PERSPECTIVE / PERSPECTIVE

Ballast-mediated animal introductions in the Laurentian Great Lakes: retrospective and prospective analyses

Igor A. Grigorovich, Robert I. Colautti, Edward L. Mills, Kristen Holeck, Albert G. Ballert, and Hugh J. MacIsaac

Abstract: Since completion of the St. Lawrence Seaway in 1959, at least 43 nonindigenous species (NIS) of animals and protists have established in the Laurentian Great Lakes, of which ~67% were attributed to discharge of ballast water from commercial ships. Twenty-three NIS were first discovered in four "hotspot" areas with a high representation of NIS, most notably the Lake Huron – Lake Erie corridor. Despite implementation of the voluntary (1989, Canada) and mandatory (1993, U.S.A.) ballast water exchange (BWE) regulations, NIS were discovered at a higher rate during the 1990s than in the preceding three decades. Here we integrate knowledge of species' invasion histories, shipping traffic patterns, and physicochemical factors that constrain species' survivorship during ballast-mediated transfer to assess the risk of future introductions to the Great Lakes. Our risk-assessment model identified 26 high-risk species that are likely to survive intercontinental transfer in ballast tanks. Of these, 10 species have already invaded the Great Lakes. An additional 37 lower-risk species, of which six have already invaded, show some but not all attributes needed for successful introduction under current BWE management. Our model indicates that the Great Lakes remain vulnerable to ship-mediated NIS invasions.

Résumé : Depuis l'ouverture de la Voie maritime du Saint-Laurent en 1959, au moins 43 espèces non indigènes (NIS) d'animaux et de protistes se sont établies dans les Grands Lacs laurentiens et la présence de ~67 % d'entre elles s'explique, croit-on, par la vidange de l'eau des ballasts des navires commerciaux. Vingt-trois des NIS ont été découvertes la première fois dans quatre « points chauds » qui abritent un grand nombre de NIS, en particulier dans le corridor du lac Huron au lac Érié. Malgré la mise en application des règlements volontaire (Canada, 1989) et obligatoire (É.-U., 1993) sur l'échange des eaux de ballasts (« ballast water exchange » (BWE)), les NIS ont été retrouvées à un taux plus élevé pendant les années 1990 que durant les trois décennies précédentes. On trouvera ici une synthèse des connaissances sur l'histoire des invasions des espèces, sur les patterns de transport maritime et sur les facteurs physicochimiques qui restreignent la survie des espèces durant leur transport dans les ballasts, ainsi qu'une évaluation des risques d'introductions futures dans les Grands Lacs. Notre modèle d'évaluation des risques identifie 26 espèces qui présentent des risques élevés et qui sont susceptibles de survivre à des transferts intercontinentaux dans les ballasts; dix de celles-ci se retrouvent déjà dans les Grands Lacs. Trente-sept espèces additionnelles, qui représentent des risques plus faibles et dont six sont déjà présentes dans les Grands Lacs, possèdent une partie seulement des caractéristiques nécessaires pour une invasion réussie dans les conditions actuelles de la gestion de BWE. Notre modèle démontre que les Grands Lacs restent vulnérables aux invasions de NIS via le transport maritime.

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Introduction

Since the settlement of North America by Europeans, human activities have facilitated introductions of nonindigenous species (NIS) into the Laurentian Great Lakes (Mills et al. 1993*a*). Thus far, some 162 aquatic species have been recognized as introduced and established in this basin (Ricciardi 2001). Discharge of ballast water by commercial ships has been identified as a major vector in the transfer of NIS to the Great Lakes over the past century (Mills et al. 1993*a*; Ricciardi 2001). Consequently, efforts to reduce the risk of future introductions have focused on ballast water management. Voluntary ballast water exchange (BWE) guidelines were initiated by the Canadian government in 1989 and made mandatory by U.S. legislation in 1993 (United States Coast Guard 1993). Vessels that carry ballast water originating from freshwater or coastal brackish-water ports outside of the Great Lakes and that declare "ballast on board" (BOB) status are subject to these regulations and are requested either to exchange ballast during their ocean voyage or to seal ballast tanks while operating on the Great Lakes (United States Coast Guard 1993). The BWE procedure is intended to purge brackish water and freshwater organisms in ballast tanks and to kill those remaining by osmotic stress (United States Coast Guard 1993).

Despite a high level of compliance with these regulations (e.g., Wiley 1995), living brackish water and freshwater species continue to arrive to the Great Lakes in vessels that report open-ocean BWE, indicating that the current ballast management strategy may not fully protect the lakes from additional invasions (Locke et al. 1993). Vessels declaring "no ballast on board" (NOBOB) status are not subject to ballast management regulations; however, they enter the Great Lakes carrying unpumpable residual ballast water and sediment that contain viable organisms (e.g., Locke et al. 1991, 1993; Bailey et al. 2003). Thus, activity of NOBOB ships may predispose the lakes to invasion risk.

Modeling ballast-mediated introductions has allowed an initial assessment of risk arising from ballast water releases from the two categories (i.e., BOB and NOBOB) of ships entering the Great Lakes (MacIsaac et al. 2002). This model predicted that NOBOB vessels apparently pose a greater collective risk of ballast-mediated introductions, largely because they dominate (~90%; Colautti et al. 2003) trade into the Great Lakes and convey live organisms or viable resting stages. Other models have sought to identify potential invaders to the Great Lakes based on species invasion histories elsewhere and inbound shipping patterns (Mills et al. 1993*b*; Ricciardi and Rasmussen 1998). These forecasts have had only limited success thus far, perhaps because the ability of NIS to survive ballast-mediated dispersal was not considered explicitly.

In this study, we conduct a retrospective analysis of the mechanisms and hypotheses associated with introductions of aquatic animals and protists into the Great Lakes since the completion of the St. Lawrence Seaway in 1959. We examine transoceanic shipping traffic in the Great Lakes during 1959–2000 to explore patterns of BWE for BOB and NOBOB ships entering this basin. Moreover, we synthesize information regarding the timing and location of first occurrence, dispersal vectors, and life history traits for NIS recorded in the Great Lakes and contrast these characteristics with patterns of shipping traffic and BWE. In addition, we develop a multistep risk-assessment approach to forecast potential invaders to the Great Lakes by integrating current knowledge of shipping traffic to the basin, species' invasion histories in potential donor regions, and life history traits that facilitate survival in ballast water.

Materials and methods

Historical and emerging patterns of introduction

We assembled a comprehensive inventory of the nonindigenous aquatic metazoans and protists recorded in the Great Lakes basin from 1959 through 1999. To appraise the emerging patterns of NIS introductions under ballast water management in this basin, we chose the mandatory BWE legislation (1993, U.S.A.). Although Wiley (1995) reported that ~90% of ships complied with the Canadian voluntary guidelines enacted in 1989, many vessels likely undertook only partial exchange (e.g., Drake et al. 2001). Both BWE regulations were considered when analysing the chronology of NIS discovery. Time trends in discovery of NIS during 1959–1988 (before the ballast regulation period) were contrasted with those during 1989–1999 (after the ballast regulation period) by comparing regression line slopes. The chronological arrangement of NIS records, however, may not fully represent the rate of invasions because of time lags between the initial inoculation of NIS and their discovery (see below).

Introduced species were defined as those that successfully spread beyond their historic or native geographic range and colonized the Great Lakes via natural or human-mediated dispersal vectors. We did not distinguish between NIS whose introductions resulted from transfer across broad geographic distances (e.g., *Schizopera borutzkyi*) and those that represented local dispersal from an adjacent area (e.g., *Cyclops strenuus*). We considered only those NIS known or suspected to be introduced to the Great Lakes since the completion of the St. Lawrence Seaway in 1959. We included *Pisidium supinum* as it was discovered shortly after the opening of this seaway, although it may have established earlier and remained undetected. Several species (e.g., *Lepisosteus platostomus*) historically occurred in close proximity to the Great Lakes basin and were found in it after 1959. Following Kolar and Lodge (2002), we considered these species as introduced. We excluded species considered indigenous to any part of the Great Lakes basin but which were subsequently introduced to other, previously uncolonized sites within the basin (e.g., *Gasterosteus aculeatus*). We focused on NIS that have been documented as present and reproducing on at least two occasions, sensu Ruiz et al. (2000). We identified 12 nonindigenous invertebrates and fishes that were reported since 1959 but not established (as above) in this basin (I. Grigorovich, unpublished data); these species are beyond the scope of this survey.

For each NIS we sought to characterize the (1) date of first appearance; (2) locality of the first observation in the basin; (3) native range before the opening of the St. Lawrence Seaway; and (4) the most plausible vector (mechanism) of introduction to the basin. Entry mechanisms were categorized as follows: (1) shipping and boating activities, including transport in liquid or solid ballast, in or on cargo, or on hulls or other components of commercial or recreational boats; (2) stocking of nontarget species resulting from aquaculture; (3) release of aquarium species; (4) bait release; (5) canal development; (6) multiple vectors involving more than one entry mechanism; in such cases, the most plausible mechanism was indicated; and (7) natural dispersal vectors (e.g., wind or birds). Parasites and epibionts (e.g., *Trypanosoma acerinae* and *Acineta nitocrae*) were assigned the same entry mechanism as that of their host species, except when they were inadvertently released through stocking activity (e.g., *Glugea hertwigi*). Where no entry mechanism was indicated in the original record of a species, we synthesized information on transfer vectors from other published and unpublished studies. We acknowledge that the inherent limitation of this approach precludes rigorous hypotheses testing.

Spatial patterns of species introductions in the Great Lakes were analyzed by mapping sites of the first observations of NIS in the basin. We selected relatively small, semi-enclosed areas, nearly surrounded by land, that encompass the highest density of sites where NIS were first discovered in the Great Lakes. Areas that contribute to the diversity of the Great Lakes' nonindigenous fauna were defined here as "invasion hotspots", featuring >1 NIS per 1000 km^2 of water surface area. Lake surface areas were measured by outputting images of sections enclosing the sites of NIS to Scion Image for Windows software, Beta 4.0.2 release, on a personal computer.

Shipping activities and ballast water discharge

We developed a comprehensive database of transoceanic ships operating on the Great Lakes during 1959–2000 using annual reports of the St. Lawrence Seaway Development Corporation (SLSDC), the U.S. Customs forms 1400 and 1401 (1981–1986), the U.S. Maritime Administration's (MARAD) reports (1987–2000), records compiled by Norm Eakins (1995, 1996, 1997, 1998, 1999, 2000, 2001), and Rene Beauchamp's unpublished data (9041 Bellerive, Montréal, QC H1L 3S5; list of sources consulted available from K. Holeck).

The principal limitation of our data set is that, for 1981–1993, we were unable to determine the ballast status of transoceanic vessels that entered U.S. ports after visiting Canadian ports because these vessels were indicated as "foreign" entrances in U.S. Customs and MARAD reports. Thus, some vessels classified as "from foreign" in these sources did not necessarily originate from overseas. Therefore, when examining the redistribution of Great Lakes' ballast water by foreign vessels, we used a subset of the data that included only those ships that proceeded to a U.S. port directly from overseas and had a clearance directly to an overseas port. From 1959 through 1979, SLSDC reports listed the combined numbers of inbound and outbound annual trips for each category (BOB and NOBOB) of transoceanic vessel. We estimated the number of inbound trips for transoceanic BOB ships by comparing numbers of inbound and outbound trips operated by transoceanic BOB ships with all inbound trips operated by transoceanic and domestic BOB ships with all inbound and outbound trips operated by all transoceanic and domestic BOB vessels. The number of inbound transits for NOBOB ships was estimated in a similar way. We inferred ballasting and deballasting operations by the type of transaction recorded at each port. For example, if cargo was unloaded, we assumed that ballasting occurred, whereas deballasting was assumed when cargo was loaded. If a ship visited several ports to load or unload cargo, we assumed that this vessel loaded or discharged ballast in proportion to the number of ports it visited. We assumed that ballast water was discharged at or near the port at which cargo was loaded, except when ships "lighten the load" by releasing some water before entering shallow passages and connecting channels (e.g., St. Clair, Detroit, and St. Mary's rivers and the Welland Canal). We ascribed ballast releases in connecting waterways to the immediate downstream lake, except the Detroit River, which was, together with the St. Clair River, ascribed to Lake St. Clair.

Forecasting introductions

Recent developments in invasion biology provide the basis for predictive risk assessment of NIS (e.g., Carlton 1996; Kolar and Lodge 2001, 2002). We developed a qualitative risk-screening framework by integrating species characteristics and factors that are important at different stages of ballast-mediated introduction. These stages (i.e., uptake, transportation, release, establishment, and spread) represent sequential transitions that NIS must complete in the invasion process (Fig. 1).

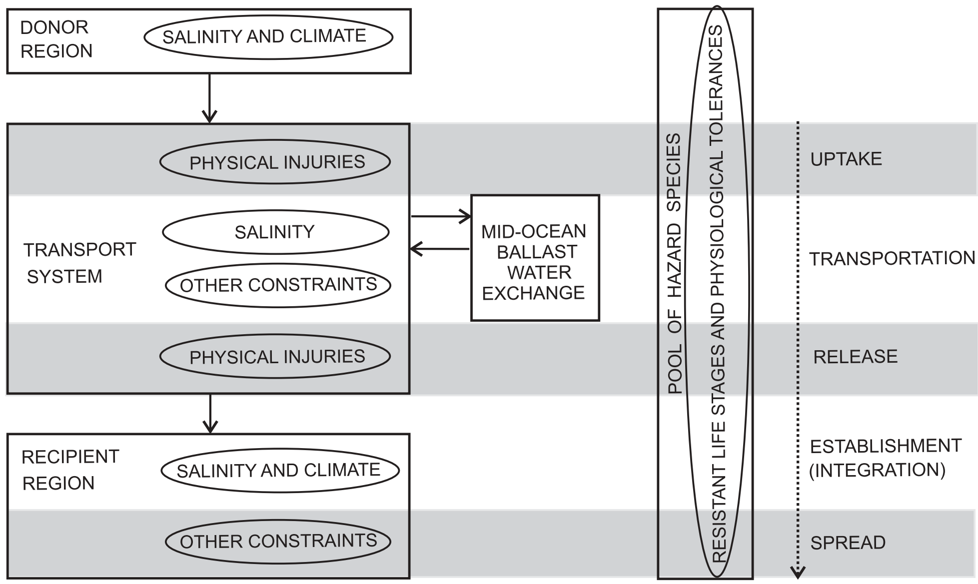
We first analyzed the geographic origin of vessels entering the Great Lakes using information on port of origin, Great Lakes' port of arrival, and whether ships carried ballast water (i.e., BOB status) or cargo (i.e., NOBOB status) while inbound (Eakins 1998; C. Major, St. Lawrence Seaway Management Corporation, Cornwall, Ont., personal communication). For the purpose of our analysis, each port of origin was assigned to broad oceanic and continental regions (as below; see Donor regions). We identified the major donor regions from whence >50% of transoceanic vessels inbound to the Great Lakes originated during 1997. We were unable to obtain similar comprehensive data for other years.

For these donor regions, we assembled a list of nonindigenous aquatic invertebrates and protists with documented invasion histories. In addition, for the Black Sea basin, we considered indigenous species that were introduced to previously uncolonized sites within this and two adjacent (Caspian and Azov seas) basins via human activities. Although our approach can be extended to other taxonomic groups (e.g., fishes), these were not considered here because of insufficient evidence of their commensalism with ballast water transport vectors in donor regions. However, Kolar and Lodge (2002) developed a predictive risk assessment for nonindigenous fishes.

From the list of potential invaders, we identified species capable of completing their life cycle entirely in Great Lakes' milieu using water temperature and salinity characteristics of their native habitats. Inferences were drawn from the published literature, unpublished reports, dissertations, and our own field observations (I. Grigorovich, unpublished data). We excluded species that are unlikely to pass through the climatic and salinity screening.

Next we judged whether species could exploit ballast water transport vectors by examining evidence for their occur-

Fig. 1. Conceptual model of ballast-mediated introduction (modified from Carlton (1985)). (Left) Donor and recipient ecosystems interact via ships carrying ballast water and associated biota. (Right) Ballast-mediated introduction process compartmentalized into sequential transitions that invading species must complete to proceed in invasion. Corresponding events on both sides are linked with shaded and blank areas. Number of propagules is predicted to decline with each subsequent transition (MacIsaac et al. 2002). Sampling of ballast tanks revealed that 80–100% of coastal organisms loaded aboard were eliminated during transoceanic transit by open-ocean ballast exchange (Wonham et al. 2001).



rence in ballast medium from ballast tank surveys. For those taxa that are likely to be transported in ships' ballast water but not recorded aboard vessels, we required evidence of unintentional secondary spread along invasion corridors (Ricciardi and MacIsaac 2000).

Then we assessed which species, at any life stage, are likely to survive the adverse conditions associated with ballast-mediated transfer. Information on species characteristics was collected from published literature, unpublished reports, and dissertations (I. Grigorovich, unpublished data). Invasion risk was assessed for (*i*) BOB ships that conduct open-ocean BWE by examining species' tolerances to salinities of 17‰ and (*ii*) NOBOB ships by examining species' ability to produce resistant life stages and (or) tolerate reduced oxygen content. Other environmental factors that may impair the physiological condition and survivorship of inoculants during transport in NOBOB ballast tanks (e.g., food limitation) were not considered because they have been studied inadequately (see Wonham et al. (2001) for list of factors). Finally, we estimated the capability of species to become established. Species that possess life history traits and environmental tolerances amenable to transportation and survival in ballast tanks were categorized as posing a high risk for establishment in the Great Lakes. Species that passed through all but the last screen were considered as posing a lower risk of invasion.

Retrospective analysis of NIS in the Great Lakes

We identified 43 aquatic animal and protist species as introduced and established in the Great Lakes basin since 1959 (Table 1). Ballast water transport by commercial vessels was invoked to explain the origin of 67% of these NIS (Fig. 2). In addition, two species, the copepod *Skistodiaptomus pallidus* and bivalve *Corbicula fluminea*, likely gained entry via boating activities not associated with ballast water. Although ballast water discharge is a very likely mechanism by which many NIS have been introduced to the Great Lakes, only a few taxa have been collected from ballast tanks: the copepod *Cyclops strenuus*, cladoceran *Bosmina coregoni*, and unidentified veligers of the bivalve *Dreissena* (Howarth 1981; Locke et al. 1993; Aquatic Sciences 1996). In most cases, possible involvement of alternative vectors was rarely examined owing to a dearth of data, and evidence of entry mechanisms was inferred after the discovery of new NIS (see Daniels (2001) for examples). For example, several entry mechanisms, including stocking, river drainage divergence, canals, ballast water release, and bait release, operating individually or jointly, may account for the introduction of *Cyclops strenuus* (Smith and Fernando 1978; Reed and McIntyre 1995; Aquatic Sciences 1996).

Even though shipping is considered the only apparent vector for four fishes and their parasites introduced since 1959 (Table 1), none of these fishes has ever been collected in ballast water (e.g., Wonham et al. 2000). Stocking of salmonid fishes from Atlantic and Pacific drainages, Europe, or other parts of the world may have served as the entry mechanism for some parasites in the Great Lakes (e.g., Crafford 2001). Furthermore, no live fish have been detected in residual water of 38 NOBOB ships sampled during 2001–2002 (S. Bailey and C. van Overdijk, Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON N9B 3P4, unpublished data). Possible reasons include the following: small apertures (typically 1–2 cm) of intake covers precluding uptake of large-bodied animals; ability of fish to avoid

Table 1. Nonindigenous metazoans and protozoans recorded in the Great Lakes basin since 1959, arranged chronologically.

No.	Taxonomic group	Species name	Year of discovery	Native region	Entry vector	Reference
1	Mollusca	*Pisidium supinum*	1959	Europe	B	Mackie 1999
2	Protista	*Glugea hertwigi* *	1960	Eurasia	S	Dechtiar 1965; Mills et al. 1993*a*
3	Pisces	*Lepisosteus platostomus*	1962	Mississippi basin	C	Fuller et al. 1999; Cudmore-Vokey and Crossman 2000
4	Crustacea	*Bosmina coregoni*	1966	Eurasia	B	Wells 1970; Deevey and Deevey 1971; Mills et al. 1993*a*
5	Crustacea	*Skistodiaptomus pallidus*	1967	Mississippi basin	B	Patalas 1969; Robertson and Gannon 1981; Mills et al. 1993*a*
6	Platyhelminthes	*Dugesia polychroa*	1968	Europe	B	Ball 1969
7	Protista	*Myxosoma cerebralis* §	1968	Unknown	M (S)	Anonymous 1988; Hoffman and Schubert 1984
8	Pisces	*Enneacanthus gloriosus*	1971	Atlantic North America	M (A)	Werner 1972; Mills et al. 1993*a*
9	Crustacea	*Cyclops strenuus*	1972	Boreal Holarctic	N ?	Selgeby 1975; Reed and McIntyre 1995
10	Crustacea	*Nitocra hibernica*	1973	Eurasia	B	Czaika 1978; Hudson et al. 1998
11	Pisces	*Notropis buchanani*	1979	Mississippi basin	M (F)	Holm and Coker 1981; Mills et al. 1993*a*
12	Mollusca	*Corbicula fluminea*	1980	Asia	M (B)	Clarke 1981; McMahon 2000
13	Annelida	*Ripistes parasita*	1980	Eurasia	B	Barton and Griffiths 1984
14	Pisces	*Alosa aestivalis*	1981	Atlantic North America	M (C)	MacNeill 1998
15	Crustacea	*Bythotrephes longimanus*	1982	Eurasia	B	Bur et al. 1986; O. Johannsson and W. Taylor, personal communication[a]
16	Annelida	*Gianius aquaedulcis*	1983	Europe	B	Farara and Ersues 1991
17	Crustacea	*Salmincola lotae* §§	1985	Eurasia	?	Lasee et al. 1988
18	Pisces	*Apeltes quadracus*	1986	Atlantic North America	M (B)	Holm and Hamilton 1988
19	Pisces	*Gymnocephalus cernuus*	1986	Eurasia	B	Simon and Vondruska 1991
20	Crustacea	*Bosmina maritima*	1988	Europe	B	De Melo and Hebert 1994
21	Crustacea	*Argulus japonicus* †	1988	Asia	A	Galarowicz and Cochran 1991; Mills et al. 1993*a*
22	Mollusca	*Dreissena polymorpha*	1988	Ponto-Caspian	B	Hebert et al. 1989
23	Mollusca	*Dreissena bugensis*	1989	Ponto-Caspian	B	May and Marsden 1992; Mills et al. 1999
24	Pisces	*Alosa chrysochloris*	1989	Hudson and Mississippi basins	C	Fago 1993; Fuller et al. 1999
25	Pisces	*Neogobius melanostomus*	1990	Ponto-Caspian	B	Jude et al. 1992
26	Pisces	*Proterorhinus marmoratus*	1990	Ponto-Caspian	B	Jude et al. 1992
27	Mollusca	*Potamopyrgus antipodarum*	1991	Australasia	B	Zaranko et al. 1997
28	Crustacea	*Onychocamptus mohammed*	1992	Holarctic	B ?	Hudson et al. 1998; P. Hudson, personal communication[b]
29	Platyhelminthes	*Dactylogyrus amphibothrium* ‡	1992	Eurasia	B	Pronin et al. 1998
30	Platyhelminthes	*Dactylogyrus hemiaphibothrium* ‡	1992	Eurasia	B	Pronin et al. 1998
31	Platyhelminthes	*Neascus brevicaudatus* ‡	1992	Eurasia	B	Pronin et al. 1998
32	Platyhelminthes	*Ichthyocotylurus pileatus* ∫	1992	Black Sea basin	B	Pronin et al. 1997
33	Protista	*Trypanosoma acerinae* ‡	1992	Eurasia	B	Pronin et al. 1998
34	Crustacea	*Echinogammarus ischnus*	1994	Ponto-Caspian	B	Witt et al. 1997; van Overdijk et al. 2003

Table 1 (*concluded*).

No.	Taxonomic group	Species name	Year of discovery	Native region	Entry vector	Reference
35	Crustacea	*Neoergasilus japonicus* ††	1994	Eastern Asia	M (S)	Hudson and Bowen 2002
36	Protista	*Sphaeromyxa sevastopoli* ∫ ‡‡	1994	Black Sea basin	B	Pronin et al. 1997
37	Platyhelminthes	*Scolex pleuronectis* ∫	1994	Black Sea basin	B	Pronin et al. 1997
38	Crustacea	*Heteropsyllus* cf. *nunni*	1996	Eurasia	B	Horvath et al. 2001
39	Protista	*Acineta nitocrae* +	1997	Europe	B	Grigorovich et al. 2001
40	Crustacea	*Cercopagis pengoi*	1998	Ponto-Caspian	B	MacIsaac et al. 1999
41	Crustacea	*Schizopera borutzkyi*	1998	Ponto-Caspian	B	Horvath et al. 2001
42	Crustacea	*Nitocra incerta*	1999	Ponto-Caspian	B	Grigorovich et al. 2001
43	Crustacea	*Daphnia lumholtzi*	1999	Australasia/Africa	N ?	Muzinic 2000; I. Grigorovich, unpublished data

Note: Keys to vectors of introduction: B, boating including recreational and ballast-mediated vectors; C, canal development; A, aquarium release; S, stocking of nontarget species with aquaculture; F, bait release; M, multiple vectors; N, natural vectors; ?, unknown or uncertain. In case of possible multiple mechanisms, the most plausible vector was indicated in parentheses. Parasite and epibiont hosts: *, *Osmerus mordax*; §, *Tubifex tubifex* and salmonid spp.; §§, *Lota lota*; †, *Carassius auratus*; ‡, *Gymnocephalus cernuus*; ∫, *Neogobius melanostomus*; ††, cyprinid, percid, and centrarchid spp.; ‡‡, *Proterorhinus marmoratus*; +, *Nitocra* spp.

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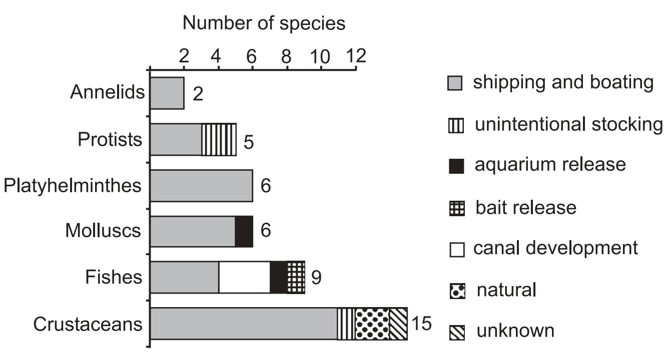
Fig. 2. Taxonomic diversity of aquatic nonindigenous metazoans and protozoans established in the Laurentian Great Lakes since 1959, sorted by entry mechanism.



sampling efforts in ballast tanks; or inhospitable environmental conditions precluding fish survival (e.g., Wonham et al. 2000).

Ballast water and sediment may provide an excellent avenue for dispersal of copepods and some branchiopods because they avoid unfavourable conditions by entering diapause or by producing resting stages (e.g., Horvath et al. 2001). Hudson et al. (1998) suggested such an entry mechanism for the copepod *Megacyclops viridis*. However, its broad Holarctic occurrences, including recent findings in the Canard River drainage, western Lake Erie basin, indicate that *M. viridis* is naturally distributed in the Great Lakes (Monchenko 1974; I. Grigorovich, unpublished data). Another copepod, *Acanthocyclops americanus*, has been collected from ships entering the Great Lakes and identified as a potential invader (Locke et al. 1993; MacIsaac 1999); but it was earlier regarded as native to Lake Michigan based on historical and biogeographical evidence (e.g., Monchenko 1974). Thus, based on circumstantial evidence, shipping has been inferred to explain the origin of these species, though, in fact, they could be Great Lakes' natives.

Several taxa that are poorly differentiated morphologically (e.g., sphaeriid bivalves and oligochaetes) may include cryptic invaders that were introduced before 1959 but have remained undetected for an extended time. These species include the oligochaetes *Stylodlilus heringianus*, *Spirosperma ferox*, *Potamothrix* spp., and *Branchiura sowerbyi* and the sphaeriid bivalve *Pisidium moitessierianum* (Cook and Johnson 1974; Grigorovich et al. 2000; Spencer and Hudson 2003). Some of these (e.g., *P. moitessierianum*) are not widely distributed in the Great Lakes basin, despite possessing a broad inland distribution in Europe (Grigorovich et al. 2003).

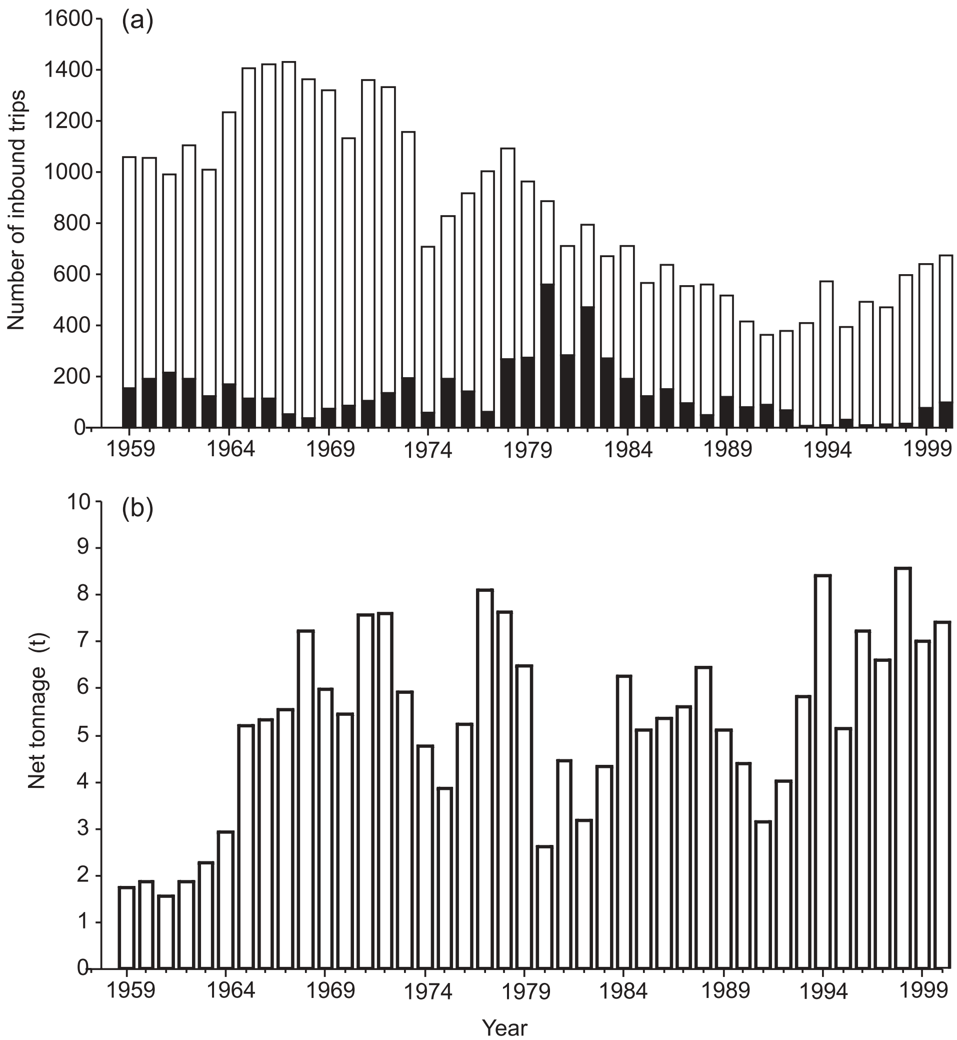
Below we analyze the temporal and spatial patterns of shipping activities in the Great Lakes to explore the involvement of ballast water transport vectors in the transfer of NIS.

Patterns of shipping activities and ballast water discharge

The overall pattern evident in transoceanic shipping traffic into the Great Lakes since 1959 is that over 90% of foreign vessels entered this system carrying cargo (i.e., NOBOB status). Only in the years 1980 and 1982 did BOB vessels outnumber NOBOB ships. The volume of transoceanic vessel traffic varied tremendously from 1959 through 2000 (Fig. 3*a*). After the opening of the St. Lawrence Seaway, traffic increased, peaking at >1430 vessels in 1967. Then traffic declined to its lowest point in 1991 (362 vessels) but increased thereafter to 675 vessels in 2000. The fraction of ballasted ships has diminished since 1992. The volume of cargo transported into the Great Lakes changed continually over the past four decades, cycling from low (e.g., 1.5 million tonnes (t) in 1961) to high (e.g., 8.6 million t in 1998) periods (Fig. 3*b*). Tonnage has increased since 1993, when the mandatory BWE legislation became effective (Fig. 3*b*). For example, average cargo volume during 1959–1992 and 1993–2000 was 4.8 and 7.0 million t·year^{-1}, respectively.

Fig. 4. Shipping activities of transoceanic vessels in the Great Lakes from 1981 through 2000: Lake Superior (solid bars), Lake Michigan (bars with grid), Lake Huron (bars with diagonal hatching), Lake Erie (shaded bars), Lake St. Clair (open bars), and Lake Ontario (bars with vertical lines). Numbers above bars represent inbound trips to United States' ports directly from overseas, based on traceable records from 1981 through 2000. (*a*) Percentage of ballast water discharges by ballasted ships into each lake. (*b*) Percentage of first port-of-call visitations by vessels carrying cargo (NOBOB status) into each lake. (*c*) Percentage of ballast water discharges by NOBOB ships into each lake.

Fig. 3. Shipping activities of transoceanic vessels in the Great Lakes from 1959 through 2000: (*a*) inbound trips of ballasted ships (solid bars) and those that declare "no ballast on board" (NOBOB) status (open bars); (*b*) net tonnage (t) of NOBOB ships.



During 1981–2000, most (~75%) BOB vessels entering the Great Lakes proceeded directly to Lake Superior, where almost all of these ships discharged their ballast load. Other recipients of ballast water from BOB ships, in order of decreasing supply, were Lake Erie, Lake Michigan, and Lake St. Clair (Fig. 4*a*).

During 1981–2000, ~72% of NOBOB vessels made their first stop at Lake Erie, where they typically unloaded cargo and loaded Great Lakes' water (Fig. 4*b*). Ports on Lake Superior received ~70% of the mixed ballast water discharges from NOBOB vessels, followed, in turn, by Lake Erie (16%), Lake Michigan (12%), and Lake St. Clair (2%) (Fig. 4*c*).

Thus, over the past four decades, the bulk of transoceanic vessels entered the Great Lakes carrying cargo and having no declarable ballast water on board. After unloading freight at Great Lakes' ports, these ships typically filled their ballast tanks with Great Lakes' water to compensate for loss of cargo weight. As a result, residual ballast water and sediment became mixed with Great Lakes' water and, after the subsequent discharging within the system, could facilitate invasions (Bailey et al. 2003). Below we examine the chronology and locations of Great Lakes' NIS discoveries to deduce their relationship to the ballast water discharge by overseas vessels.

Emerging invasion patterns

We identified four invasion "hotspots": the Lake Huron – Lake Erie corridor (10 species), Lake Erie – Lake Ontario

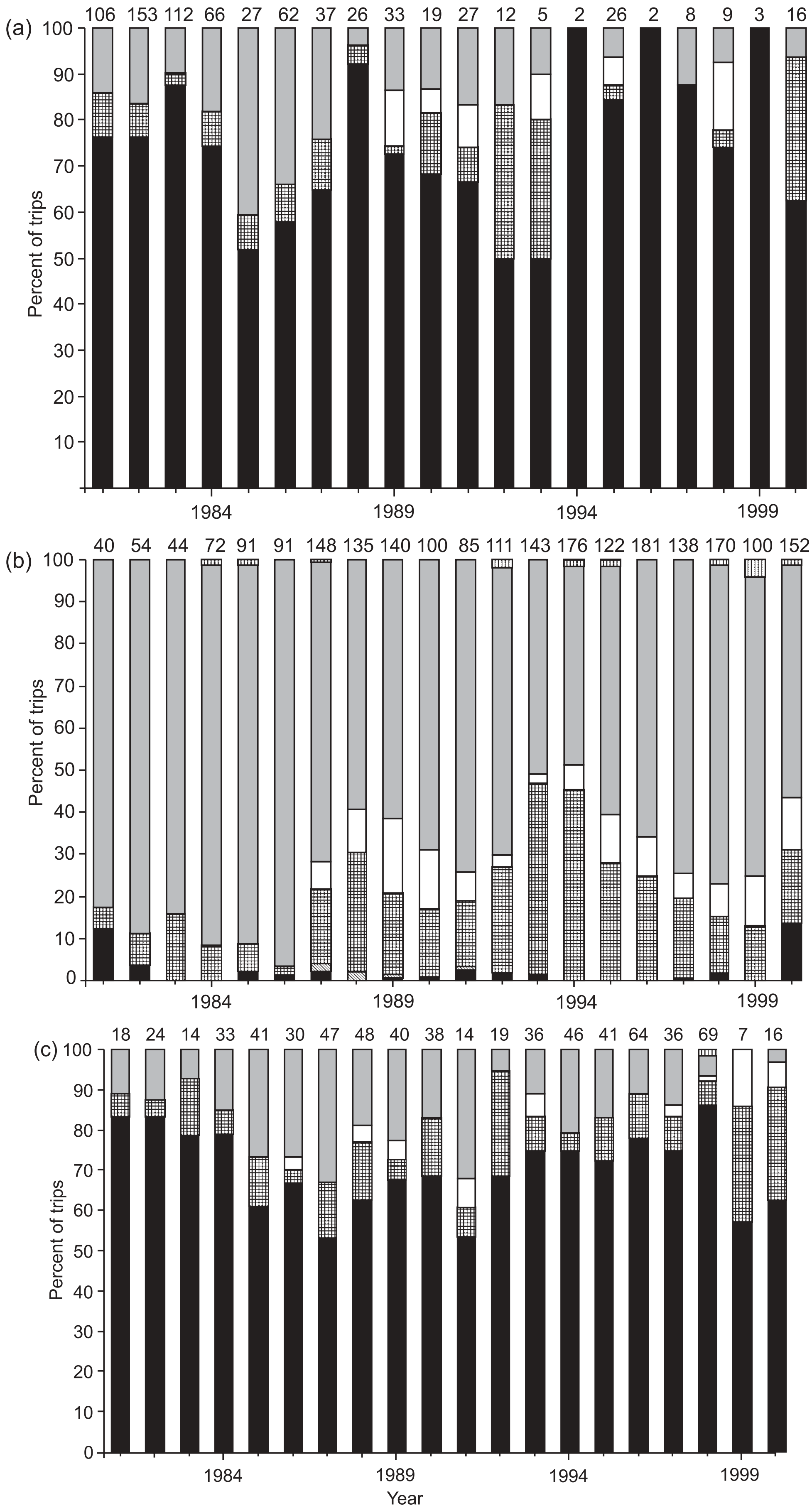
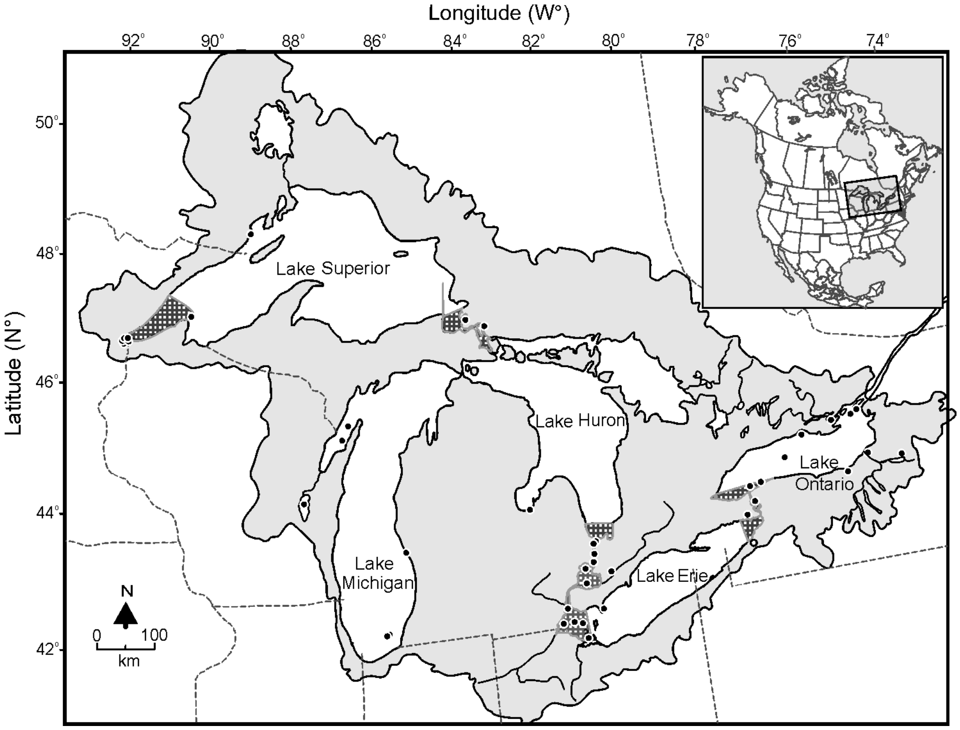

(a)
106 153 112 66 27 62 37 26 33 19 27 12 5 2 26 2 8 9 3 16
Percent of trips
100 90 80 70 60 50 40 30 20 10
1984 1989 1994 1999
(b)
40 54 44 72 91 91 148 135 140 100 85 111 143 176 122 181 138 170 100 152
Percent of trips
100 90 80 70 60 50 40 30 20 10 0
1984 1989 1994 1999
(c)
18 24 14 33 41 30 47 48 40 38 14 19 36 46 41 64 36 69 7 16
Percent of trips
100 90 80 70 60 50 40 30 20 10 0
1984 1989 1994 1999
Year

Fig. 5. Map of the Laurentian Great Lakes drainage (shaded) showing sites of the first discovery for established nonindigenous aquatic animals and protists (●) 1959–1999. Fish hatchery location, where *Myxosoma cerebralis* was first discovered in North America, is indicated by ○. Invasion "hotspots" featuring high concentrations of new nonindigenous species are indicated by hatching of lake surface area.

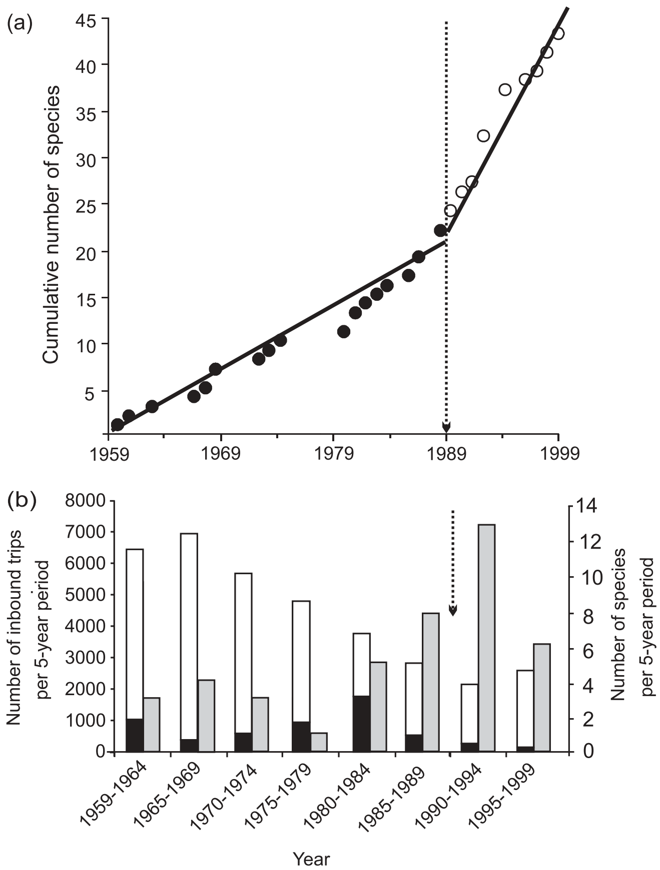


corridor (4 species); Lake Superior – Lake Huron corridor (2 species); and the western end of Lake Superior (7 species) (Fig. 5). Collectively these hotspots compose <5.6% of the total Great Lakes' water surface area but account for ~ 53.5% of NIS recorded since 1959. Thus, the concentration of NIS sites in these hotspots is more than 19 times that in the remaining lake surface area. The density of NIS sites ranges from >2/1000 km^2 in the Lake Huron – Lake Erie corridor to ~1/1000 km^2 in the Lake Superior – Lake Huron corridor. At a large spatial scale, these hotspots generally correspond to the major areas of ballast water discharge by ocean-going vessels, including western Lake Superior, the Lake Huron – Lake Erie corridor, and the Lake Erie – Lake Ontario corridor (Aquatic Sciences 1996). Also, these hotspots are all fairly shallow water areas. It is possible that before entering the shallow passages, ships "lighten up" by discharging some ballast water to reduce draft, in accordance with safety operational requirements (Carlton et al. 1995). Some of the NIS findings in the interconnecting channels could be explained by drift from upstream locations (e.g., western Lake Erie from the Detroit River). Further research is necessary to determine why NIS are concentrated in hotspot areas.

Although the "propagule pressure" hypothesis attributes invasion outcome to the quantity of NIS propagules delivered, formal records of ballast water discharge are a poor predictor of the extent of ballast-mediated invasions in the Great Lakes (Grigorovich et al. 2003). For example, despite receiving a disproportionate ballast water and presumably propagule supply, the western end of Lake Superior supports relatively few (~14%) NIS (species 17, 19, and 29–33 in Table 1). Five of these NIS (species 29–33) were likely transported with their host (*Gymnocephalus cernuus*) and, as such, may represent a single inoculation event. A number of hypotheses may account for the relative rarity of NIS in this lake (see Grigorovich et al. 2003).

The rate of discovery of nonindigenous invertebrates and protists in the Great Lakes has changed dramatically through time (Fig. 6*a*). The number of new NIS recorded between 1989 and 1999 increased to three times the rate observed between 1959 and 1988 (Fig. 6*b*). This pattern may be real, reflecting changes in vector type and magnitude between these periods. Alternatively, this pattern may be an artifact of sampling bias, reflecting increasing awareness of, and sampling efforts for, NIS (e.g., Ricciardi 2001). Between 1959 and 1999, there was no consistent relationship between the number of new NIS discovered in the Great Lakes and volume of shipping activities per 5-year period (Fig. 6*b*). Some NIS (e.g., *Daphnia lumholtzi*) are associated with vectors other than shipping. Inherent time lags between the initial inoculation of NIS and their identification in the field may also partially account for the "accelerating" accumulation of introduced species during the 1980s and 1990s. Records of deliberate introductions indicate that successfully introduced populations may remain undetected for an extended time following initial stocking, from 1 year (Karpevich 1975) to 20 years (reviewed in Grigorovich et al. 2002). Likewise, time lags between the initial inoculation and detection are anticipated for inadvertently introduced NIS (Sakai et al. 2001). However, no data exist allowing for an accurate estimation of the duration of time lags in the Great Lakes. The problem of time lags may be particularly acute when new invaders

Fig. 6. Time trends in introductions of nonindigenous metazoans and protozoans in the Great Lakes from 1959 through 1999. (*a*) Cumulative number of introduced species recorded over the preregulation period (1959–1988; slope = 0.621, r^2_{adj} = 0.963) and after ballast regulation period (1989–1999; slope = 1.880, r^2_{adj} = 0.956). The species accumulation rate during the period before ballast water regulation (0.621) lies outside the 95% confidence (1.543–2.216) interval of the postregulation period. (*b*) Number of species discovered (shaded bars) and volume of inbound traffic by overseas ballasted (solid bars) and cargo-carrying ships (open bars) per 5-year period. Implementation of the voluntary guidelines for the control of ballast water discharges (1989) is indicted by arrows.



are not demonstrably distinct in morphology from taxa already resident in the system. For example, the time lag extended over 100 years for the morphologically cryptic sphaeriid bivalve, *Pisidium moitessierianum*, established in the Great Lakes (Grigorovich et al. 2000). Only 10 NIS (~23%) in our survey (species 8, 12, 13, 15, 19, 22, 25, 26, 40, and 43 in Table 1) are deemed clearly distinctive morphologically from species resident in the system, whereas the remaining NIS may have been subject to time lags.

The ecological profile of nonindigenous fauna introduced through ships' ballast water has changed over the period of 1959–1999. Nonindigenous species inhabiting the water–sediment interface have become predominant since 1993 (Table 1). This change may reflect a shift in transport vectors from those associated with BOB vessels to those associated with NOBOB vessels (see Fig. 2*a*). Six NIS species discovered after 1993 (species 38–43 in Table 1), excluding parasites of previously established fishes, may have been transported to the Great Lakes in ballast tanks of NOBOB ships. An additional species, *Echinogammarus ischnus*, was present in western Lake Erie in 1994 and may have been introduced as early as 1993 (van Overdijk et al. 2003).

Forecasting ballast-mediated introductions

Our risk-assessment framework predicts potential invertebrate invaders and estimates the risk of their successful introduction in the Great Lakes using a sequence of "screens" (after Hayes 1998; Haugom et al. 2002). Each screen may independently preclude invasion or establishment of NIS (Fig. 7). These screens include the following: (1) strong shipping pathways and vector activities linking high-risk donor regions with the Great Lakes; (2) history of invasiveness and commensalism with humans; (3) salinity and climate matches between recipient and donor regions; (4) interface with ballast water vectors and availability for ballast intakes; and (5) life histories and environmental tolerances that may enhance inoculant survival during uptake and transportation in ballast tanks.

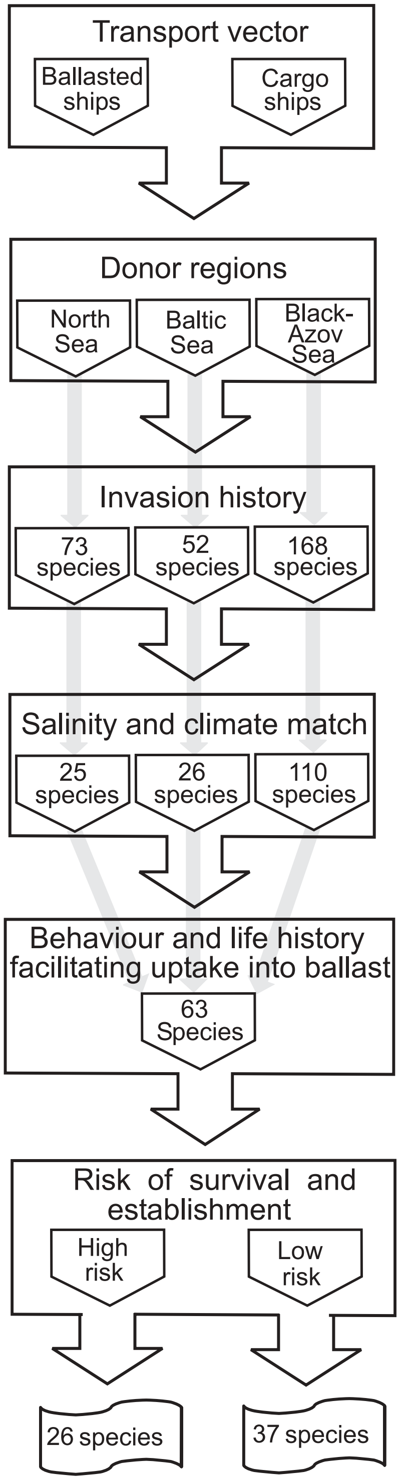
Donor regions

From 1983 through 1998, trade into the Great Lakes was dominated by vessels arriving from European ports (~88%), followed by those originating from South and Central America. In total, we identified 460 different last ports-of-call, representing virtually all regions of the world, from whence Great Lakes shipping traffic originated. In 1997, five regions accounted for >72% of Great Lakes' inbound traffic, namely the North Sea, the Baltic Sea, the South American Atlantic, the North American Atlantic, and Black Sea basins (Fig. 8). Of these, basins of the North, Baltic, and Black seas contributed ~55% of inbound vessels. Although a high proportion of overseas vessels do not operate on regular, defined routes (Niimi 2000), the former two basins remained the primary sources of Great Lakes' shipping traffic during 1983–1998, whereas vessel traffic from the Black Sea basin was difficult to discern but clearly was much lower than that from the former two regions (Colautti et al. 2003). The North American Atlantic region was not considered here because it is a source of cabotage trade. The South American Atlantic region was excluded because of insufficient information on the extent of NIS introductions in this region and because of its pronounced climatic mismatch with the Great Lakes region (as below) precluding establishment of propagules. Thus, some species posing a risk of invasion cannot be predicted by our model because certain ports of ballast origin were not considered.

Invasion history

We identified 73 and 52 nonindigenous invertebrates that have documented invasion histories in the North Sea and Baltic Sea basins, respectively (Gollasch and Leppäkoski 1999; Kelleher et al. 1999; Van der Velde et al. 1999; Hopkins 2001; Bij de Vaate et al. 2002). We also identified 168 invertebrate species that have been deliberately or accidentally introduced in the Ponto-Caspian basins and thus are likely to

Fig. 7. Risk-assessment framework for prediction of ballast-mediated introductions into the Laurentian Great Lakes. Risk-assessment screens may independently or jointly preclude transfer, survival, or establishment of species in the invasion process. Screening of target species originating from individual donor regions is indicated by shading.



interface with relevant vectors for transfer of aquatic species elsewhere (Grigorovich et al. 2002; see Grigorovich et al. (2003) for updated list of nonindigenous and cryptogenic metazoans and protists in the Great Lakes). Twenty-seven species, including 16 Ponto-Caspian natives, have documented invasion histories in either the Baltic Sea or North Sea basins (Gollasch and Leppäkoski 1999; MacIsaac et al. 2001; Bij de Vaate et al. 2002). Putative sources of recent NIS in the Great Lakes are generally consistent with these three regions (Ricciardi and MacIsaac 2000; MacIsaac et al. 2001). Thus, we identified a total of 238 species with histories of introductions in the areas from whence most Great Lakes' shipping traffic originates.

Salinity and climate matches

We used water temperature and salinity parameters of their native habitats to determine whether species could become established. For example, water temperature was judged to deter the gastropod *Melanoides tuberculata* from establishment as it needs minimum temperatures of ~18°C (Duggan 2002). Temperature changes in ballast tanks could further decrease the probability of its survival during transit to the Great Lakes.

We excluded species that were judged unlikely to survive or reproduce in fresh water. For the latter reason, the Chinese mitten crab, *Eriocheir sinensis*, has failed to establish self-sustaining populations, even though it has been repeatedly transported to the Great Lakes (Nepszy and Leach 1973; Council of Great Lakes Fishery Agencies 2001). Likewise, the Atlantic–Mediterranean peracarid crustaceans *Gammarus aequicauda* and *Idotea baltica*, which are capable of surviving at salinity as low as ~0.1‰, were rejected because they require a mixohaline environment (1–30‰) for reproduction (Karpevich 1975).

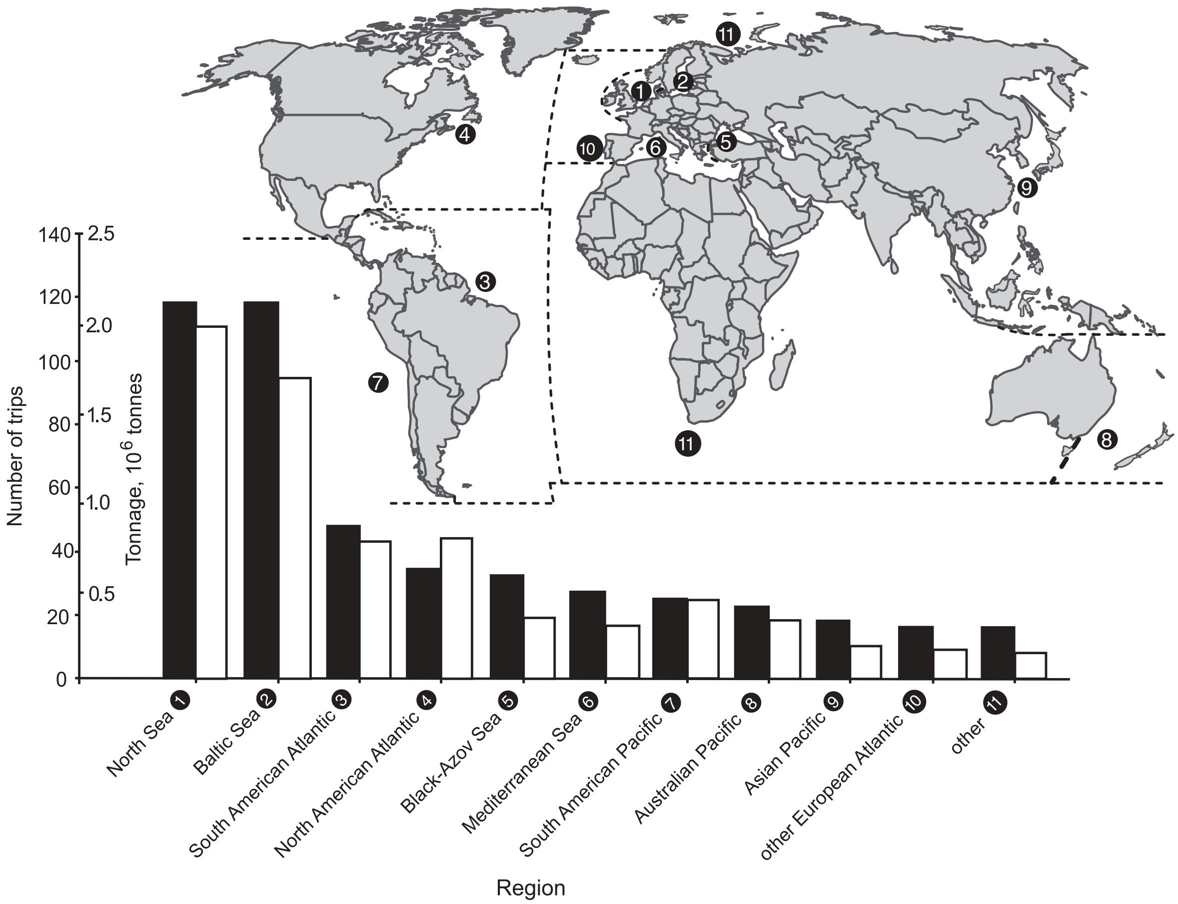
The resulting 139 species, including euryhaline forms and freshwater specialists, were judged likely to pass through the climate screening as their potential source regions — the coasts of the North, Baltic, and Black seas — are climatically compatible with the Great Lakes region (e.g., Reid and Orlova 2002).

Shipping vector interface

Organisms occurring in the water column in sufficient quantities, including holoplankton, meroplankton, and nekton, were judged likely to be loaded with ballast water (following Carlton 1985; Carlton and Geller 1993; Haugom et al. 2002). We excluded fish parasites (e.g., parasitic helminthes of Amur cyprinid fishes) for which establishment relies on the introduction of their host. We screened out aquatic organisms with behavioural and life history features that make them unavailable for ballast water intake, including sessile taxa with short planktonic stages and absent dormant life stages (e.g., bryozoan *Urnatella gracilis*) and molluscs that burrow in sediment (e.g., brooding sphaeriids, *Pisidium* spp.). In addition, we rejected large-bodied crayfishes (e.g., *Astacus leptodactylus*) because they may be precluded from uptake by intake hatch screens and because they are unlikely to be present in the water column during the ballasting phase.

Sediment stirring in shallow ballasting ports may enable benthic organisms to be drawn into ballast intake streams (e.g., Gollasch and Leppäkoski 1999). Therefore, we also included free-living nektonic (e.g., gammarid amphipods) and benthic organisms, including those dwelling in attached tubes but which migrate occasionally (e.g., corophiid amphipods,

Fig. 8. Source regions of cargo-carrying ships (NOBOB) inbound to the Great Lakes in 1997. Shipping activity is represented by number of inbound trips (open bars) and by net tonnage (solid bars). In addition to 444 inbound trips operated by NOBOB vessels in 1997, Eakins (1998) reported 31 trips by ballasted vessels.



ampharetid polychaetes). Analysis of the transfer mechanisms for these species revealed that dispersal beyond their natural range may have involved shipping or multiple, interacting transport vectors (Grigorovich et al. 2002).

A total of 63 species likely pass through the ballasting phase of the ballast water transfer sequence. These species represent a variety of life styles (plankton, benthos, and nekton), life history strategies (*r*- and *K*-selected strategies), and salinity tolerances (freshwater–oligohaline, mesohaline, euryhaline).

Ballast tank survival

We estimated the likelihood of potential survival of target species for NOBOB and BOB vessels. Using salinities of species' natural habitats, we first gauged the risk of propagule survival in ballasted vessels that comply with BWE legislation. We considered coastal and estuarine species that have evolved osmoregulatory mechanisms allowing for rapid ion exchange regulation when moving between salt water and freshwater habitats (e.g., Mordukhai-Boltovskoi 1960, 1970). Species that naturally occur at salinities of 17‰ (e.g., amphipods *Echinogammarus warpachowskyi* and *Dikerogammarus villosus*; Derzhavin 1951; Bruijs et al. 2001) were judged to survive a partial to complete BWE, provided that they have not been flushed out from ballast tanks in the process. We considered eight species to have a high probability of surviving ballast-mediated transfer and establishment (Table 2). Of these, the littoral gammarid amphipod *Pontogammarus maeoticus* is likely to be taken on board in small quantities, deterring its establishment. Therefore, we considered it as a low-risk species. The remaining target species were not considered for BOB ships, as they are not known to survive at high salinities (as above). Also, we did not assess risk level for dormant life stages of freshwater species in BOB ships, because limited data suggest that high salinity water may reduce their viability (Bailey et al. 2003).

When assessing the risk of propagule survival in NOBOB vessels, we considered various invertebrate taxa that tolerate some exposure to anoxia, feed on detritus or sediment, and show burrowing behaviours. These taxa were judged likely to survive in NOBOB ballast tanks as evidenced from sampling residual ballast water and sediment (Gollasch and Leppäkoski 1999; S. Bailey, Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON N9B 3P4, unpublished data). Six species (13–18 in Table 2) were judged to have a high likelihood of surviving ballast-mediated transfer because they may enter diapause as adults and thereby survive anoxic conditions in ballast tanks.

Benthic organisms that lack resistant pelagic life stages or behaviours (e.g., gastropods except *Potamopyrgus antipodarum* assessed for risk above) were judged likely to have low density in residual ballast water resulting from the fewer

Table 2. List of species predicted to invade the Great Lakes using risk-based model of ballast-mediated introduction.

No.	Risk level	Taxonomic group	Species name	Donor region	Ship category
1	High	Coelenterata	*Cordylophora caspia* *+	N, B, P	BOB
2		Crustacea	*Daphnia cristata* ‡	P	BOB, NOBOB
3			*Bosmina coregoni* *‡	P	BOB, NOBOB
4			*Bosmina obtusirostris* ‡	P	BOB, NOBOB
5			*Bythotrephes longimanus* *‡	N, B, P	BOB, NOBOB
6			*Cercopagis pengoi* *‡	B, P	BOB, NOBOB
7			*Cornigerius maeoticus maeoticus* ‡	P	BOB, NOBOB
8			*Podonevadne trigona ovum* ‡	P	BOB, NOBOB
9			*Eurytemora affinis* *‡	P	BOB, NOBOB
10			*Heterocope appendiculata* ‡	P	NOBOB
11			*Heterocope caspia* ‡	P	NOBOB
12			*Calanipeda aquae-dulcis* ‡	P	BOB, NOBOB
13			*Cyclops kolensis* ‡	P	NOBOB
14			*Ectinosoma abrau*	P	NOBOB
15			*Paraleptastacus spinicaudata triseta*	P	NOBOB
16			*Schizopera borutzkyi* *	P	NOBOB
17			*Nitocra incerta* *	P	NOBOB
18			*Onychocamptus mohammed* *	P	NOBOB
19			*Hemimysis anomala* +	N, B, P	BOB, NOBOB
20			*Echinogammarus ischnus* *+	N, B, P	BOB, NOBOB
21			*Echinogammarus warpachowskyi* +	P	BOB, NOBOB
22			*Dikerogammarus villosus* +	N, P	BOB, NOBOB
23			*Dikerogammarus haemobaphes* +	N, P	BOB, NOBOB
24			*Pontogammarus aralensis* +	P	BOB, NOBOB
25			*Pontogammarus robustoides* +	B, P	BOB, NOBOB
26		Mollusca	*Potamopyrgus antipodarum* *+	N, B, P	BOB, NOBOB
27	Low	Platyhelminthes	*Dendrocoelum romanodanubiale*	N	NOBOB
28			*Apophallus muehlingi*	P	NOBOB
29			*Nicolla skrjabini*	P	NOBOB
30			*Rossicotrema donicum*	P	NOBOB
31		Annelida	*Hypania invalida*	N, P	NOBOB
32			*Hypaniola kowalevskyi*	P	NOBOB
33			*Potamothrix bedoti* *	B	NOBOB
34			*Potamothrix heuscheri*	B	NOBOB
35			*Potamothrix moldaviensis* *	B	NOBOB
36			*Potamothrix vejdovskyi* *	B	NOBOB
37		Crustacea	*Paramysis lacustris*	B, P	NOBOB
38			*Paramysis intermedia*	P	NOBOB
39			*Limnomysis benedeni*	N, B, P	NOBOB
40			*Pterocuma pectinata*	P	NOBOB
41			*Pseudocuma cercaroides*	P	NOBOB
42			*Proasellus coxalis*	N	BOB, NOBOB
43			*Proasellus meridianus*	N	BOB, NOBOB
44			*Jaera sarsi*	P	NOBOB
45			*Jaera istri*	N	NOBOB
46			*Gammarus tigrinus*	N, B	BOB, NOBOB
47			*Gmelinoides fasciatus*	B, P	NOBOB
48			*Pontogammarus maeoticus* +	P	BOB, NOBOB
49			*Pontogammarus subnudus*	P	NOBOB
50			*Pontogammarus crassus*	P	NOBOB
51			*Pontogammarus obesus*	P	NOBOB
52			*Echinogammarus berilloni*	N	NOBOB
53			*Echinogammarus trichiatus*	N, P	NOBOB
54			*Iphigenella shablensis*	P	NOBOB
55			*Corophium curvispinum*	P	NOBOB
56		Mollusca	*Theodoxus fluviatilis*	P	NOBOB

Table 2 (*concluded*).

No.	Risk level	Taxonomic group	Species name	Donor region	Ship category
57			*Theodoxus pallasi*	B, P	NOBOB
58			*Lithoglyphus naticoides*	N, B, P	NOBOB
59			*Corbicula fluminea* *	N	NOBOB
60			*Corbula gibba*	N	NOBOB
61			*Dreissena polymorpha* *	N, B, P	NOBOB
62			*Dreissena bugensis* *	P	NOBOB
63			*Hypanis colorata*	P	NOBOB

Note: Species occurring at salinities of 17‰ are indicated by +. Species that have already established in the Great Lakes are marked with *. Species producing resistant life stages are indicated by ‡. Keys to donor regions: N, North Sea basin (lower Rhine River); B, Baltic Sea basin; P, Black Sea – Azov Sea basin. Invasion risk was assessed for ballasted (BOB) and those that declare "no ballast on board" (NOBOB) status.

propagules loaded during the ballasting phase or poor survivorship during transit. Consequently, they were considered to pose a lower risk of establishment. Obligate sexual reproduction may further deter these taxa from becoming established owing to Allee effects (species 37–55 in Table 2). For example, the Ponto-Caspian amphipod *Corophium mucronatum* was found, but has not established, in Lake St. Clair, perhaps because of demographic limitations (Grigorovich and MacIsaac 1999). Consequently, these organisms were considered to pose a lower risk of establishment (see Table 2 for list of species).

In addition, species that are known to produce resistant life stages (e.g., ephippia, resting eggs, cysts), and thereby survive transfer in residual ballast water or sediments in NOBOB vessels, were judged likely to pose a relatively high risk of introduction and establishment. Bailey et al. (2003) have experimentally assessed the viability of resting stages for rotifer, cladoceran, and calanoid copepod species in ballast tanks of NOBOB ships.

Predicted and actual invertebrate invaders

Our model identified 63 species that pose an invasion risk to the Great Lakes. Of these, 26 species are considered high-risk invaders, including 10 species that invaded the lakes between 1959 and 1999 (Table 2). These NIS may have been transported directly from the Black Sea basin (species 1, 3, 5, 6, 9, 16–18, 20, and 26 in Table 2) or indirectly from the North Sea (species 5, 20, and 26) or Baltic Sea (species 1, 6, 20, 26) basins, which may serve as "distribution hubs" (sensu Ricciardi and Rasmussen 1998). The remaining 16 high-risk species have not yet been reported in the Great Lakes. This group consists of four cladoceran, six copepod, and six peracarid crustaceans. Five peracarid crustaceans (species 19, 21–23, and 25 in Table 2) native to the Ponto-Caspian basins have established in the Rhine River or Baltic Sea basins (e.g., MacIsaac et al. 2001). Euryhaline adaptations of these species, in conjunction with their establishment in staging areas that are linked to the Great Lakes via "invasion corridors", may facilitate their transfer in ships' ballast tanks to the Great Lakes (e.g., Bruijs et al. 2001). Each cladoceran and copepod species from this group possesses at least two features that render them suitable to a ballast water vector: (1) ability to enter diapause as an adult; (2) production of dormant life stages; (3) single-parent reproduction; or (4) short generation times. The ubiquity of these features in NIS established since 1993 may have fostered survival of adverse conditions associated with ballast-mediated transfer and ensured rapid population growth in novel habitats.

An additional group of 37 species is considered to pose a lower risk of invasion to the Great Lakes under the mandatory BWE legislation. Of these, three species of tubificid oligochaetes (species 33, 35, and 36 in Table 2) and three species of bivalves (species 59, 61, and 62) established before implementation of BWE regulations. Five of these species are Ponto-Caspian natives, and one, *Corbicula fluminea*, is native to Southeast Asia. The oligochaetes have an invasion history in the Baltic Sea and may have gained entry to the Great Lakes in solid ballast before the early 1900s (see Mills et al. 1993*a*). Possible geographical sources of the zebra mussel, *Dreissena polymorpha*, include the regions of the Black, North, or Baltic seas, whereas the quagga mussel, *Dreissena bugensis*, could originate only from the Ponto-Caspian basins (Mills et al. 1999; Grigorovich et al. 2002; Vanderploeg et al. 2002).

A remaining 31 species pose a lower risk of invasion and have not yet been found in the Great Lakes. These species typically lack physiological tolerances or life history traits that enhance survival during unfavourable conditions encountered during ballast water transfer. This group includes 19 peracarid crustacean, four platyhelminth, five mollusc, and three annelid species. These species may be introduced directly from their native habitats or indirectly from invaded Baltic Sea and North Sea habitats. NOBOB vessels may facilitate these introductions, as they are exempt from BWE regulations.

In conclusion, we identified 43 nonindigenous animal and protist species established in the Great Lakes basin since 1959. More than 53% of these NIS were first recorded in four invasion hotspots where ballast water is likely discharged from overseas vessels. The overall rate of invasion of NIS increased dramatically in the 1990s, although several factors may account for this pattern. Using species invasion histories, shipping traffic to the Great Lakes, species characteristics, and factors critical to invasion success, we predict that an additional 47 invertebrate species pose a hazard of invasion. We identify 16 species that are capable of surviving ballast-mediated transport and pose a high risk for establishment in the Great Lakes. Additionally, 31 species are considered to pose a lower risk of invasion. The shift in shipping from BOB to NOBOB vessels during the 1980s may have served as a filter that favoured invasion of species capable of diapause or production of resistant life stages. This change may signal a new phase in the history of anthropogenic transformations of the Great Lakes' biota.

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