involving dispersal by natural mechanisms (e.g. seeds in wind), we explore their utility to invasions of aquatic ecosystems owing to human-mediated ones (e.g. transport in ballast water).

The Great Lakes experience

In order to expand on classical concepts of the processes that mediate invasions in aquatic environments, we use as a model aquatic system the history and possible future of invasions in the Laurentian Great Lakes, North America. The Great Lakes serve as a useful model for the basic invasion concept because they have the benefit of a rich biological diversity data base extending back into the 19th century, possess a large number of both native and introduced species, and have been the subject of increasingly intensive study on invasion phenomena, patterns and processes for the last 25 years. Four recent studies have explored patterns of NIS introductions to the Great Lakes during the past decade. Mills et al. (1993) assessed the temporal sequence, probable date, source and mode of entry, and the lake of first discovery for 139 NIS in the Great Lakes. Ricciardi and Rasmussen (1998) identified NIS likely to invade the Great Lakes based upon three primary criteria: species with previous invasion histories, species present in major waterways that are used by commercial ships bound for North America, and species with broad salinity tolerance; the latter attribute could prove beneficial in instances where ships destined for the Great Lakes undergo only partial ballast water exchange while on the open sea, resulting in brackish conditions (Locke et al. 1993). MacIsaac (1999) conducted a similar analysis, with a focus on invaders established or likely to establish in Lake Erie. Most recently, Ricciardi (2001) updated the NIS complement of the Great Lakes to 162 identified, established NIS through summer 2001. Ricciardi (2001) also noted that the number of NIS discoveries was positively correlated ($r^2 = 0.62$) with shipping activities to the

Great Lakes. Collectively these reviews provide a comprehensive history of species invasions in the Great Lakes. Consequently, the purpose of this paper is not to reiterate these findings, but to use the Great Lakes basin invasion experience to explore and develop invasions concepts. Below we review historical concepts of species invasions, provide basic models of the invasion process, and apply these perspectives to the post-1980 history of invasions in the Great Lakes.

Models of invasion

Two basic models may be constructed to describe invasion patterns. The reaction–diffusion model (Figure 1) was initially used to forecast spread of mutant alleles. Demographically this model consists of initial establishment and local exponential or logistic population growth of an invading species, followed by diffusion to adjacent areas (Skellam 1951). This model predicts that the velocity of radial spread from an invasion site is proportional to a population's growth rate and to its diffusion coefficient (Skellam 1951). It predicts a wave-like outward movement of a population front, with probability of invasion related to proximity to the population epicentre and to time since initial colonization (Figure 1). Variants of the model allow for directional movement of dispersing individuals in, for example, prevailing winds or water currents (Shigesada et al. 1995). The model successfully predicted spread of invading collared doves (*Streptopelia decaocto*) and other terrestrial taxa (Hengeveld 1989; Shigesada and Kawasaki 1997).
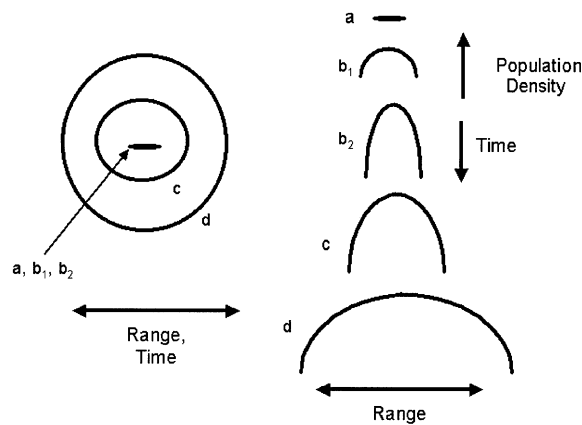
Stratified diffusion is an alternative model of range expansion that involves elements of local reaction–diffusion growth and long distance or 'jump' dispersal (Hengeveld 1989; Shigesada et al. 1995; Brown and Lomolino 1998; Neubert and Caswell 2000). Jump dispersal involves long-distance transport of a small proportion of individuals great distances from the population epicentre owing to a 'fat-tailed' redistribution kernel. In addition to predominant local neighbourhood growth, isolated invasion 'foci' establish considerable distances from the parental colony (Hengeveld 1989; Kot et al. 1996; Lewis 1997; Neubert and Caswell 2000). Stratified diffusion is consistent with dispersal patterns of herbaceous plants (Neubert and Caswell 2000), trees (Clark 1998; Higgins and Richardson 1999) and fruit flies (Kot et al. 1996). In contrast to the reaction–diffusion model, the probability of colonization of distant localities is directly dependent on the availability of long-distance dispersants and dispersal opportunities, and much less so on the distance from the source and time since initial colonization (Figure 2). For naturally dispersed taxa, long-distance dispersal opportunities could be determined by factors including major storms that present unusual dispersal opportunities in strong winds or ephemeral connections between discrete aquatic ecosystems owing to flooding.
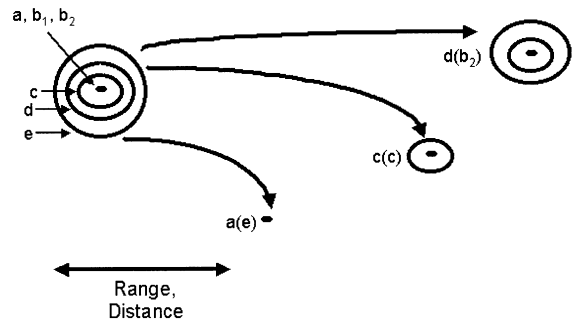

Figure 1. Reaction–diffusion invasion model. Invasion consists of initial colonization (a), followed by local population growth (b_1, b_2) before the population distribution expands in a wave-like manner. The probability of population establishment is directly proportional to time since initial invasion and inversely related to distance from colonization site.

Figure 2. Human-vectored invasion model. Letters refer to the stage of population growth from Figure 1; letters in parentheses indicate the stage of the source population when humans transported propagules to initiate a new invasion. Invasion begins at the site on the left of the figure. This population establishes and begins local population growth (b_1, b_2). Humans disperse propagules to a distant site(s), where population establishment and growth occur (to stage d), before or attendant with significant local diffusion of the initial colonist population (>stage b_2). Here, the probability of peripheral colonization is directly proportional to propagule 'load', and much less so on distance from the source population or time.

Stratified diffusion may result in a dramatic increase in area occupied by the NIS, although it is very difficult to identify where new colonies will establish on the periphery (Kot et al. 1996; Lewis 1997).

An increasingly important variant of jump dispersal is associated with humans (Figure 2). Here, dispersal is determined by the probability of propagule movement by humans from the source to the recipient site, and is much less dependent on time or on distance between source and recipient ecosystems. This is an important distinction from the reaction–diffusion model because it permits a much higher probability of very long-range invasions over short time intervals. Human-vectored dispersal may also differ from natural stratified diffusion because the destination of long-distance migrants may be discernable (see below). It is also important because it focuses attention on invasion opportunities, the first key step of any invasion, rather than simply on characteristics of species or of habitats, as a determinant of invasion success. One possibility exists wherein distance could influence invasion opportunity. Ships laden with ballast water move large populations of many species around the world. Survival of live organisms in ballast water may decline exponentially (e.g. Smith et al. 1999). This decline may stem from reduced food quantity or quality, or to variation in light or temperature (Carlton 1985). If live organisms were unable to tolerate ambient conditions in the ballast water during transit, successful invasion at the recipient port would depend on availability of diapausing propagules (e.g. cysts, ephippia) in discharged ballast water. Consequently, more distant ports-of-call should receive fewer live organisms in deballasted water than closer destinations.

Human-vectored dispersal is more capable than reaction–diffusion dispersal of accounting for a number of invasion patterns observed in European water bodies. For example, the Ponto-Caspian (i.e. Black, Azov and Caspian Seas) amphipod *Corophium curvispinum* invaded the British Isles decades before it established in many European waterways (Jażdżewski 1980). Likewise, the Baltic Sea has been invaded by 10 species native to the Atlantic coast of North America, by at least 17 species endemic to the Ponto-Caspian region, and by others native to the Pacific Ocean (Nikolaev 1979; Olenin and Leppäkoski 1999). These and other examples demonstrate at both regional and global scales that reaction–diffusion models cannot predict the movement of aquatic species, particularly if humans constitute major dispersal vectors.

Analysis of zebra mussel distributions in North America reveals the importance of reaction–diffusion and human vector dispersal. The initial discovery of this species was made during 1988 in Lake St Clair, although the species likely colonized in 1985 or 1986 (Hebert et al. 1989). In a reconstruction of the invasion pattern for the Great Lakes, Griffiths et al. (1991) noted that distribution expanded between 1986 and 1987 to occupy most of the western basin of Lake Erie, downstream of Lake St Clair, as well as a small portion of central Lake Erie. The downstream, wave-like population front continued to expand during 1988 and by 1989, had 'spilled' over into Lake Ontario. By 1990, most of the southern and western margins of Lake Ontario were populated (Griffiths et al. 1991). All of these invasions may have occurred naturally via passive drift of planktonic larvae in currents. Populations established at upstream locations in Lake Superior and Lake Huron in 1989, and in Lake Michigan in 1990 (Griffiths et al. 1991). As well, a population established in the St Lawrence River in 1989, well ahead of the invasion front in western Lake Ontario. Human activities are likely responsible for dispersal of all upstream populations as well as the one in the St Lawrence River. Dispersal mechanisms associated with humans are myriad, but include transport of adults and/or larvae by commercial ships or by recreational boats (Johnson and Carlton 1996; Johnson et al. 2001). Thus, the initial long-distance colonization of the Great Lakes likely resulted from dispersal in ballast water contained within a trans-oceanic vessel, while other human-mediated and natural dispersal mechanisms were responsible for its subsequent spread. Johnson and Carlton (1996) suggested that the species may be dispersal-limited in Europe, as it spread slowly to unconnected ecosystems even though it quickly colonized connected waterways. Similarly, Kraft and Johnson (2000) determined that invasion of inland lakes in North America occurred at a slower rate than dispersal through connected waterways. A particularly important mechanism of inland invasion appears to be the movement of trailered pleasure boats laden with stranded macrophytes and attached zebra mussels; using a probabilistic model, Johnson et al. (2001) showed that this mechanism likely resulted in 170 dispersal events to inland waters within a single summer season from a single boat launch on Lake St Clair.

In what may be the best-documented test of reaction–diffusion versus human vector invasion models, Buchan and Padilla (1999) examined the

correspondence between zebra mussel (*Dreissena polymorpha*) spatial invasion patterns in Wisconsin lakes and recreational boat traffic within the state. Buchan and Padilla (1999) determined that application of a reaction–diffusion model underestimated the maximum rate and the geographic extent of invasions within the state, but overestimated the invasion of suitable habitats in closer proximity to invasion sources. This observed pattern was consistent with expectations based upon human-vectored, stratified diffusion. More recently, Bossenbroek et al. (2001) developed a production-constrained gravity model to relate location and number of lakes in Illinois, Indiana, Michigan and Wisconsin with location and number of recreational boats (i.e. vectors) to predict spread of *Dreissena*. While the model was unable to make specific source–destination predictions, it accurately simulated dispersal of the species to specific regions of Wisconsin and Michigan.

Borbely (2001) employed a doubly constrained gravity model to predict invasion patterns of the spiny waterflea (*Bythotrephes longimanus*) to inland lakes in Ontario. In a backcasting analysis, invasion sequence for lakes with defined invasion dates was positively correlated with the intensity of human vector activity from invasion sources (initially the Great Lakes) (Borbely 2001). In a forecasting analysis, vector activity to 'noninvaded' lakes (from invaded sources) that were subsequently invaded was significantly greater than that to lakes that remained noninvaded. Analysis of vector pathways also revealed that the primary invasion of the Great Lakes from Eurasia was followed by secondary, tertiary and possibly even quaternary invasions of inland lakes, consistent with a 'stepping-stone' dispersal model (Ruiz et al. 2000). Each of the above studies confirm the utility of identifying and quantifying invasion vectors, and demonstrate that invasion of inland lakes occurs as a result of a nonrandom process that may produce patterns similar to natural stratified diffusion. It remains to be determined whether gravity models can be successfully applied to predicting invasion patterns in other heterogeneous landscapes (e.g. terrestrial plant communities).

Invasion corridors to the Great Lakes

Ballast water has been the leading mechanism responsible for invasion of NIS in the Great Lakes for most of the 20th century, whereas prior to 1900 most introductions resulted from transfer of sand, mud or gravel ballast (see the review in Mills et al. 1993). Indeed, the relative importance of ballast water appears to have grown during the part of the century (Ricciardi and MacIsaac 2000; Horvath et al. 2001; Ricciardi 2001). Approximately 75% of the 40 NIS that have been introduced to and established in the Great Lakes since 1959, when the St Lawrence Seaway was completed, can be attributed to ballast water discharge (Mills et al. 1993; MacIsaac 1999; Ricciardi 2001). Since 1985, approximately 75% of the NIS that have established in the Great Lakes have originated from Eurasia, with 57% from the Ponto-Caspian region (Ricciardi and MacIsaac 2000; Horvath et al. 2001; Ricciardi 2001). These species include a wide array of taxa including mussels (*Dreissena polymorpha, D. bugensis*), amphipods (*Echinogammarus ischnus*), cladocerans (*Cercopagis pengoi*), harpacticoid copepods (*Nitocra incerta* and *Schizopera borutzkyi*) and fishes (*Neogobius malanostomus, Proterorhinus marmoratus, Gymnocephalus cernuus*). Ten additional free-living and parasitic species (46%) have Eurasian distributions (see Appendix 1 in Ricciardi 2001). Parasites were likely transported to the Great Lakes with their host fishes directly from their native Ponto-Caspian range (see the review in Grigorovich et al. 2001). Ballast water introductions are consistent with human-vectored, stratified diffusion because propagules of NIS are transferred long distances from population sources. The dominance of Ponto-Caspian taxa among recent invaders to the Great Lakes seems to contradict this model since little vessel traffic links these regions (Colautti et al. 2002). These divergent patterns may, however, be reconciled by considering invasion pathways within Europe that facilitate transfer of these species to key western and northern European ports. Once established in these ports, they may be loaded into ballast by Great Lakes-bound vessels. The overall pattern is consistent with the development of new invasion 'hubs' from which new invasion spokes (i.e. routes) facilitate secondary invasions (Carlton 1996). Ricciardi and MacIsaac (2000) proposed the existence of 'invasion corridors' between the Great Lakes and the Ponto-Caspian region (Figure 3). Invasion corridors may also link East Asian ports and San Francisco Bay (Cohen and Carlton 1998; Ruiz et al. 2000) or various Australian ports (e.g. see Jones 1991).

Ponto-Caspian and other taxa may utilize up to five major shipping corridors to reach North America
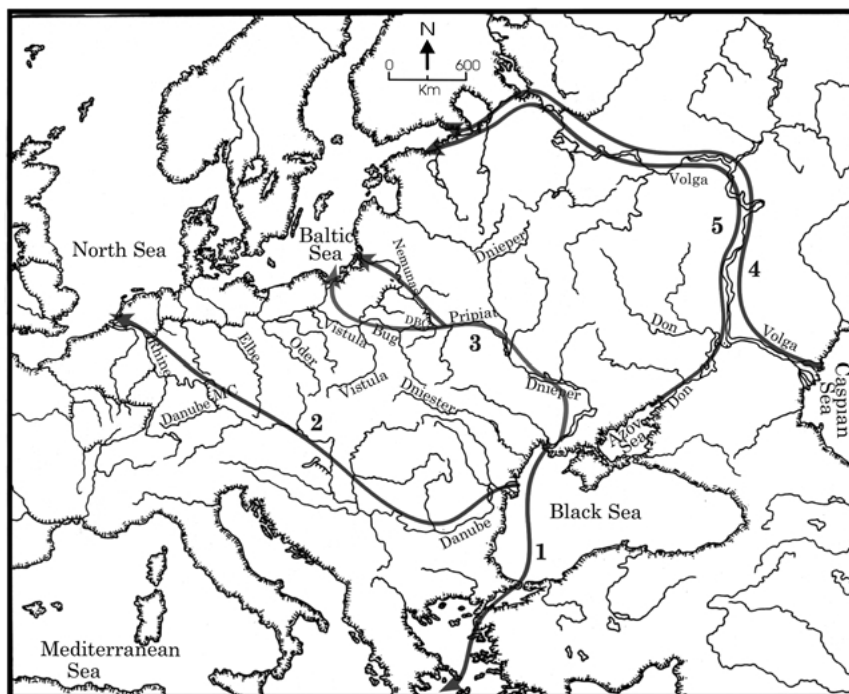
Figure 3. Proposed invasion corridors for the transfer of Ponto-Caspian taxa to the Laurentian Great Lakes. Corridors are considered routes and associated mechanisms that facilitate long-distance dispersal of different life stages of an array of species. A direct corridor may transfer taxa from Black and Azov sea estuaries or adjacent rivers (route 1). Four indirect corridors may facilitate the transfer of species to the Great Lakes only as secondary invasions from other waterways in Europe. These include: a corridor between the Danube River–Main Canal–River Rhine network (MC; see text for details) (route 2); the Black Sea via the Dnieper River–Pripiat River–Dnieper–Bug Canal–either the Nemunas or Vistula Rivers to the Baltic Sea (route 3); Caspian Sea through the Volga River system, Volga-Baltic Canal, to the Baltic Sea (route 4); or Black and Azov Seas–Don River–Volga–Don Canal–Volga River and Volga-Baltic Canal, to the Baltic Sea (route 5). Canals are indicated as hatch marks on lines connecting major rivers. DBC = Dnieper–Bug Canal, a major link between Black Sea (Dnieper, Pripiat rivers) and Baltic Sea (Vistula, Bug Rivers) basins that has facilitated the transfer of Ponto-Caspian species into central and western Europe. Route numbers are identified on the map. Modified from Jażdżewski (1980).

(Figure 3). First, they may be transferred in ballast water directly from ports on the Black (Kherson, Nikolaev, Kakhovka, Belgorod-Dniestrovskii, Galati, Izmail, Tulcea) or Azov Seas (Melitopol, Taganrog) to the Great Lakes. Second, they may be dispersed from Black or Azov Sea ports via the Danube River, the Rhine–Main–Danube Canal and the Rhine River, to the North Sea. Third, they may move from ports on the Black or Azov Seas through the Dnieper and Pripiat Rivers and the Dnieper–Bug Canal into the Vistula or Neman Rivers, and then into the Baltic Sea. Fourth, they may be dispersed from the Caspian Sea through the Volga River and its reservoir system, into the Volga–Baltic Canal, the Neva River and the Baltic Sea. Finally, ships can travel from ports on the Black or Azov Seas through the Don River, the Volga–Don Canal, and into the Volga River. All of the routes except the first one require that European

ports serve as donor regions for other ships that subsequently transport species to the Great Lakes in secondary invasions. Evidence exists to link most of these corridors to invasions in Europe and the Great Lakes. For example, quagga mussels likely entered the Great Lakes directly from a port on the Black Sea (route 1; Spidle et al. 1994). *Cercopagis* most likely used route 3, but routes 1 and 5 cannot be excluded (MacIsaac et al. 1999; Cristescu et al. 2001). The mysid *Hemimysis anomala* and numerous other Ponto-Caspian taxa used route 2 to invade reservoirs in the lower River Rhine (Pinkster et al. 1992; van den Brink et al. 1993a,b; Rajagopal et al. 1997; Ketelaars et al. 1999; Table 1). Some of these species have also been introduced to the Baltic Sea (Table 1). In fact, it is possible that these species initially invaded the Baltic Sea drainage basin via the Dnieper and Pripiat Rivers (Black Sea drainage basin) and their connections to Rivers Bug and

Table 1. Ponto-Caspian taxa that have invaded the Baltic Sea and Rhine River basins (Nikolaev 1979; Olenin and Leppäkoski 1999; Ketelaars et al. 1999; van der Velde et al. 2000).

Phylum	Taxonomic group	Species	Established in Baltic Sea basin?	Established in Rhine River?
Cnidaria	Hydrozoan	*Cordylophora caspia*	Yes	Yes
Annelida	Oligochaete	*Potamothrix vejdovskyi*[a]	Yes	No
		Paranais frici[*]	Yes	No
	Polychaete	*Hypania invalida*	No	Yes
Mollusca	Bivalve	*Dreissena polymorpha*	Yes	Yes
	Gastropod	*Theodoxus pallasi*	Yes	No
Crustacea	Onychopod	*Cercopagis pengoi*	Yes	No
	Amphipod	*Corophium curvispinum*	Yes	Yes
		Echinogammarus ischnus	Yes	Yes
		Echinogammarus warpachowskyi	Yes	No
		Dikerogammarus villosus	No	Yes
		Dikerogammarus haemobaphes	No	Yes
		Pontogammarus crassus	Yes	No
		Pontogammarus robustoides	Yes	No
	Mysidacean	*Limnomysis bendeni*	Yes	Yes
		Hemimysis anomala	Yes	Yes
		Paramysis lacustris	Yes	No
Chordata	Acipencerid fish	*Acipenser gueldenstaedti*	Yes	No
		Acipenser ruthenus	Yes	No
	Gobiid fish	*Neogobius melanostomus*	Yes	No

[a] Species of unresolved origin.

Vistula by man-made canals (Dediu 1980; Figure 3). Once established in the Baltic Sea drainage, species could utilize other rivers and canals to spread into central and western Europe. Examples of species that may have utilized this network of rivers and canals to disperse from the Black Sea basin into northern and then central and western Europe include *Echinogammarus ischnus, Dreissena polymorpha* and *Corophium curvispinum* (Dediu 1980; Jażdżewski 1980). Den Hartog et al. (1992) attributed the successful invasion of the River Rhine by *Corophium curvispinum* to the river's increasing salinity, among other factors.

Ponto-Caspian taxa have invaded all of the major river systems adjacent to the Black, Azov and Caspian Seas, and could therefore be picked up in ballast water loaded on connected rivers, in estuaries or on the main waterbodies. The number of Ponto-Caspian taxa potentially available for uptake into ballast water would depend, however, on the ships' position on the rivers. Mordukhai-Boltovskoi (1964) reported that 69 Ponto-Caspian invertebrate species were found in the Danube River delta adjacent to the Black Sea, while only 20 species were found 100–150 km farther upstream. Likewise, 56 species were found in the lower Don River (Rostov-on-Don), while only 14 species

were found 250 km upstream in Tsimlyansk Reservoir (Mordukhai-Boltovskoi 1964). Finally, >30 species of malacostracans were found in the Volga River delta at Astrakhan, but only 20 species were found 700 km upstream at Saratov (Mordukhai-Boltovskoi 1979).

Witt et al. (1997) proposed that some Ponto-Caspian crustaceans may have succeeded in invading the Great Lakes because they are not affected by current ballast water treatment measures to the extent that strictly freshwater species would be. This difference may stem from evolved salinity tolerance by some Ponto-Caspian species owing to the geological, climatological and biogeographical history of their native region. Over its geological history the Caspian Sea has experienced periods during which freshwater inflows, primarily from the Volga River, were reduced or eliminated, which altered the salinity regime of the basin (Dumont 1998). Even today pronounced salinity gradients exist within the basin, from freshwater at the Volga inflow in the north, to highly brackish conditions in the south, to near saline conditions in Kara-Bogaz Lake in the east (Dumont 1998). Current guidelines require that ships entering the Great Lakes exchange fresh or estuarine ballast water for highly saline, open-ocean water (United States Coast Guard 1993). This procedure is thought to reduce the

probability of freshwater invasions because freshwater organisms would be purged or killed by exposure to salt water. However, ballast water exchange is often incomplete, and some of the species resident in the Ponto-Caspian basin tolerate a relatively wide range of salinity, opening the possibility that they might survive ballast exchange. Carlton et al. (1995) reported survival of some euryhaline, freshwater taxa following salt-water ballast exchange, a capability they termed the 'Malinska effect'.

It is important to note that not all current residents of Ponto-Caspian waters have the same evolutionary history or salinity tolerance. Mordukhai-Boltovskoi (1964) noted that most of the taxa in the Ponto-Azov basin are mesohaline (5–18‰) taxa, with a smaller group of oligohaline (0.5–5‰) species. There exists approximately as many oligo- to mesohaline taxa as oligohaline taxa, though most live at salinity values between 0‰ and 9‰. Finally, there is a smaller group of brackish water fauna (2–18‰), which prefer waters between 2‰ and 11‰ (Mordukhai-Boltovskoi 1964). Thus, it should be recognized that not all species from Ponto-Caspian basins could tolerate exposure to oceanic waters. Nevertheless, recent invasions in the Great Lakes are skewed toward Ponto-Caspian taxa that possess some degree of salinity tolerance (see Ricciardi and Rasmussen 1998; MacIsaac et al. 1999; Ricciardi and MacIsaac 2000). This pattern raises the possibility that ballast water exchange procedures employed on the Great Lakes may be less effective than desired in preventing invasions (Locke et al. 1993) or that invasions result from hatching of dormant stages, most of which are more tolerant of adverse environmental conditions than active stages (Carlton et al. 1995). Considering the number of Ponto-Caspian and other species with invasion histories that have established in major European ports, additional invasions of the Great Lakes may be anticipated.

Salinity barriers to invasion?

One hypothesis that could account for the recent success of Ponto-Caspian migrants in the Great Lakes is convergence of conditions (i.e. salinity) of the basins. Salinity in most of the Great Lakes increased substantially since the turn of the last century (Beeton 1965; Dobson 1984). Since 1900, absolute increases in major cation and anion concentrations have been greatest in Lakes Ontario and Erie and least in Lake Superior

(Beeton 1965). Sheath (1987) suggested that eight species of benthic marine algae invaded the Great Lakes owing to a tripling of ion concentrations over the past century. Could increased salinity of the Great Lakes account for recent invasions by Ponto-Caspian taxa? It is difficult to test this hypothesis, although we feel that it is unlikely to account for recent patterns. Lake Ontario salinity remains very low both in absolute terms and relative to that of Ponto-Caspian basins. For example, Lake Ontario had only 0.65% of the salt content of mean ocean water by 1981 (Dobson 1984). Spring salinity in Lake Ontario averaged 0.23‰ in 1984 (Dobson 1984) and 0.20‰ in 1990–1993 (V. Richardson, personal communication). Salinity in the Caspian Sea differs among basins, with the lowest values recorded in the north region (0.2–12‰) and higher values in the central and southern regions (12–13.5‰; Dumont 1998). Thus, 1990–1993 spring salinity in Lake Ontario is up to 67 times lower than that of the Caspian Sea, and between 45 and 85 times lower than that of the main region of the Sea of Azov (Zenkevitch 1963). Coastal salinity in the Gulf of Tananrog, Sea of Azov (~1–45 times higher) and in the Dnieper–Bug tidal estuary, Black Sea (~1.5–85 times higher) is typically more similar to that of Lake Ontario (Mordukhai-Boltovskoi 1960; Zhuravlieva 1989). The overall pattern of salinity differences between these basins and Lake Ontario ranges from profound in the main Black, Azov and Caspian seas, to minimal in estuaries of major river inflows to these basins. Most of the NIS that have invaded the Great Lakes are associated with these river–estuary regions. A similar pattern exists for salinity of Lake Erie, where values ranged from 0.20‰ in 1966 (Kramer 1968) to 0.20‰ in 1978 (Richards 1981) to 0.17‰ between 1994 and 1995 (V. Richardson, personal communication). Because salinity appears to have changed little in Lakes Ontario and Erie in recent decades, changes in salinity cannot account for the recent influx of Ponto-Caspian invaders to these Great Lakes.

Directions for future research

The huge number of species invasions reported from ecosystems around the world has provided ecologists with tremendous opportunities to test and advance invasions theory, yet progress has been slow. In our view, progress will be hastened if ecologists adopt different approaches to their studies of aquatic invasions,

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including modelling, meta-analysis exploration of existing concepts, and full utilization of pre- and post-invasion data sets (where they exist) to test emerging concepts. In particular, we expect that modelling approaches that incorporate human vector activity are best able to predict spread of NIS; greater emphasis should be placed on ranking human vectors and invasion corridors. We argue that analysis of invasions of inland lakes holds particular promise in this regard since ecosystem boundaries are clearly delineated, accurate vector flows may be established, and species lists and environmental data often incorporate pre- and post-invasion phases.

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