PERSPECTIVES

Predicting the identity and impact of future biological invaders: a priority for aquatic resource management

Anthony Ricciardi and Joseph B. Rasmussen

Abstract: The identification and risk assessment of potential biological invaders would provide valuable criteria for the allocation of resources toward the detection and control of invasion threats. Yet, freshwater biologists have made few attempts at predicting potential invaders, apparently because such efforts are perceived to be costly and futile. We describe some simple, low-cost empirical approaches that would facilitate prediction and demonstrate their use in identifying high-risk species from an important donor region: the Ponto-Caspian (Black, Caspian, and Azov seas) basin. This region is the source of several freshwater organisms already invading North America, including the zebra mussel (*Dreissena polymorpha*), quagga mussel (*Dreissena bugensis*), ruffe (*Gymnocephalus cernuus*), and round goby (*Neogobius melanostomus*). Based on a thorough literature review, we identify 17 additional Ponto-Caspian animals that have recent invasion histories and are likely to be transported overseas in ship ballast water; moreover, their broad salinity tolerance could allow them to survive an incomplete ballast-water exchange. These results suggest that, unless current vectors are more effectively controlled, the Great Lakes – St. Lawrence River system and other North American inland waterways will continue to receive and be impacted by invasive Eurasian species.

Résumé : L'identification des espèces susceptibles de devenir envahissantes et l'évaluation des risques qu'elles peuvent poser permettraient de définir des critères utiles pour l'affectation de ressources à la détection et à l'élimination des espèces nuisibles. Jusqu'ici, pourtant, les biologistes des eaux douces n'ont guère consacré de temps à cette question, de telles études paraissant être considérées comme coûteuses et inutiles. Nous décrivons ici des méthodes de prévision empiriques, simples et peu coûteuses et nous montrons comment les utiliser pour identifier les espèces à fort potentiel de nuisibilité d'une région qui peut être une importante source de ce genre d'organismes : le bassin pontocaspien (comprenant la mer Noire, la mer Caspienne et la mer d'Azov). C'est en effet de cette région que proviennent plusieurs des espèces qui ont déjà envahi les eaux douces nord-américaines et notamment la moule zébrée (*Dreissena polymorpha*), la moule quagga (*Dreissena bugensis*), la grémille (*Gymnocephalus cernuus*) et le gobie arrondi (*Neogobius melanostomus*). Dans une revue documentaire approfondie, nous avons relevé 17 autres espèces animales d'origine pontocaspienne qui ont récemment envahi d'autres régions et qui pourraient vraisemblablement être transportées jusqu'ici dans l'eau de ballast des bateaux arrivant d'outremer; de plus, comme ces espèces tolèrent des conditions de salinité très variées, elles pourraient survivre dans une eau de ballast incomplètement changée. Ces résultats donnent à penser qu'à défaut d'un contrôle plus rigoureux des vecteurs actuels, de nouvelles espèces envahissantes continueront d'être introduites d'Eurasie et de provoquer des dégâts dans le bassin des Grands Lacs et du Saint-Laurent, ainsi que dans d'autres bassins hydrographiques de l'intérieur des terres en Amérique du Nord.

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Introduction

One of the most pervasive and ecologically damaging effects of human activities is the widespread movement of species beyond their natural range. In most countries, 10^2–10^4 nonindigenous species have been documented and their numbers are increasing (Lodge 1993). In North America, hundreds of exotic plants and animals have become established in aquatic habitats during this century (e.g., Mills et al. 1993*a*, 1996; Cohen and Carlton 1998). Biological invasions will continue to occur, particularly as expanding global trade increases the volume of flora and fauna that is shuttled from one geographic realm to another (e.g., in the ballast water of ships; Carlton and Geller 1993). The aquarium industry, for example,

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Table 1. Some hypothesized general attributes of invasive aquatic species (based on Ehrlich 1986; Groves and Burdon 1986; Lodge 1993; Morton 1979, 1997).

1.	Abundant and widely distributed in original range
2.	Wide environmental tolerance
3.	High genetic variability
4.	Short generation time
5.	Rapid growth
6.	Early sexual maturity
7.	High reproductive capacity
8.	Broad diet (opportunistic feeding)
9.	Gregariousness
10.	Possessing natural mechanisms of rapid dispersal
11.	Commensal with human activity (e.g., ship ballast-water transport)

has deliberately moved thousands of foreign species into North America, paving the way for many unintentional introductions (Welcomme 1984).

Typically, only a small proportion (<10%) of introduced species cause significant impacts (Williamson and Fitter 1996), but some of these have had enormous ecological and economic consequences (OTA 1993). Advance information on invasive and potentially harmful organisms would provide valuable criteria for control measures, such as quarantines and import restrictions (Groves and Burdon 1986; Willan 1987; Jenkins 1996), for allocating resources to maximize detection and for guiding decisions about proposed introductions (e.g., Townsend and Winterbourn 1992). Yet, despite the ecological and economic damage caused by exotics such as the sea lamprey (*Petromyzon marinus*), purple loosestrife (*Lythrum salicaria*), Eurasian watermilfoil (*Myriophyllum spicatum*), zebra mussel (*Dreissena polymorpha*), and others (OTA 1993; Mills et al. 1993*a*), there have been few formal attempts at forecasting unplanned invasions in North American freshwater habitats (but see Mandrak 1989; Mills et al. 1993*b*). This is likely the result of what Rejmanek (1996) described as a "widespread pessimism regarding the prospect of predicting which species are likely to become successful invaders." Such pessimism may have led administrators to ignore the warning of consultants contracted by the Canadian government in 1980 to study the occurrence of foreign organisms in ship ballast water; the consultants reported the transport of living veliger larvae to the Great Lakes in European vessels and predicted the establishment of the zebra mussel in North America (Bio-Environmental Services Ltd. 1981).

Clearly, the science and management of exotic species need to become more proactive to prevent or mitigate invasion threats. In this perspective, we propose that limited, but valuable predictions of the invasion success of different aquatic organisms can be made using documented information. We suggest a few simple, low-cost approaches that would facilitate the identification of potential future aquatic invaders.

Guidelines for identifying potential aquatic invaders

Because any organism can potentially expand its population when introduced into a favorable environment, it would be impractical to construct a comprehensive list of potential invaders based solely on environmental tolerances. A more cost-effective strategy is to identify species with exceptionally high invasion and impact potential. Using concepts currently being developed in both marine and terrestrial invasion biology (e.g., Forcella et al. 1986; Carlton 1996; Mack 1996; Rejmanek 1996), we suggest the following guidelines for such a selection process.

1. Identify potential donor regions and dispersal pathways of future invaders

An essential first step toward predicting invasions is the identification of a potential geographic donor region. Active donor "hot spots" may be identified by their disproportionate numerical contribution to the floras and faunas of various recipient regions using updated species lists (e.g., Mills et al. 1993*a*, 1996; Cohen and Carlton 1998). Regions with similar climates may have a higher potential of successfully exchanging species, although predictions based on this assumption have had varied success (Mack 1996). Potential donor regions may also be identified by large-scale shipping patterns. The global dispersal of aquatic organisms has been achieved primarily through transoceanic shipping (Williams et al. 1988; Carlton and Geller 1993), with ports acting as distribution hubs (Morton 1987; Willan 1987). Therefore, because the bulk of international trade is carried by ships, regions with growing economies should be considered as potential future donors of exotic species.

The presence of strong dispersal pathways and vector activity between the potential donor and target regions may indicate a high probability of future invasion. For example, repeated ballast-water discharges by European shipping using the St. Lawrence Seaway have resulted in the establishment of numerous species of exotic algae, invertebrates, and fishes in the Great Lakes; in fact, over 30% of all invasions in the Great Lakes have occurred following the opening of the Seaway (Mills et al. 1993*a*). Similarly, an increase in the net tonnage of ships arriving from East Asian ports over the past three decades has coincided with introductions of a variety of Asian invertebrates into Pacific North American estuaries (Cordell et al. 1992; Cohen and Carlton 1998). Therefore, Carlton (1996) suggested that an analysis of shipping traffic from regions containing known invaders such as the zebra mussel (e.g., the Great Lakes) or the Japanese crab *Hemigrapsus sanguineus* (e.g., Long Island Sound) could help predict where these species will next invade. While the probability of future North American invasions should be reduced by recent U.S. and Canadian regulations requiring oceanic exchange of ballast water, not all ships comply and incomplete ballast-water exchanges are common (Locke et al. 1993). Because organisms with saline-tolerant life stages could survive an incomplete ballast-water exchange and remain in the residual water or tank bottom sediments (Carlton 1985; Carlton and Geller 1993; Locke et al. 1993), it is likely that ships will continue to introduce new aquatic species into North America.

2. Select potential invaders using biological criteria

After having identified a potential donor region, a pool of probable invaders could be selected based on a general biological profile of invasive species. Some hypothesized attributes of successful aquatic invaders are listed in Table 1. Few of these generalizations have been confirmed by rigorous

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Table 2. Ponto-Caspian fauna established in the Great Lakes – St. Lawrence River system (data from Mills et al. 1993*a*; Witt et al. 1997; Zaranko et al. 1997).

Taxon	Species	Common name	Year of discovery	Mode of invasion
Cnidarians	*Cordylophora caspia*	Hydroid	1956	Unknown
Amphipods	*Echinogammarus ischnus*	Gammarid amphipod	1995	Ship ballast water
Bivalves	*Dreissena polymorpha*	Zebra mussel	1988	Ship ballast water
	Dreissena bugensis	Quagga mussel	1989	Ship ballast water
Fishes	*Cyprinus carpio*	Common carp	1879	Intentional introduction
	Gymnocephalus cernuus	Ruffe	1987	Ship ballast water
	Neogobius melanostomus	Round goby	1990	Ship ballast water
	Proterorhinus marmoratus	Tubenose goby	1990	Ship ballast water

statistical and experimental studies, and each has exceptions (Simberloff 1989; Lodge 1993); however, they apply well to a wide variety of invasive organisms and thus provide a useful basis for prediction. For example, a species with high genetic variability, wide tolerance limits, and natural mechanisms for rapid dispersal (e.g., the zebra mussel; Garton and Haag 1991) is more likely to colonize a large geographic range (Ehrlich 1986; Groves and Burdon 1986). Studies on herbaceous plants have shown that the size of the current distribution of a species is often a good predictor of invasiveness (Forcella et al. 1986; Roy et al. 1991; Rejmanek 1996). In fact, a large range is possessed by many invasive freshwater plants and animals, e.g., water hyacinth (*Eichornia crassipes*) (Groves and Burdon 1986), brown trout (*Salmo trutta*) (MacCrimmon et al. 1970), the cladoceran *Daphnia lumholtzi* (Havel et al. 1995), the hydrobiid snail *Potamopyrgus antipodarum* (Zaranko et al. 1997), and the Asiatic clam *Corbicula fluminea* (Morton 1997).

The most consistent attribute of an invasive species is human commensalism. Most successful invaders, particularly major pest species, use dispersal mechanisms that involve human activity (Ehrlich 1986; Groves and Burdon 1986; Morton 1979, 1997). Many invasive bivalves and crustaceans possess planktonic larvae that are more easily transported in ship ballast water (Morton 1979; Carlton 1985; Carlton and Geller 1993). Moreover, recent introductions of the amphipod *Echinogammarus ischnus* (Witt et al. 1997) and round goby (*Neogobius melanostomus*) (Jude et al. 1995) demonstrate that at least some organisms that lack a true planktonic stage can be transported by this mechanism. We recommend that profile-based predictions focus on the ability of an organism to exploit ballast-water transport and that particular attention be given to euryhaline organisms that are either planktonic (pelagic) or have planktonic life stages or behaviours.

3. Use invasion history as a predictive criterion

More reliable predictions can be made by assuming that invasive species will continue to invade elsewhere if conditions permit and opportunities arise (Daehler and Strong 1993; Carlton 1996). This premise can be combined with the previous profile-based approach by focusing on species that have an invasion history and an ability to interface with human-mediated dispersal mechanisms, particularly transoceanic shipping. Predictive power can be further enhanced by considering only species that have recently invaded sites (new potential donor regions) from which subsequent dispersal to the target region is more likely. Using this method, Mills et al. (1993*b*) successfully predicted the invasion of the Great Lakes by *P. antipodarum*, a snail with an extensive invasion history in Europe; it was recently reported from Lake Ontario (Zaranko et al. 1997). Similarly, *Limnoperna fortunei*, an Asian freshwater mussel that is currently expanding its range in both the Western Pacific and South America, is predicted to become established in North America (Ricciardi 1998).

Application to predicting invasions: the Great Lakes – Ponto-Caspian example

To demonstrate these approaches, we have selected the Great Lakes – St. Lawrence River as the target region and the Ponto-Caspian (Black, Caspian, and Azov seas) basin as a potential donor region. The former has been colonized by >140 exotic species, of which more than half are of Eurasian origin (Mills et al. 1993*a*; Witt et al. 1997; Zaranko et al. 1997). The Ponto-Caspian basin possesses a diverse endemic fauna (Mordukhai-Boltovskoi 1979*a*), is linked to North America by extensive shipping traffic (Locke et al. 1993; Mills et al. 1993*a*), and is the source of numerous invasive animals characterized by a broad ecological adaptability derived from having evolved under extremely variable hydrological and saline conditions (Zenkevitch 1963). Several Ponto-Caspian species are already established in the Great Lakes system (Table 2); with perhaps one exception, tubenose goby (*Proterorhinus marmoratus*), each of these has had a previous invasion history. Most (75%) were introduced by ballast water within the last 15 years. In fact, several ballast-water introductions of Eurasian fauna into the Great Lakes in the 1970s and 1980s had established a pattern of invasion prior to the arrival of the zebra mussel (Mills et al. 1993*a*). A focused search of other species likely to use this pathway would have identified the zebra mussel as a probable invader on the basis of its rapidly expanding European range, life history traits that facilitate ballast-water transport (i.e., planktonic larvae, wide salinity tolerance), and occurrence in estuarine waters where shipping traffic is frequent.

Using recent European literature (published after 1960) and Ponto-Caspian species lists provided by Mordukhai-Boltovskoi (1979*a*), we applied a combination of our predictive approaches to identify a pool of potential North American invaders. We considered 82 euryhaline macroinvertebrates that are endemic to freshwater regions of the Caspian Sea basin. From these, we selected species that belong to taxonomic

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Table 3. Ponto-Caspian fauna predicted to invade the Great Lakes – St. Lawrence River system.

Taxon	Species	Common name	Literature source[a]
Polychaetes	*Hypania invalida*	Polychaete worm	9, 10, 11, 14, 15, 16, 23
Amphipods	*Corophium curvispinum*	Corophiid amphipod	1, 4, 6, 7, 10, 11, 17, 19, 20, 21, 22, 23
	Corophium sowinskyi	Corophiid amphipod	7, 10, 11, 15
	Dikerogammarus haemobaphes	Gammarid amphipod	6, 9, 10, 11, 16
	Dikerogammarus villosus	Gammarid amphipod	10, 11, 13, 16
	Pontogammarus obesus	Gammarid amphipod	6, 7, 10, 11
	Pontogammarus robustoides	Gammarid amphipod	6, 10, 11, 16
	Obesogammarus crassus	Gammarid amphipod	6, 7, 10, 11
Mysids	*Limnomysis benedeni*	Mysid shrimp	10, 11, 12, 16
	Paramysis intermedia	Mysid shrimp	10, 11, 12, 18
	Paramysis lacustris	Mysid shrimp	3, 10, 11, 12
	Paramysis ullskyi	Mysid shrimp	10, 11, 12, 18
	Hemimysis anomala	Mysid shrimp	10, 11, 24
Bivalves	*Hypanys* (*Monodacna*) *colorata*	Cardiid clam	8, 10, 11, 12, 15, 23
Fishes	*Clupeonella caspia*	Tyulka; Caspian kilka	5, 10, 11, 12
	Benthophilus stellatus	Starry goby	10, 11, 12, 23
	Neogobius fluviatilis	Monkey goby	2, 10, 11, 12, 23

[a]Sources of information used in our literature survey: 1, Bachmann et al. 1997; 2, Biro 1972; 3, Bondarenko and Yablonskaya 1979; 4, Bortkevitch 1987; 5, Hoestland 1991; 6, Jazdzewski 1980; 7, Jazdzewski and Konopacka 1988; 8, Kogan 1970; 9, Lvova et al. 1996; 10, Mordukhai-Boltovskoi 1964; 11, Mordukhai-Boltovskoi 1979*a*; 12, Mordukhai-Boltovskoi 1979*b*; 13, Musko 1989; 14. Nagy 1979; 15, Pirogov et al. 1991; 16, Pligin and Yemel'yanova 1989; 17, Pygott and Douglas 1989; 18, Tarasov 1996; 19, Taylor and Harris 1986; 20, Tittizer et al. 1995; 21, van den Brink et al. 1993; 22, van der Velde et al. 1994; 23, Zenkevitch 1963; 24, Salemaa and Hietalahti 1993.

groups whose life history stages are likely to survive oceanic transport in ship ballast water (cf. Carlton 1985; Carlton and Geller 1993; Locke et al. 1993). From the resulting set (59 species), we identified those that had a documented invasion history, i.e., recent evidence of having successfully invaded habitats outside their natural range; for species that were introduced deliberately into new basins during stocking programs, we required evidence of unintentional secondary spread. Species that are currently invasive in Europe but that were judged unlikely to be transported in ship ballast water (e.g., the crayfish *Astacus leptodactylus*; Holdich and Reeve 1991) were rejected. Other groups (e.g., copepods, cladocerans) were not considered because of taxonomic inconsistencies or insufficient information on invasion history. Our survey (meant primarily to be illustrative rather than comprehensive) revealed 17 Ponto-Caspian invertebrates that have high invasion potential and are likely to survive an incomplete ballast-water exchange and thus should be considered as probable future immigrants to the Great Lakes (Table 3).

High-risk species: potential impact of Ponto-Caspian fauna

Can we predict the ecological impact of a Great Lakes' invasion by any of these species? An effective approach toward predicting the impact of an invader is to identify patterns in multiple, spatially independent invasions (e.g., Ricciardi et al. 1995, 1996, 1997; Grosholz and Ruiz 1996). While correlative analyses are often limited by a scarce amount of comparable quantitative data, descriptive information on the impacts of previous invasions may still provide a basis for useful predictions, although with a high degree of uncertainty (e.g., Grosholz and Ruiz 1996; Moyle and Light 1996). Simple, but powerful predictions may result by assuming that invaders will cause significant impacts in the target region if they have already done so in other regions (e.g., Forcella et al. 1986; Townsend and Winterbourn 1992; Ricciardi et al. 1995; Grosholz and Ruiz 1996). Arguably, this approach would have identified Eurasian invaders like the zebra mussel, ruffe (*Gymnocephalus cernuus*), and *Bythotrephes* as species of high impact potential prior to their arrival in North America. Therefore, we searched the literature for evidence of ecosystem alterations by our 17 Ponto-Caspian invertebrates or closely related species. Recognizing that these results are both speculative and subjective, our review suggests that each of the following species would have a significant ecological impact in the Great Lakes – St. Lawrence River system

Corophium spp.

The suspension-feeding amphipods *Corophium curvispinum* and *Corophium sowinskyi* inhabit fresh and brackish waters of lakes and rivers (Taylor and Harris 1986) and have been spreading across Europe since ca. 1900, using newly constructed canals and shipping traffic to enter adjacent river basins (Jadzewski 1980). Both species live in massive networks of mud tubes constructed on stable substrata. In the 1980s, *C. curvispinum* invaded the Rhine, colonizing hundreds of kilometres of the river and establishing enormous densities ($100\,000 - 750\,000 \cdot m^{-2}$) within only a few years (van den Brink et al. 1993). Similar high densities ($>100\,000 \cdot m^{-2}$) have been recently recorded in other European rivers (Tittizer et al. 1995; Bachmann et al. 1997). By fixing thick layers (1–4 cm) of mud to the surfaces of stones, *C. curvispinum* displaced filter-feeding caddisflies (*Hydropsyche* sp.) and the zebra mussel from the Dutch Lower Rhine; zebra mussel larvae were

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denied suitable settling surfaces, and adult mussels were smothered to death by muddy encrustations (van der Velde et al. 1994). Competition for particulate food may also have occurred. Reductions in total organic carbon and suspended material in the lower Rhine have been attributed to the explosive population growth and filtration activity of the amphipod (van den Brink et al. 1993). These observations suggest that the introduction of Ponto-Caspian corophiids could significantly alter littoral communities and food webs in North American river systems.

Mysids

Mysid shrimp are diverse and abundant in shallow littoral areas of Ponto-Caspian deltas and estuaries (Mordukhai-Boltovskoi 1964, 1979*a*). A few species have demonstrated high invasion potential. Recognized as an important food item for fish, *Hemimysis anomala* and *Paramysis* spp. (*P. lacustris*, *P. intermedia*, *P. ullskyi*) have been intentionally transplanted, with remarkable success, into numerous lakes and reservoirs in Eurasia and the Baltic Peninsula, in which they have rapidly formed dense populations (Mordukhai-Boltovskoi 1964, 1979*a*). Another mysid, *Limnomysis benedeni*, was accidentally introduced into Dnieper reservoirs (Pligin and Yemel'yanova 1989) and has also spread 1700 km up the Danube River. These species have continued to expand their ranges in recent decades (Mordukhai-Boltovskoi 1979*a*, 1979*b*; Salemaa and Hietalahti 1993; Tarasov 1996).

Ponto-Caspian mysids differ strikingly from their North American relatives by their adaptation to shallow, warm waters; for example, the metabolic rate of *P. lacustris* at 20°C is similar to that of cold-water mysids at 10°C (Bondarenko and Yablonskaya 1979). This being the case, *Paramysis* and others could potentially invade a large number of North American lakes that are currently devoid of mysids. Their impact in these lakes would likely include a reduction of zooplankton (with concomitant negative effects on planktivorous fishes and higher consumers; cf. Spencer et al. 1991) and biomagnification of contaminants at higher trophic levels through a lengthening of the food chain; PCB and mercury levels in pelagic fishes have been shown to be higher in North American lakes containing mysids than in mysid-free lakes (Rasmussen et al. 1990; Cabana et al. 1994).

Clupeonella caspia

Three fishes from the Ponto-Caspian region, the ruffe, round goby, and tubenose goby, were introduced into the Great Lakes by ballast-water discharge in the 1980s (Mills et al. 1993*a*; Jude et al. 1995). Additional species that may arrive in the future include a Caspian herring, the "tyulka" (*Clupeonella caspia*). This pelagic planktivore is a fast-growing, eurythermal, and euryhaline species that has historically inhabited coastal waters of the Black and Caspian seas, but has expanded its range throughout the Volga, Don, and Kama rivers in recent decades (Hoestland 1991). In Volga River reservoirs, the tyulka is reported to have become abundant and suppressed native fishes (Mordukhai-Boltovskoi 1979*b*). It is capable of extreme population fluctuations, and mass winter mortalities in reservoirs have been reported (Hoestland 1991). We predict that the tyulka would cause reductions of native planktivores (e.g., coregonids, shiners, yellow perch (*Perca flavescens*)) in the Great Lakes system, similar to the observed impacts of another introduced clupeid, the alewife (*Alosa pseudoharengus*) (Brandt et al. 1987). The tyulka poses the added threat of invading lakes that are currently devoid of important pelagic forage fish, which could result in increased contaminant levels in piscivores, an effect already documented for introduced smelt (Vander Zanden and Rasmussen 1996).

Conclusion: using predictive approaches as an early-warning system

We have demonstrated how simple, low-cost approaches could be used to identify species with high invasion and impact potential. In spite of any perception that "the worst is over" (i.e., all significant invaders have already arrived), our results suggest that the Great Lakes – St. Lawrence River system and other North American inland waterways will continue to receive and be impacted by invasive Eurasian fauna.

Because the ecological and economic costs of invasion are high (OTA 1993), resources should be allocated towards prevention. Preventative measures depend on advance knowledge of invasion threats, which can be gained from careful monitoring of information networks (e.g., literature, the internet, symposia), and the application of the guidelines we have described. Such endeavors would be aided greatly by the development of a broadly accessible electronic inventory of aquatic invaders, with information about their life history, habitat requirements, dispersal patterns, and methods of control. Even when invasion is imminent, advance knowledge could prepare us for dealing with the ecological and technological impacts that may follow. Given the detrimental effects of invasive aquatic organisms on fisheries, biodiversity, outdoor recreation, and water supply systems (e.g., Morton 1979, 1997; Kaufman 1992; Lodge 1993; Mills et al. 1993*a*; OTA 1993), the identification of future invaders should be a common priority among scientists and policy makers.

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References

Bachmann, V., Usseglio-Polatera, P., Cegielka, E., Wagner, P., Poinsaint, J.F., and Moreteau, J.C. 1997. Premières observations sur la coexistence de *Dreissena polymorpha*, *Corophium curvispinum* et *Corbicula* spp. dans la rivière Moselle. Bull. Fr. Pêche Piscicult. **344/345**: 373–384.

Bio-Environmental Services Ltd. 1981. The presence and implication of foreign organisms in ship ballast waters discharged into the Great Lakes. Report prepared for the Environmental Protection Service, Environment Canada, Ottawa, Ont.

Biro, P. 1972. *Neogobius fluviatilis* in Lake Balaton: a Pontocaspian goby new to the fauna of central Europe. J. Fish Biol. **4**: 249–256.

Bondarenko, M.V., and Yablonskaya, E.A. 1979. The rate of oxygen consumption by the mysid *Paramysis lacustris* (Czern.) from the northern Caspian Sea. *In* Effect of water management on the biological productivity of the Azov and Caspian seas. VNIRO, Moscow. pp. 65–69. (In Russian with English summary.)

Bortkevitch, L.V. 1987. Ecology and production of *Corophium curvispinum* in the estuarine sections of rivers of the northwest Black Sea coast. Hydrobiol. J. **23**: 91–93.

Brandt, S.B., Mason, D.M., MacNeill, D.B., Coates, T., and Gannon,

© 1998 NRC Canada

J.E. 1987. Predation by alewives on larvae of yellow perch in Lake Ontario. Trans. Am. Fish. Soc. **116**: 641–645.

Cabana, G., Tremblay, A., Kalff, J., and Rasmussen, J.B. 1994. Pelagic food chain structure in Ontario lakes: a determinant of mercury levels in lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. **51**: 381–389.

Carlton, J.T. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanogr. Mar. Biol. Annu. Rev. **23**: 313–371.

Carlton, J.T. 1996. Pattern, process, and prediction in marine invasion ecology. Biol. Conserv. **78**: 97–106.

Carlton, J.T., and Geller, J.B. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. Science (Washington, D.C.), **261**: 78–82.

Cohen, A.N., and Carlton, J.T. 1998. Accelerating invasion rate in a highly invaded estuary. Science (Washington, D.C.), **279**: 555–558.

Cordell, J.R., Morgan, C.A., and Simenstad, C.A. 1992. Occurrence of the Asian calanoid copepod *Pseudodiaptomus inopinus* in the zooplankton of the Columbia River estuary. J. Crustacean Biol. **12**: 260–269.

Daehler, C.C., and Strong, D.R., Jr. 1993. Prediction and biological invasions. Trends Ecol. Evol. **8**: 380.

Ehrlich, P.R. 1986. Which animal will invade? *In* Ecology of biological invasions of North America and Hawaii. *Edited by* H.A. Mooney and J.A. Drake. Springer-Verlag, New York. pp. 79–95.

Forcella, F., Wood, J.T., and Dillon, S.P. 1986. Characteristics distinguishing invasive weeds within *Echium* (Bugloss). Weed Res. **26**: 351–364.

Garton, D.W., and Haag, W.R. 1991. Heterozygosity, shell length and metabolism in the European mussel, *Dreissena polymorpha*, from a recently established population in Lake Erie. Comp. Biochem. Physiol. A Comp. Physiol. **99**: 45–48.

Grosholz, E.D., and Ruiz, G.M. 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. Biol. Conserv. **78**: 59–66.

Groves, R.H., and Burdon, J.J. (*Editors*). 1986. Ecology of biological invasions. Cambridge University Press, New York.

Havel, J.E., Mabee, W.R., and Jones, J.R. 1995. Invasion of the exotic cladoceran *Daphnia lumholtzi* into North American reservoirs. Can. J. Fish. Aquat. Sci. **52**: 151–160.

Hoestland, H. 1991. Clupeidae, Anguillidae. Vol. 2. The freshwater fishes of Europe. AULA-Verlag, Wiesbaden.

Holdich, D.M., and Reeve, I.D. 1991. Distribution of freshwater crayfish in the British Isles, with particular reference to crayfish plague, alien introductions and pollution. Aquat. Conserv. Mar. Freshwater Ecosyst. **1**: 139–158.

Jazdzewski, K. 1980. Range extensions of some gammaridean species in European inland waters caused by human activity. Crustaceana Suppl. (Leiden), **6**: 84–107.

Jazdzewski, K., and Konopacka, A. 1988. Notes on the gammaridean Amphipoda of the Dniester River basin and eastern Carpathians. Crustaceana Suppl. (Leiden), **13**: 72–89.

Jenkins, P.T. 1996. Free trade and exotic species introductions. Conserv. Biol. **10**: 300–302.

Jude, D.J., Janssen, J., and Crawford, G. 1995. Ecology, distribution and impact of the newly introduced round (and) tubenose gobies on the biota of the St. Clair and Detroit rivers. *In* The Lake Huron ecosystem: ecology, fisheries and management. *Edited by* M. Munawar, T. Edsall, and J. Leach. SPB Academic Publishing, Amsterdam, The Netherlands. pp. 447–460.

Kaufman, L. 1992. Catastrophic change in species-rich freshwater ecosystems. BioScience, **42**: 846–858.

Kogan, A.V. 1970. The food resources of Tsimlyansk Reservoir and the extent of their utilization by common fish species. J. Ichthyol. **10**: 667–674.

Locke, A., Reid, D.M., van Leeuwen, H.C., Sprules, W.G., and Carlton, J.T. 1993. Ballast water exchange as a means of controlling dispersal of freshwater organisms ships. Can. J. Fish. Aquat. Sci. **50**: 2086–2093.

Lodge, D.M. 1993. Biological invasions: lessons for ecology. Trends Ecol. Evol. **8**: 133–137.

Lvova, A.A., Pally, A.V., and Sokolova, N.Y. 1996. Ponto-Caspian immigrants in the Moscow River within Moscow City. Zool. Zh. **75**: 1273–1275. (In Russian with English summary.)

MacCrimmon, H.R., Marshall, T.L., and Gots, B.L. 1970. World distribution of brown trout, *Salmo trutta*: further observations. J. Fish. Res. Board Can. **27**: 811–818.

Mack, R.N. 1996. Predicting the identity and fate of plant invaders: emergent and emerging approaches. Biol. Conserv. **78**: 107–121.

Mandrak, N.E. 1989. Potential invasion of the Great Lakes by fish species associated with climatic warming. J. Great Lakes Res. **15**: 306–316.

Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C.L. 1993*a*. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. J. Great Lakes Res. **19**: 1–54.

Mills, E.L., Leach, J.H., Secor, C.L., and Carlton, J.T. 1993*b*. What's next? The prediction and management of exotic species in the Great Lakes. Report to the Great Lakes Fishery Commission, Ann Arbor, Mich.

Mills, E.L., Scheuerell, M.D., Strayer, D.L., and Carlton, J.T. 1996. Exotic species in the Hudson River basin: a history of invasions and introductions. Estuaries, **19**: 814–823.

Mordukhai-Boltovskoi, F.D. 1964. Caspian fauna beyond the Caspian Sea. Int. Rev. Gesamten Hydrobiol. **53**: 357–408.

Mordukhai-Boltovskoi, F.D. 1979*a*. Composition and distribution of Caspian fauna in the light of modern data. Int. Rev. Gesamten Hydrobiol. **64**: 1–38.

Mordukhai-Boltovskoi, F.D. 1979*b*. The River Volga and its life. W. Junk Publishers, The Hague, The Netherlands.

Morton, B. 1979. Freshwater fouling bivalves. *In* Proceedings of the First International Corbicula Symposium (1977). *Edited by* J.C. Britton. Texas Christian University, Fort Worth, Tex. pp. 1–14.

Morton, B. 1987. Recent marine introductions into Hong Kong. Bull. Mar. Sci. **41**: 503–513.

Morton, B. 1997. The aquatic nuisance species problem: a global perspective and review. *In* Zebra mussels and aquatic nuisance species. *Edited by* F. D'Itri. Ann Arbor Press, Chelsea, Mich. pp. 1–53.

Moyle, P.B., and Light, T. 1996. Fish invasions in California: do abiotic factors determine success? Ecology, **77**: 1666–1670.

Musko, I.B. 1989. Amphipoda (Crustacea) in the littoral zone of Lake Balaton (Hungary): qualitative and quantitative studies. Int. Rev. Gesamten Hydrobiol. **74**: 195–205.

Nagy, S. 1979. Erster Fund des Polychaeten *Hypania invalida* (Polychaeta, Ampharetidae) im Tschehoslowakischen Donauabschnitt. Vestn. Cesk. Spol. Zool. **43**: 132–137. (In German with English summary.)

Office of Technology Assessment (OTA). 1993. Harmful nonindigenous species in the United States. Report No. OTA-F-565, U.S. Government Printing Office, Washington, D.C.

Pirogov, W., Pilchakov, V.A., Zinchenko, T.D., Karpiuk, M.I., and Edskyi, L.V. 1991. The new elements in benthic fauna of the reservoirs of the Volga-Kama Cascade. Hydrobiol. J. **27**: 53–58.

Pligin, Y.V., and Yemel'yanova, L.V. 1989. Acclimatization of Caspian invertebrates in Dnieper reservoirs. Hydrobiol. J. **25**: 1–9.

Pygott, J.R., and Douglas, S. 1989. Current distribution of *Corophium curvispinum* Sars. var. *devium* Wundsch (Crustacea: Amphipoda) in Britain with notes on its ecology in the Shropshire Union Canal. Naturalist (Leeds), **114**: 15–17.

Rasmussen, J.B., Rowan, D.J., Lean, D.R.S., and Carey, J.H. 1990. Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. Can. J. Fish. Aquat. Sci. **47**: 2030–2038.

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Rejmanek, M. 1996. A theory of seed plant invasiveness: the first sketch. Biol. Conserv. **78**: 171–181.

Ricciardi, A. 1998. Global range expansion of the Asian mussel *Limnoperna fortunei* (Mytilidae): another fouling threat to freshwater systems. Biofouling. In press.

Ricciardi, A., Whoriskey, F.G., and Rasmussen, J.B. 1995. Predicting the intensity and impact of *Dreissena* invasion on native unionid bivalves from *Dreissena* field density. Can. J. Fish. Aquat. Sci. **52**: 1449–1461.

Ricciardi, A., Whoriskey, F.G., and Rasmussen, J.B. 1996. Impact of *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence River. Can. J. Fish. Aquat. Sci. **53**: 1434–1444.

Ricciardi, A., Whoriskey, F.G., and Rasmussen, J.B. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Can. J. Fish. Aquat. Sci. **54**: 2596–2608.

Roy, J., Navas, M.L., and Sonié, L. 1991. Invasion by annual brome grasses: a case study challenging the homocline approach to invasions. *In* Biogeography of Mediterranean invasions. *Edited by* R.H. Groves and F. Di Castri. Cambridge University Press, Cambridge, U.K. pp. 207–224.

Salemaa, H., and Hietalahti, V. 1993. *Hemimysis anomala* G.O. Sars (Crustacea: Mysidacea) — immigration of a Pontcaspian mysid into the Baltic Sea. Ann. Zool. Fennici, **30**: 271–276.

Simberloff, D. 1989. Which insect introductions succeed and which fail? *In* Biological invasions: a global perspective. *Edited by* J.A. Drake et al. John Wiley & Sons, New York. pp. 61–75.

Spencer, C.N., McClelland, B.R., and Stanford, J.A. 1991. Shrimp stocking, salmon collapse, and eagle displacement. BioScience, **41**: 14–21.

Tarasov, A.G. 1996. Macrocrustaceans (Malacostraca) in the Ural River. Hydrobiol. J. **32**: 18–30.

Taylor, P.M., and Harris, R.R. 1986. Osmoregulation in *Corophium curvispinum* (Crustacea: Amphipoda), a recent coloniser of freshwater. I. Sodium ion regulation. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. **156**: 323–329.

Tittizer, T., Leuchs, H., and Banning, M. 1995. The consequences of river impoundments for the macrozoobenthos — demonstrated at the example of the River Danube in Germany. Misc. Zool. Hung. **10**: 73–84.

Townsend, C.R., and Winterbourn, M.J. 1992. Assessment of the environmental risk posed by an exotic fish: the case of the proposed introduction of channel catfish (*Ictalurus punctatus*) to New Zealand. Conserv. Biol. **6**: 273–282.

van den Brink, F.W.B., van der Velde, G., and bij de Vaate, A. 1993. Ecological aspects, explosive range extension and impact of a mass invader, *Corophium curvispinum* Sars, 1895 (Crustacea: Amphipoda), in the Lower Rhine (The Netherlands). Oecologia (Heidelb.), **93**: 224–232.

van der Velde, G., Paffen, B.G.P., van den Brink, F.W.B., bij de Vaate, A., and Jenner, H.A. 1994. Decline of zebra mussel populations in the Rhine: competition between two mass invaders (*Dreissena polymorpha* and *Corophium curvispinum*). Naturwissenschaften, **81**: 32–34.

Vander Zanden, M.J., and Rasmussen, J.B. 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. Ecol. Monogr. **68**: 451–477.

Welcomme, R.L. 1984. International transfers of inland fish species. *In* Distribution, biology, and management of exotic fishes. *Edited by* W.R. Courtnay, Jr., and J.R. Stauffer, Jr. Johns Hopkins University Press, Baltimore, Md. pp. 22–40.

Willan, R.C. 1987. The mussel *Musculista senhousia* in Australia: another aggressive alien highlights the need for quarantine at ports. Bull. Mar. Sci. **41**: 475–489.

Williams, R.J., Griffiths, F.B., van der Wal, E.J., and Kelly, J. 1988. Cargo vessel ballast water as a vector for the transport of non-indigenous marine species. Estuarine Coastal Shelf Sci. **26**: 409–420.

Williamson, M., and Fitter, A. 1996. The varying success of invaders. Ecology, **77**: 1655–1661.

Witt, J.D.S., Hebert, P.D.N., and Morton, W.B. 1997. *Echinogammarus ischnus*: another crustacean invader in the Laurentian Great Lakes basin. Can. J. Fish. Aquat. Sci. **54**: 264–268.

Zaranko, D.T., Farara, D.G., and Thompson, F.G. 1997. Another exotic mollusc in the Laurentian Great Lakes: the New Zealand native *Potamopyrgus antipodarum* (Gray 1843) (Gastropoda, Hydrobiidae). Can. J. Fish. Aquat. Sci. **54**: 809–814.

Zenkevitch, L. 1963. Biology of the seas of the U.S.S.R. George Allen and Unwin Ltd., London, U.K.

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