Biological invasions in Lake Ontario: past, present and future

Ian C. Duggan[1]*, Sarah A. Bailey[1], Robert I. Colautti[1], Derek K. Gray[1], Joseph C. Makarewicz[2], and Hugh J. MacIsaac[1]

[1] *Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON N9B 3P4*

[2] *Department of Environmental Science and Biology, State University of New York at Brockport, Brockport, NY. USA. 14420*

*Contact: Dr. I. Duggan, ph: (519) 253-3000 ext. 2734; Fax: (519) 971-3616; email: iduggan@uwindsor.ca

Abstract

Lake Ontario has an extensive history of biological invasions, extending more than 170 years. The rate of invasion began to increase during the 1870s, and accelerated after the opening of the St. Lawrence Seaway in the 1950s. Currently, there exist approximately 60 nonindigenous species (NIS) of vertebrate and invertebrate animals, protozoans, algae and aquatic macrophytes established in the lake. Fish are the most widely represented taxon (15 species), followed by algae (14 species), molluscs (11 species) and crustaceans (8 species), respectively. Vectors responsible for NIS introductions vary temporally and by taxon. Before 1920, deliberate release and solid shipping ballast were the dominant vectors for NIS introduction. Ships' ballast water was the dominant vector between 1961 and 2002. All algal species, and most of the crustaceans and protozoans, were introduced via ballast water discharge, whereas fish vectors consisted of deliberate introductions, canals, accidental introductions, ballast water discharge, and bait release. Identified mollusc vectors include solid or liquid ballast discharge, movement through canals and aquarium release. Since all transoceanic vessels entering the Great Lakes system must pass through Lake Ontario, these ships could potentially introduce new species,

State of Lake Ontario (SOLO) – Past, Present and Future
Edited by M. Munawar
© Ecovision World Monograph Series
2003 Aquatic Ecosystem Health and Management Society

either by ballast water discharges or hull fouling. Approximately 17% of all the ships entering the Great Lakes with saline ballast water discharge into Lake Ontario, potentially exposing the lake to euryhaline NIS such as the crustacean *Cercopagis pengoi* and the diatom *Thalassiosira baltica*. Lake Ontario is the first port-of-call for 43% of non-ballasted vessels, which may expose port areas to NIS introduction via hull fouling. Additionally, about 5% of non-ballasted vessels will load and then discharge ballast water while operating on Lake Ontario, potentially allowing NIS contained in ballast residuals to establish in the lake. Alternative vectors, including the baitfish and aquarium trades, and particularly the commercial sale of live freshwater fishes for human consumption, may add to the complement of established NIS in the lake. NIS is now abundant components of the lake's phytoplankton, invertebrate and fish communities, and jeopardize effective management of the lake. Despite recent implementation of ballast water exchange legislation, Lake Ontario remains highly vulnerable to future invasions. Management efforts must focus on identifying and eliminating vectors that may bring additional NIS to Lake Ontario and the other Great Lakes.

Introduction

Lake Ontario is part of the largest freshwater resource utilized by mankind. However, the Laurentian Great Lakes are becoming increasingly affected by a wide array of human activities, including introduction of nonindigenous species (NIS). NIS pose the leading threat to the biological integrity of lakes (Sala et al., 2000) and may interact with other ecosystem stressors, including climate change and toxic contaminants, potentially compounding their effects (e.g. Mazak, et al. 1997; Stachowicz et al., 2002).

The Great Lakes have an extensive history of NIS introductions (Mills et al., 1993; Ricciardi and Rasmussen, 1998; Ricciardi, 2001; Grigorovich et al., in press (a)). The cumulative number of NIS established in this system presently stands at approximately170 species (A. Ricciardi, McGill University, pers. comm.). Grigorovich et al. (in press (a)) demonstrated that the apparent rate of NIS introductions tripled during the period 1989-1999 in comparison to the preceding 40 years. This pattern was unexpected since the latter period represents an interval during which ballast water exchange was either voluntary (1989-1992) or mandatory (1993 onward; United States Coast Guard, 1993). Before these controls, ships arriving to the Great Lakes were free to discharge fresh water ballast loaded at international ports. Ballast water exchange, whereby vessels purge fresh- or brackish-ballast water and replace it with highly-saline, open-ocean water, was thought to protect the Great Lakes from additional invasions (United States Coast Guard, 1993). While clearly troubling, the recent increase in NIS introductions in the Great Lakes is consistent with patterns observed world-wide including in Chesapeake Bay (Ruiz et al., 2000), San Francisco Bay (Cohen and Carlton, 1998), the Baltic Sea (Leppäkoski et al., 2002), and the Mediterranean Sea (Galil and Zenetos, 2002).

Factors that may account for the acceleration of NIS recorded in the Great Lakes include facilitative interactions amongst invaders, greater efforts by researchers to identify NIS in the basin and changes in the types or strengths of vectors. Positive interactions amongst some invaders have caused some biologists to question the age-old wisdom that progressive saturation of a community with immigrating species renders the community immune to subsequent invasion. Indeed, it is now clear that some NIS, like zebra mussels (*Dreissena polymorpha*), strongly facilitate the establishment of species that arrive after them through provision of habitat or food resources (MacIsaac, 1996; Simberloff and Van Holle, 1999; Ricciardi, 2001).

It is important to consider the Great Lakes as a single system when considering risk of additional biological invasions because natural connections between the lakes allow for passive or active dispersal once NIS become established in any part of the system. In addition, transfer of ballast water within the system, mainly from lower to upper lakes, may allow long-distance transfers between systems. For example, the waterflea *Cercopagis pengoi* was first recorded in Lake Ontario in 1998, but appeared in Lake Michigan in 1999, and western Lake Erie in 2001 (Therriault et al., 2002). The Lake Michigan population likely resulted from transfer of Lake Ontario ballast water, while the Lake Erie population could have been seeded from either Lake Ontario or Lake Michigan. The amphipod *Echinogammarus ischnus* was first detected in the lower Detroit River in 1994(Witt et al., 1997; van Overdijk et al., 2003), but quickly spread to Lake Erie (van Overdijk et al., 2003), Lake Michigan (Nalepa et al., 2001) and Lake Superior (Grigorovich et al, in press (b)). Thus, the invasion of any one of the Great Lakes often foreshadows the invasion of the others. Despite this pattern, individual risks differ between each Great Lake with respect to initial invasion by new NIS because the vectors that supply NIS to each system differ. For instance, Colautti et al., (in press) determined that Lake Superior should have the greatest risk of new NIS introductions because far more ballast water discharges occur there than in any other Great Lake. Despite these risk differences between lakes, invasion reviews or surveys have been conducted only for Lakes Erie (MacIsaac, 1999) and Superior (Grigorovich et al., in press (b)) and for the overall system (Ricciardi and Rasmussen, 1998; Kolar and Lodge, 2002; MacIsaac et al., 2002a). In this paper, we review the rate and taxonomic composition of NIS invasions in Lake Ontario, the vectors associated with these invasions, and how these vectors have changed in importance over time.

Methods

We compiled a list of NIS recorded from Lake Ontario by literature review. As a starting point, we searched for occurrences in Lake Ontario of NIS known from the Great Lakes basin, using Mills et al. (1993) and Grigorovich et al. (in press (a)) as primary sources. We recorded the first report for each NIS within Lake Ontario proper (i.e. not including the catchment basin), likely vectors of release, and whether Lake Ontario was the site of first introduction in the Great Lakes. We acknowledge that for many taxa, introduction may have occurred some time before being first recorded in the lake (i.e. unknown time lags exist between introduction and first detection). If we could not find published accounts of taxa known from the wider Great Lakes in Lake Ontario, we assumed that they were not found here. Our estimate of established NIS is, therefore, likely to be conservative.

We did not consider records of annelids purported to be nonindigenous. We believe that taxonomic difficulties and/or wide geographical distributions render difficult decisions of the native region for many oligochaete taxa; consequently, we treat these species as cryptogenic (Carlton, 1996) rather than nonindigenous (e.g. Mills et al., 1993; Spencer and Hudson, 2003). For higher plants, only submerged macrophytes that grow within the lake itself were considered (i.e. marginal swamp plants and shoreline trees were excluded).

For assessment of vectors of introduction, we followed the categories used by Mills et al. (1993). Based on our resulting dataset, we plotted the cumulative number of NIS recorded in Lake Ontario over time, and explored the relationships between invaders and time using linear and non-linear regression (least-squares fit; Systat 8.0). The numbers of species introduced from each major taxonomic group was examined, and comparison made of the dominant vector of introduction for each. Temporal changes in the importance of vectors were also examined by classifying invasions into four time intervals: early period (1830-1880); pre-industrial (1881-1920); industrial (1921-1960); and post-opening of the St. Lawrence Seaway (1961-2002).

Shipping profiles for Lake Ontario were compiled from data on transoceanic shipping activity published in Colautti et al., (in press). We used cargo movement to infer the number of ships declaring ‘no ballast on board’ (NOBOB), and those carrying ‘ballast on board’ (BOB), that visited a port on Lake Ontario before visiting any of the other Great Lakes. BOB vessels were assumed to have discharged brackish or salt water at the first port-of-call where they loaded cargo. Conversely, NOBOB vessels, which offload cargo at their first port-of-call, were assumed to have loaded Great Lakes’ water. This uptake of fresh water may stimulate hatching of invertebrates from diapausing stages in residual sediments, making them available for release at subsequent ports (Bailey et al., in press). To estimate the threat posed by mixed ballast in NOBOB ships, we recorded the proportion of ports on

Lake Ontario where NOBOB vessels loaded cargo, and thus presumably discharged ballast.

History of Invasions

We tabulated 60 different NIS of vertebrate and invertebrate animals, protists, algae and aquatic (submerged) macrophytes established in Lake Ontario (Table 1). The rate of accumulation was distinctly non-linear since the initial invasion by sea lamprey (*Petromyzon marinus*) sometime around 1830 (Fig. 1). A forty-three year period elapsed before the next invaders, alewife (*Alosa pseudoharengus*) and Chinook salmon (*Oncorhynchus tshawytscha*), entered the system (Table 1). Thereafter, the rate of accumulation was relatively constant through the early 1940s (~0.20 species year^{-1}). The rate increased dramatically between 1950 and 2002, to ~0.83 species year^{-1} (Figure 1). While early invaders were exclusively fish, recently established NIS first reported in Lake Ontario include the diatom *Thalassiosira baltica* (~1988), blueback herring (*Alosa aestivalis*) (1995), waterflea *Cercopagis pengoi* (1998), and the parasitic microsporidian *Heterosporis* sp. (2002; a likely NIS) (Table 1). Thus, the diversity of taxa recorded

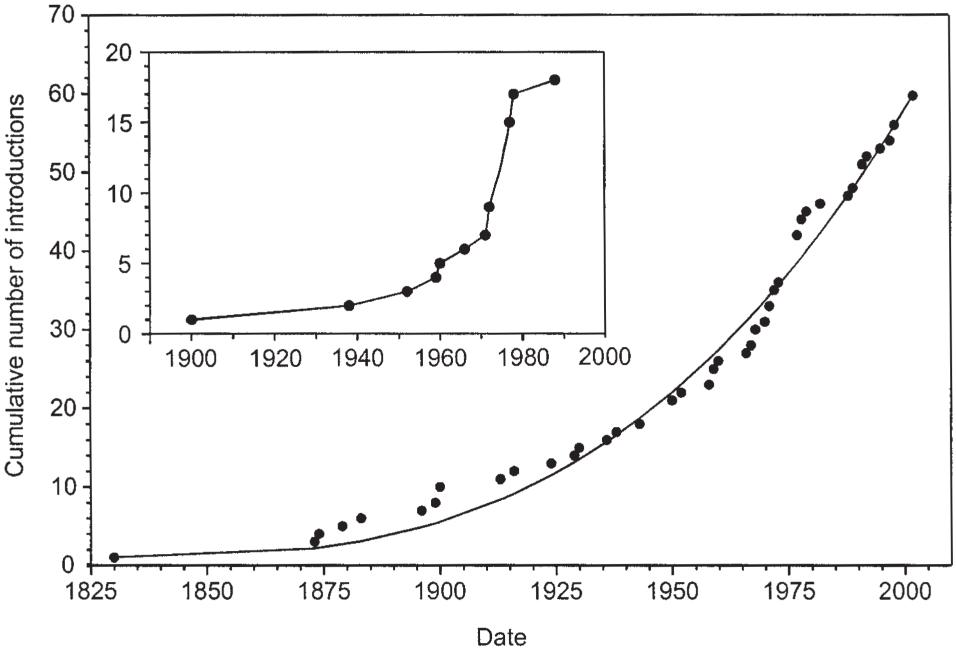

Fig. 1. Cumulative number of NIS identified in Lake Ontario, exclusive of oligochaetes. Least-squared nonlinear regression was used to fit the line (NIS = 1+ 0.0002*post-1830 years$^{2.863}$). Inset: cumulative number of submerged aquatic macrophyte and algal species in Lake Ontario.

Table 1. List of species introduced to Lake Ontario ordered by date of introduction. Key to vectors of introduction: A – accidental, AQ – aquarium release, BW – ballast water, C – canal, D – deliberate, F – unintentional establishment associated with fish release, SB – solid ballast, U – unknown. Multiple vectors are listed in order of importance.

Taxon	Species Name	Year of Introduction	Vector	Reference
Pisces	*Petromyzon marinus*	1830	C,F	Mills et al. 1993
Pisces	*Alosa pseudoharengus†*	1873	C	Mills et al. 1993
Pisces	*Oncorhynchus tshawytscha*	1873	D	Mills et al. 1993
Pisces	*Carassius auratus*	1874*	D,AQ,F,A	Mills et al. 1993
Mollusca	*Bithynia tentaculata*	1879	SB,D	Mills et al. 1993
Pisces	*Salmo trutta†*	1883	A	Mills et al. 1993
Pisces	*Cyprinus carpio‡*	1896**	D	Scott and Crossman 1973
Mollusca	*Pisidium amnicum†*	1899	SB	Grigorovich et al. 2003a
Pisces	*Oncorhynchus mykiss*	1900	D	Dueck and Danzmann 1996
Plant	*Potamogeton crispus*	1900	D,F	Stuckey 1979
Mollusca	*Valvata piscinalis†*	1913	SB	Grigorovich et al. 2003a
Mollusca	*Pisidium henslowanum†*	1916	SB	Grigorovich et al. 2003a
Mollusca	*Sphaerium corneum†*	1924	U	Grigorovich et al. 2003a
Pisces	*Osmerus mordax*	1929***	D	Fuller et al. 1999
Mollusca	*Radix auricularia*	1930	AQ	Mills et al. 1993
Mollusca	*Gillia altilis‡*	1936	C	Mills et al. 1993
Algae	*Actinocyclus normanii*	1938	BW	Mills et al. 1993
Insecta	*Tanysphyrus lemnae*	1943	U	Mills et al. 1993
Insecta	*Acentropus niveus†*	1950	A	Mills et al. 1993
Pisces	*Morone americana‡*	1950	C	Mills et al. 1993
Pisces	*Oncorhynchus nerka*	1950	D	Mills et al. 1993
Algae	*Stephanodiscus binderanus*	1952	BW	Mills et al. 1993
Crustacea	*Eurytemora affinis*	1958	BW	Mills et al. 1993
Mollusca	*Pisidium supinum†*	1959	U	Grigorovich et al. 2003a
Plant	*Trapa natans*	1959	A,AQ	Mills et al. 1993
Plant	*Myriophyllum spicatum*	1960	AQ	Mills et al. 1993
Algae	*Bangia atropurpurea*	1966	BW,F	Damann 1979
Crustacea	*Skistodiaptomus pallidus†*	1967	A,F	Mills et al. 1993
Platyhelminthes	*Dugesia polychroa†*	1968	BW	Mills et al. 1993
Crustacea	*Bosmina coregoni*	1968	BW	Mills et al. 1993
Pisces	*Oncorhynchus kisutch*	1970	D	Fuller et al. 1999
Microsporidia	*Glugea hertwigi*	1971	F	Nepszy 1988
Algae	*Cyclotella atomus*	1971	BW	Duthie and Sreenivasa 1972

Table 1. Contd.

Taxon	Species Name	Year of Introduction	Vector	Reference
Plant	*Hydrocharis morsus-ranae*	1972	AQ,D,F	Mills et al. 1993
Algae	*Stephanodiscus subtilis*	1972	BW	Mills et al. 1993
Crustacea	*Nitocra hibernica*†	1973	BW	Grigorovich et al. 2003a
Algae	*Cyclotella cryptica*	1977	BW	Stoermer 1978
Algae	*Cyclotella pseudostelligera*	1977	BW	Stoermer 1978
Algae	*Skeletonema potamos*	1977	BW	Stoermer 1978
Algae	*Skeletonema subsalsum*	1977	BW	Stoermer 1978
Algae	*Thalassiosira pseudonana*	1977	BW	Stoermer 1978
Algae	*Thalassiosira weissflogii*	1977	BW	Stoermer 1978
Algae	*Chroodactylon ramosum*	1978	BW	Sheath and Morison 1982
Algae	*Nitellopsis obtusa*	1978	BW	Crowder and Painter 1991
Pisces	*Oncorhynchus gorbuscha*	1979	A	Fuller et al. 1999
Crustacea	*Bythotrephes longimanus*†	1982	BW	Grigorovich et al. 2003a
Algae	*Thalassiosira baltica*	1988	BW	Edlund et al. 2000
Pisces	*Scardinius erythrophthalamus*‡	1989	F	Crossman et al. 1992
Mollusca	*Dreissena bugensis*	1991	BW	Mills et al. 1993
Mollusca	*Dreissena polymorpha*	1991	BW	Mills et al. 1993
Mollusca	*Potamopyrgus antipodarum*†	1991	BW	Grigorovich et al. 2003a
Crustacea	*Onychocamptus mohammed*†	1992	BW	Grigorovich et al. 2003a
Pisces	*Alosa aestivalis*‡	1995	C	Owens et al. 1998
Crustacea	*Echinogammarus ischnus*	1997	BW	Dermott et al. 1998
Crustacea	*Cercopagis pengoi*†	1998	BW	Grigorovich et al. 2003a
Pisces	*Neogobius melanostomus*	1998	BW	Fuller et al. 1999
Rhizopoda	*Psammonobiotus communis*	2002	BW	Nicholls and MacIsaac unpb
Rhizopoda	*Psammonobiotus dziwnowii*†	2002	BW	Nicholls and MacIsaac unpb
Rhizopoda	*Psammonobiotus linearis*†	2002	BW	Nicholls and MacIsaac unpb
Microsporidia	*Heterosporis* sp.†	2002	F	MacIsaac et al. 2002b

* although Grigorovich et al. (2003a) note occurrence in drainage basin of Lake Ontario as early as 1700s
** thought to have escaped into public waters at this time from Newmarket, Ontario
*** it is debatable whether the Lake Ontario population is native or introduced
† first recorded sighting in Lake Ontario proper
‡ first recorded sighting in drainage basin of Lake Ontario
Note: Fishes *Noturus insignis* and *Enneacanthus gloriosus* and bladderwort *Utricularia inflata* were first recorded in Lake Ontario drainage, but are not recorded from Lake Ontario proper, and are therefore excluded from this list.

entering the system in recent years is much greater than that in earlier years. The overall “Accumulation of New NIS” (AN-NIS) in Lake Ontario since 1830 fits a non-linear model very well (r^2=0.98):

$$\text{AN-NIS} = 1 + 0.0002\ (\text{years since } 1830)^{2.863}$$

This nonlinear model conceals a punctuated pattern of invasion records. For example, a distinct surge in discoveries of NIS of phytoplankton was recorded in 1977 (Table 1, Figure 1 inset), due wholly to a Great Lakes-wide survey by Stoermer (1978). Likewise, four protozoans (a microsporan and three testate amoebae) were detected in two studies during 2002. It is highly likely that the NIS identified during both of these time intervals involve detection of previously unidentified but pre-existing species. In other words, species are detected only after studies are conducted specifically targeting particular taxonomic groups, even though they may have been resident in the lake for an undetermined number of years. Time lags in detecting NIS are likely to occur for most taxonomic groups, unless the new species imparts particularly strong effects on the lake ecosystem or its resident species.

Of the NIS complement in Lake Ontario, 18 of the species were new records for the Great Lakes, as were an additional eight records in the lake’s watershed. These taxa represent a wide array of taxonomic groups, from fishes to parasitic protozoans (see Table 1).

Species Composition of NIS in Lake Ontario

Fishes are the numerically dominant group of established NIS in Lake Ontario (15 species), followed in order by algae (14 species), molluscs (11 species) and crustaceans (8 species) (Figure 2). Comparatively small numbers of NIS of submerged macrophytes, insects and platyhelminth worms are established in the lake (Figure 2).

New fish species have been recorded in the lake as early as 1830 and as recently as 1998 (Table 1). NIS of algae were first detected in 1938 and as recently as 1998. Conversely, the first crustacean species, the copepod *Eurytemora affinis*, did not invade until 1958. The first nonindigenous protozoan, the microsporan *Glugea hertwigi*, was not reported in the lake until 1971. Recently, the fish parasite *Heterosporis* sp. was identified in the Bay of Quinte (see MacIsaac et al., 2002b), and three testate rhizopod amoebae were identified in Lake Ontario and other Great Lakes (Nicholls and MacIsaac, unpublished report)

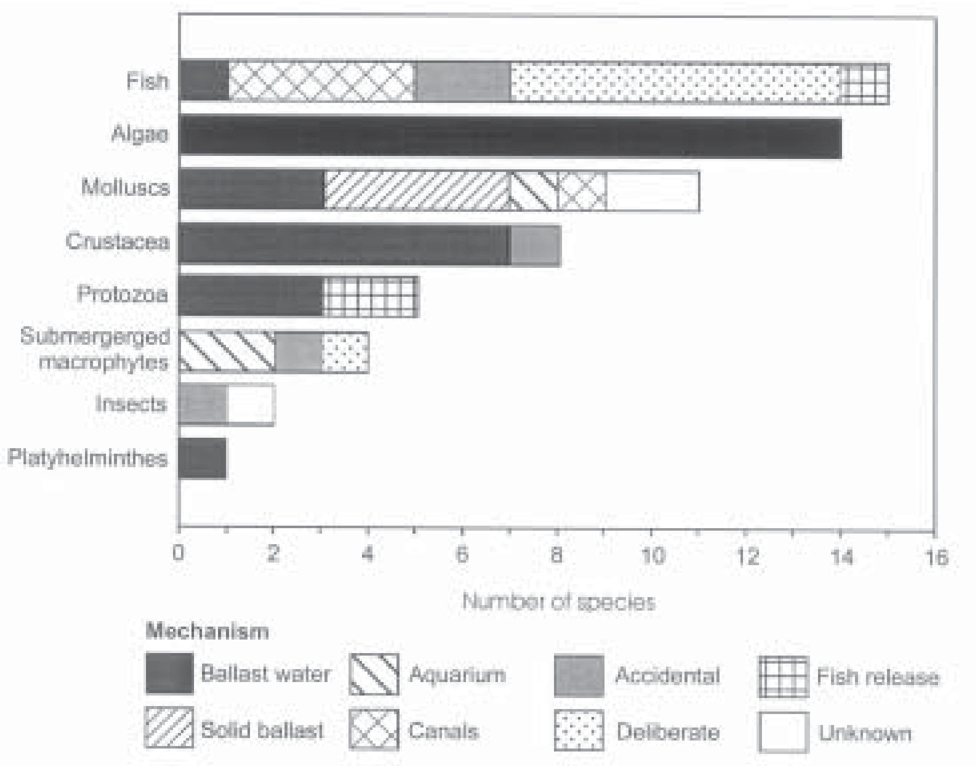

Fig. 2. Taxonomic composition and vector of entry for NIS introduced to Lake Ontario. Vectors follow the definitions given by Mills et al. (1993). Deliberate releases are those that have been introduced with the implicit purpose of establishing populations within the lake or Great Lakes basin. Fish release includes that of unused baitfish, or disease pathogens released unintentionally with fish. Accidental release includes species that were introduced unintentionally, and incidentally, to other organisms.

Vectors of NIS Invasions

Vectors responsible for introduction of NIS to Lake Ontario have varied tremendously through time. For example, during the early period of invasion (1830-1880), vectors were limited to deliberate or canal introductions (fishes) and solid ballast (mollusc *Bithynia*) (Figure 3). Solid ballast was the most important vector in the pre-industrial interval (1881-1920), followed by deliberate introductions. The first recorded introductions mediated by ballast water occurred in 1938, during the industrialization period (Figure 3). Other vectors responsible for introductions during this interval included aquarium releases, canals, deliberate stocking of NIS, and accidental introductions. The completion of the St. Lawrence Seaway in 1959 opened the Great Lakes to international shipping. Between 1961 and 2002, ballast

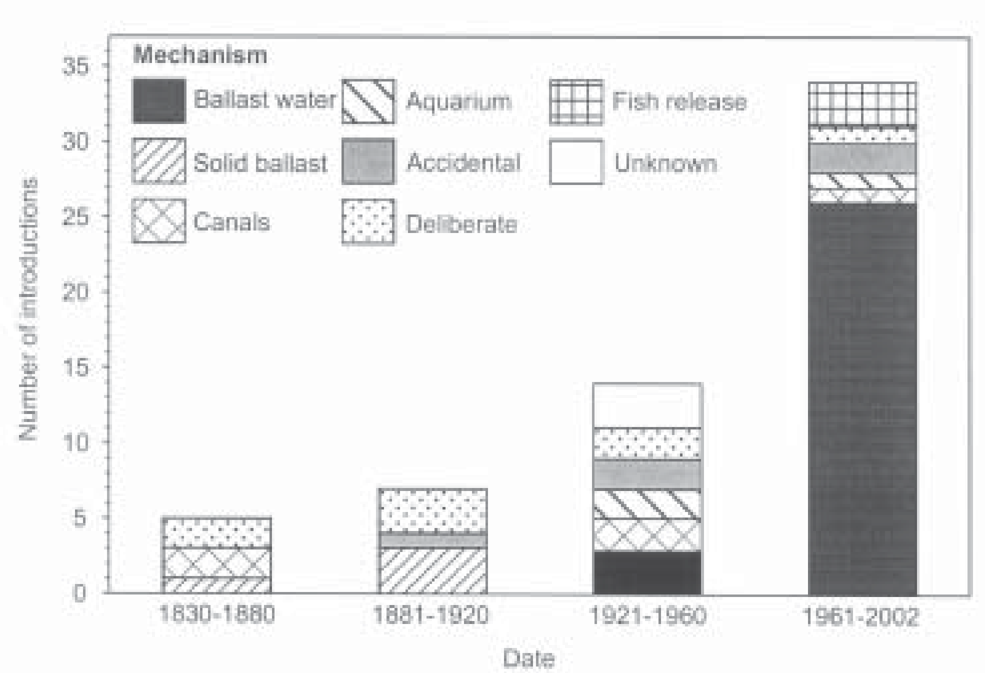

Fig. 3. Temporal sequence and mechanisms of NIS introductions into Lake Ontario.

water was implicated in the vast majority (~77%) of NIS introduced to Lake Ontario. This pattern is consistent with the correlation between shipping activity in the Great Lakes (estimated by the net tonnage of domestic and foreign cargo ships) and the number of NIS recorded in the basin (Ricciardi, 2001).

Two international classes of ships trade on the Great Lakes: those entering without cargo, whose ballast tanks are loaded with saline water (i.e. BOB ships), and vessels entering loaded with cargo and only residual water and sediment in their ballast tanks (i.e. NOBOB ships). If the NIS is fouled to ships' hulls, either class of vessel could introduce species from freshwater locales overseas, or from other parts of North America. Port areas might be particularly vulnerable to initial establishment since NIS propagules would be 'focused' in a relatively small volume of water as compared to the open lake. Secondly, species may commence reproduction soon after vessels have docked in port, as has been observed in Hawaii (Apte et al., 2000). The threat of hull-fouling introductions to Lake Ontario appears to be greatest for NOBOB vessels since they dominate inbound trade to the Great Lakes and because ~44% of these vessels have first-ports-of-call on Lake Ontario (Figure 4). Ships transiting freshwater canals and rivers within North America are more likely to successfully introduce biofouling organisms than are transoceanic vessels. In the latter case, biofouling organisms would have to survive the high salinity and colder temperatures of the open ocean.

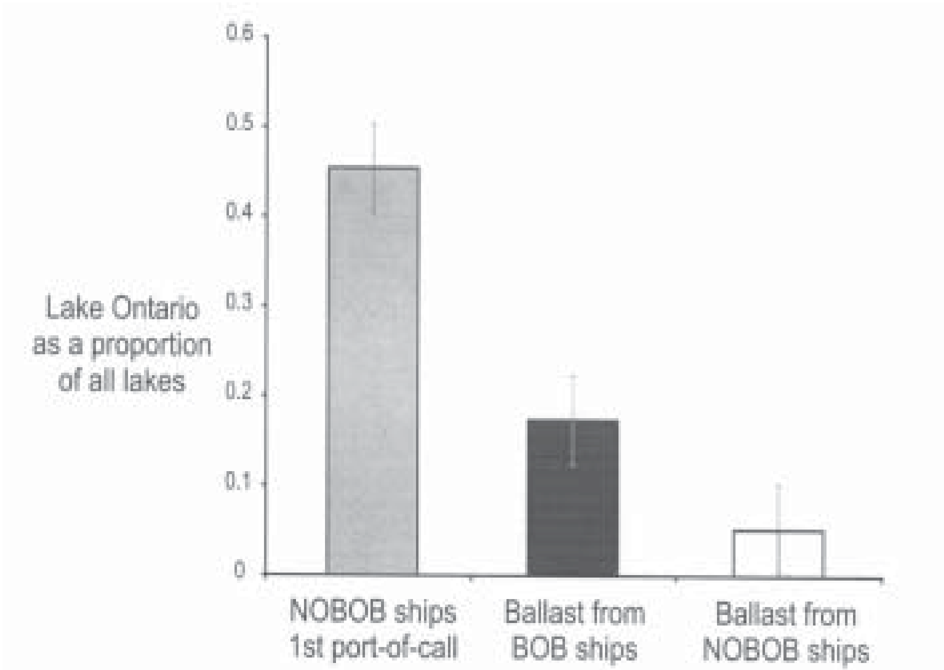

Fig. 4. Average (+/- 95% C.I.) shipping activity on Lake Ontario from 1994 to 2000 as a proportion of all Great Lakes. Ports on Lake Ontario were the first ports-of-call for almost half of all ships entering the Great Lakes declaring 'No Ballast On Board' (NOBOB; grey). However, less than 20% of ships that declared 'Ballast On Board' (BOB; black) loaded cargo at ports on Lake Ontario, and presumably discharged ballast there. Less than 5% of NOBOB ships loaded cargo and discharged ballast at Lake Ontario ports after having loaded Great Lakes ballast water at an earlier port (white).

The nature of the ship vector to the Great Lakes changed during the latter part of the 20th century. While there has always been a combination of BOB and NOBOB vessels entering the lakes, the importance of the latter class of vessels increased during the 1990s (Colautti et al., in press). Indeed, NOBOB vessels constitute >90% of inbound traffic to the lakes today. BOB and NOBOB vessels may represent different threats to Lake Ontario. BOB vessels may harbour euryhaline species capable of surviving in Lake Ontario. Few freshwater species are likely to survive in mid-ocean water (~35‰ salinity). However, studies of inbound vessels to the Great Lakes noted that some ships that declared having undergone ballast water exchange at sea contained brackish rather than saline water, and live freshwater zooplankton, in their tanks (Locke et al., 1991, 1993). It is possible, therefore, that some NIS introduced to Lake Ontario in recent years (e.g. *Thalassiosira baltica*, *Cercopagis pengoi*) may have arrived in BOB vessels. Because other fresh and brackish-water species occur in international ports that trade with the Great Lakes (Grigorovich et al., in press (a)), this vector cannot be assumed to have been eliminated. Nevertheless, a modeling exercise suggested that BOB vessels pose relatively little risk of introducing strictly freshwater species to the Great Lakes if ballast water exchange is thorough (MacIsaac et al., 2002a).

Few vessels that enter the Great Lakes in NOBOB status discharge mixed Great Lakes water and residual ballast water into Lake Ontario (Figure 4). The residual water may be of fresh or brackish origin, and live NIS could therefore be discharged directly into the lake. In addition, resting stages of invertebrate species contained in residual ballast sediments may hatch after Great Lakes water is pumped into ballast tanks (Bailey et al., in press); if this water is subsequently released into Lake Ontario, there would be an as yet undetermined risk of NIS invasion. However, due to the low volumes of water entering Lake Ontario by this mechanism relative to the other Great Lakes (Figure 4), the risk of invasion is likely to be comparatively minor. For ballast-mediated introductions, Lake Ontario is probably more at risk from the subsequent spread of species from other lakes. Domestic cargo vessels (i.e. "lakers") move much more ballast water than do transoceanic vessels, and thus pose a high risk of intra-basin transfer (Aquatic Sciences, 1996).

Alternative Vectors

Two NIS of macrophyte (*Hydrocharis morus-ranae*, *Myriophyllum spicatum*) and one mollusc (*Radix auricularia*) are thought to have invaded Lake Ontario via release from private aquaria (Table 1; Mills et al. 1993). In addition, goldfish (*Carassius auratus*) and European water chestnut (*Trapa natans*) are also thought to have been introduced by this vector, along with other mechanisms (Table 1, Mills et al., 1993). Blue-spotted sunfish (*Enneacanthus gloriosus*), which has been recorded from the Lake Ontario watershed but not within the lake itself, is also an aquarium release (Mills et al., 1993). Release of aquarium organisms is likely to occur mainly due to hobbyists discarding taxa either when they grow tired of them or when they become too large or prolific for home-based tanks (Courtenay, 1999; Crossman and Cudmore, 1999a). It is common practise to liberate fish into public waters as a perceived humane method of disposal (Courtenay, 1999). Private aquaria containing fish, macrophytes and molluscs are common in many North American homes and workplaces; in fact, approximately 10% of households in the United States maintain ornamental fish (Ramsay, 1985; Chapman et al., 1997). With large and growing human populations around Lake Ontario, particularly in the Toronto area, the rate of release of organisms from private aquaria into the lake may be large and increasing. Although the aquarium trade has not been a particularly important vector to date, with human population growth, possible curtailment of ballast-mediated introductions, and with an increasingly wide array of aquarium organisms available, it is anticipated that invasion risk from this vector will increase in the future. Release of aquarium fish may also inadvertently release new fish parasites into the system. For example, few of the fish in the United States aquarium trade are cultured domestically, but rather are imported as either wild caught or foreign-cultured species (Chapman et al., 1997). Mouten et al. (2001) recorded a number of protozoan and monogenean parasites on aquarium fish imported into South Africa. Thus, importation of aquarium species into the Lake Ontario basin could result in unanticipated introductions of species capable of surviving in the lake.

Release of live baitfish is another important method by which fish have become established unintentionally in Lake Ontario and the Great Lakes basin. Rudd (*Scardinius erythrophthalmus*) likely entered the lake by this mechanism. Also, both alewife (*Alosa pseudoharengus*) and green sunfish (*Lepomis cyanellus*) have likely experienced increases in distribution in the Great Lakes basin owing to baitfish release (Mills et al., 1993; Litvak and Mandrak, 1999). In Ontario alone, baitfish was a US $29 million industry in 1991 (Litvak and Mandrak, 1993). Despite the prohibition of baitfish release into waters other than where they were originally collected in this province, a survey of baitfish users found approximately half released their unused baitfish at their final destinations throughout Ontario (Litvak and Mandrak, 1993). Examining the native ranges of fish and the destination of anglers, Litvak and Mandrak (1993) also found 18 of the 28 species used were potentially utilised in areas outside of their known distribution ranges. Release of live baitfish is therefore likely to remain a risk for invasion into Lake Ontario and surrounding regions.

The importation of live food for human consumption is another potentially important future vector. In the Greater Toronto area, Crossman and Cudmore (1999b) noted that there were at least 14 dealers of live fish for human consumption, primarily servicing the local Asian population. As the Asian population in Toronto grows, so too may the demand for live fish and also the threat of introduction by this vector. Fish from these markets apparently originate primarily from fish farms in the southern United States, and include a variety of fish not yet established in Lake Ontario. Of particular concern is the sale of live bighead carp (*Hypophthalmichthys nobilis*) in Toronto-area markets (C. Rixon and N. Bergeron, University of Windsor, pers. comm.). Three individuals of bighead carp have been recorded on three separate occasions in Lake Erie in recent years, and one individual was discovered in a fountain pool in downtown Toronto, not far from Lake Ontario (Crossman and Cudmore, 1999b). Large numbers (~900,000) of live Asian carp are trucked into Ontario every year (B. Lafferty, Ontario Ministry of Natural Resources, pers. comm.). On-going legal trade of live individuals of these and other species pose an immediate risk to Lake Ontario and the other Great Lakes. Considering that these fishes likely originate from southern U.S. fish farm operations, the possibility also exists that associated parasitic fauna could be released into the Great Lakes.

As we learn more about the invasion routes and vectors of NIS introductions, our basic understanding of how NIS invade and integrate into communities – and how native communities respond to NIS – will grow. Clearly, Lake Ontario and the Great Lakes are not resistant to NIS introductions. Research linking theoretical and empirical studies on resource and invasion opportunities, and the importance of natural enemies and of physical conditions in affecting the NIS invasion rate, is warranted.

Nonindigenous species are very important components of the Lake Ontario food web (see Makarewicz et al., 2001; Benoit et al., 2002; Vanderploeg et al., 2002). For example, the diatom *Thalassiosira baltica* is one of the most abundant algal species in the lake (Edlund et al., 2000), and *Cercopagis pengoi* is a dominant zooplankton species (Laxson et al., in press). Moreover, zebra mussels (*Dreissena polymorpha*) and especially quagga mussels (*D. rostriformis*; = *D. bugensis*; T. Therriault, Fisheries and Oceans Canada, pers. comm.) are very important benthic species, while alewife, white perch (*Morone americana*), round goby (*Neogobius melanostomus*) and Pacific salmonids are dominant fishes. Thus, over the past 170 years, and especially over the past two decades, the Lake Ontario community has experienced dramatic, unplanned changes in species composition and dominance (Laxson et al., in press). Invasions will interact with other ecosystem stressors – notably climate change and toxic contaminants – further altering the lake in a myriad of unpredictable, uncontrollable ways. We therefore believe it to be prudent that management attention, and financial and human resources, be devoted to stanching the growing numbers of NIS entering Lake Ontario and the other Great Lakes.

Acknowledgements

We thank Dr. M. Munawar and anonymous reviewers for editorial assistance, and financial support from New York Sea Grant, U.S. Environmental Protection Agency, NSERC and Ontario PREA (JM and HJM). Additional support from U.S. National Sea Grant (ID), University of Windsor (RC), NSERC Industrial Scholarship (SB) is gratefully acknowledged.

References

Apte, S., Holland, B.S., Godwin, L.S., Jonathan, P.A., 2000. Jumping ship: A stepping stone event mediating transfer of a non-indigenous species via a potentially unsuitable environment. Biol. Invas. 2, 75-79.

Aquatic Sciences, Inc., 1996. Examination of aquatic nuisance species introductions to the Great

Lakes through commercial shipping ballast water and assessment of control options. Phase I and Phase II. ASI project E9225/E9285. St. Catharines, Ontario.

Benoit, H.O., Johannsson, O.E., Warner, D.M., Sprules, W.G., Rudstam, L.G., 2002. Assessing the impact of a recent predatory invader: the population dynamics, vertical distribution, and potential prey of *Cercopagis pengoi* in Lake Ontario. Limnol. Oceanogr. 47, 626-636.

Bailey, S.A., Duggan, I.C., van Overdijk, C.D.A., Jenkins, P.T., MacIsaac, H.J., (in press). Viability of invertebrate diapausing stages collected from residual ballast sediment. Limnol. Oceanogr.

Carlton, J.T., 1996. Biological invasions and cryptogenic species. Ecology 77, 1653-1655.

Chapman, F.A., Fitz-Coy, S.A., Thunberg, E.M., Adams, C.M., 1997. United States of America trade in ornamental fish. J. World Aquacult. Soc. 28, 1-10.

Cohen, A.N., Carlton, J.T., 1998. Accelerating invasion rate in a highly invaded estuary. Science 279, 555-558.

Colautti, R., Niimi, A., van Overdijk, C.D.A., Mills, E.L, Holeck, K., MacIsaac, H.J., (in press). Spatial and temporal analysis of shipping vectors to the Great Lakes. In: G.M. Ruiz, J.T. Carlton (Eds.), *Bioinvasions: Pathways, Vectors, and Management Strategies.* Island Press, Washington, D.C.

Courtenay, W.R. Jr., 1999. Aquariums and water gardens as vectors of introduction. In: R. Claudi, J.H. Leach (Eds.), *Nonindigenous freshwater organisms: vectors, biology, and impacts*. pp. 127-128. Lewis Publishers, Boca Raton, Florida.

Crossman, E.J., Cudmore, B.C., 1999a. Summary of North American fish introductions through the aquarium/horticultural trade. In: R. Claudi, J.H. Leach (Eds.), *Nonindigenous freshwater organisms: vectors, biology, and impacts*. pp. 129-134. Lewis Publishers, Boca Raton, Florida.

Crossman, E.J., Cudmore, B.C., 1999b. Summary of North American introductions of fish through the aquaculture vector and related human activities. In: R.Claudi, J.H. Leach (Eds.), *Nonindigenous freshwater organisms: vectors, biology, and impacts*. pp. 297-303. Lewis Publishers, Boca Raton, Florida.

Crossman, E.J., Holm, E., Cholmondeley, R., Tuininga, K., 1992. First record for Canada of the Rudd, *Scardinius erythrophthalmus*, and notes on the introduced Round Goby, *Neogobius melanostomus*. Can. Field-Nat. 106, 206-209.

Crowder, A., Painter, D.S., 1991. Submerged macrophytes in Lake Ontario: current knowledge, importance, threats to stability, and needed studies. Can. J. Fish. Aquat. Sci. 48, 1539-1545.

Damann, K.E., 1979. Occurrence of the red alga *Bangia atropurpurea* in Lake Ontario. Bull. Torrey Bot. Club 106, 43-44.

Dermott, R., Witt, J., Um, Y.M., Gonzales, M., 1998. Distribution of the Ponto-Caspian amphipod *Echinogammarus ischnus* in the Great Lakes and replacement of native *Gammarus fasciatus*. J. Great Lakes Res. 24, 442-452.

Dueck, L.A., Danzmann, R.G., 1996. Matriarchal population structure of introduced rainbow trout (*Oncorhynchus mykiss*) in the Lake Ontario watershed. Can. J. Fish. Aquat. Sci. 53, 2100-2114.

Duthie, H.C., Screenivasa, M.R., 1972. The distribution of diatoms on the superficial sediments of Lake Ontario. Proc. 15th Conf. Great Lakes Res. 45-52.

Edlund, M.B., Taylor, C.M., Schelske C.L., Stoermer E.F., 2000. *Thalassiosira baltica* (Grunow) Ostenfeld (Bacillariophyta), a new exotic species in the Great Lakes. Can. J. Fish. Aquat. Sci. 57, 610-615.

Fuller, P.L., Nico, L.G., Williams, J.D., 1999. Nonindigenous fishes introduced into inland waters of the United States. Amer. Fish. Soc., Special Publication 27, Bethesda, Maryland.

Galil, B.S., Zenetos. A., 2002. A sea of change – exotics in the Mediterranean Sea. In: E. Leppäkoski, S. Gollasch, S. Olenin (Eds.), *Aquatic invasive species of Europe. Distribution, impacts and management*. Kluwer Academic Publishers.

Grigorovich, I.A., Colautti, R.I., Mills, E.L., Holeck, K.H., MacIsaac, H.J., (in press (a)).Ballast-mediated animal introductions in the Laurentian Great Lakes: retrospective and prospective analyses. Can. J. Fish. Aquat. Sci.

Grigorovich, I.A., Gray, D.K., Duggan, I.C., Colautti R.I., MacIsaac, H.J., (in press (b)). Lake Superior: an invasion coldspot. Hydrobiol.

Kolar, C.S., Lodge, D.M., 2002. Ecological predictions and risk assessment for alien fishes in North America. Science 298, 1233-1236.

Laxson, C.L., McPhedran, K.N., Makarewicz, J.C., Telesh, I.V., MacIsaac, H.J., (in press). Effects of the nonindigenous cladoceran *Cercopagis pengoi* on the lower food web of Lake Ontario. Freshwat. Biol.

Leppäkoski, E., Gollasch, S., Gruszka, P., Ojaveer, H., Olenin, S., Panov, V., 2002. The Baltic - a sea of invaders. Can. J. Fish. Aquat. Sci. 59, 1175-1188.

Litvak, M.K., Mandrak, N.E., 1993. Ecology of freshwater baitfish use in Canada and the United States. Fisheries 18, 6-13.

Litvak, M.K., Mandrak, N.E., 1999. Baitfish trade as a vector of aquatic introductions. In: R.Claudi, J.H. Leach. (Eds.). *Nonindigenous freshwater organisms: vectors, biology, and impacts*. pp. 163-180. Lewis Publishers, Boca Raton, Florida.

Locke, A., Reid, D.M., Sprules, W.G., Carlton, J.T., van Leeuwen, H., 1991. Effectiveness of mid-ocean exchange in controlling freshwater and coastal zooplankton in ballast water. Can. Tech. Rep. Fish. Aquat. Sci. #1822. 93p.

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

MacIsaac, H.J., 1996. Potential abiotic and biotic effects of zebra mussels on inland waters of North America. Amer. Zool. 36, 287-299.

MacIsaac, H.J., 1999. Biological invasions in Lake Erie: past present and future. In: M. Munawar, T. Edsall (Eds.), *State of Lake Erie: past, present and future*. pp. 305-322. Backhuys, Leiden.

MacIsaac, H.J., Robbins, T.C., Lewis., M.A., 2002a. Modeling aquatic species invasions. Can. J. Fish. Aquat. Sci. 59, 1245-1256.

MacIsaac, H.J., Bandoni, S., Colautti, R., van Overdijk, C., Amundsen, A., 2002b. Economic impacts of invasive nonindigenous species in Canada: a case study approach. pp. 179-180. Office of the Auditor General of Canada.

Makarewicz, J.C., Grigorovich, I., Mills, E., Damaske, E., Cristescu, M., Pearsall, W., LaVoie, M., Keats, R., Rudstam, L., Hebert, P., Halbritter, H., Kelly, T., Matkovich, C., MacIsaac, H.J., 2001. Distribution and population characteristics of *Cercopagis pengoi* in Lake Ontario. J. Great Lakes Res. 27, 19-32.

Mazak, E.J., MacIsaac, H.J., Servos, M.R., Hesslein, R., 1997. Influence of feeding habits on organochlorine contaminant accumulation in Great Lakes waterfowl. Ecol. Applic. 7, 1133-1143.

Mills, E.L., Leach, J.H., Carlton, J.T., Secor, C.L., 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. J. Great Lakes Res. 19, 1-57.

Mouten, A., Basson, L., Impson, D., 2001. Health status of ornamental freshwater fishes imported to South Africa: a pilot study. Aquarium Sciences and Conservation 3, 327-333.

Nalepa, T.F., Schlosser, D.W., Pothoven, S.A., Hondorp, D.W., Fanslow, D.L., Tuchman, M.L., Fleischer, G.W., 2001. First finding of the amphipod *Echinogammarus ischnus* and the mussel *Dreissena bugensis* in Lake Michigan. J. Great Lakes Res. 27, 384-391.

Nepszy, S.J. (Ed), 1988. Parasites of fishes in the Canadian waters of the Great Lakes. Technical Report No. 51, Great Lakes Fishery Commission, Ann Arbor, Michigan.

Owens, R.W., O'Gorman, R., Mills, E.L., Rudstam, L.G., Hasse, J.J., Kulik, B.H., MacNeill, D.B.,

1998. Blueback herring (*Alosa aestivalis*) in Lake Ontario: first record, entry route, and colonization potential. J. Great Lakes Res. 24, 723-730.

Ramsay, J.S., 1985. Sampling aquarium fishes imported by the United States. J. Ala. Acad. Sci. 56, 220-244.

Ricciardi, A., 2001. Facilitative interactions among aquatic invaders: evidence of 'invasional meltdown' in the Great Lakes. Can. J. Fish. Aquat. Sci. 58, 2513-2525.

Ricciardi, A., Rasmussen, J.B., 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Can. J. Fish. Aquat. Sci. 55, 1759-1765.

Ruiz, G.M., Fofonoff, P.W., Carlton, J.T., Wonham, M.J., Hines, A.H., 2000. Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. Ann. Rev. Ecol. Syst. 31, 481-531.

Sala, O.E., Chapin III, F.S., Armesto, J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770-1774.

Scott, W.B., Crossman, E.J., 1973. Freshwater fishes of Canada. Bull 184, Fish. Res. Bd. Canada, Ottawa.

Sheath, R.G., Morison, M.O., 1982. Epiphytes on *Cladophora glomerata* in the Great Lakes and St. Lawrence Seaway with particular reference to the red alga *Chroodactylon ramosum* (=*Asterocytis smargdina*). J. Phycol. 18, 385-391.

Simberloff, D.,Van Holle, B., 1999. Positive interactions of nonindigenous species: invasional meltdown? Biol. Invas. 1, 21-32.

Spencer, D.R., Hudson P.L., 2003. The Oligochaeta (Annelida, Clitellata) of the St. Lawrence Great Lakes Region: an update. J. Great Lakes Res. 29, 89-104.

Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B., Osman, R.W., 2002. Linking climate change and biological invasion: ocean warming facilitates nonindigenous species invasions. Proc. Nat. Acad. Sci. (USA) 99, 15497-15550.

Stoermer, E.F., 1978. Phytoplankton assemblages as indicators of water quality in the Laurentian Great Lakes. Trans. Amer. Micros. Soc. 97, 2-16.

Stuckey, R.L., 1979. Distributional history of *Potamogeton crispus* (curly pondweed) in North America. Bartonia 46, 22-42.

Therriault, T.W., Grigorovich, I.A., Kane, D., Haas, E., Culver, D., MacIsaac, H.J., 2002. Range expansion of the exotic zooplankter *Cercopagis pengoi* (Ostroumov) into western Lake Erie and Muskegon Lake. J. Great Lakes Res. 28, 698-701.

United States Coast Guard, 1993. Ballast water management for vessels entering the Great Lakes. Code of Federal Regulations 33-CFR Part 151.1510.

Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K., Liebig, J.R., Grigorovich, I.A. Ojaveer, H., 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 59, 1209-1228.

van Overdijk, C.D.A., Grigorovich, I.A., Mabee, T., Ray, W., Ciborowski, J.J.H., MacIsaac. H.J., 2003. Microhabitat selection by the amphipods *Echinogammarus ischnus* and *Gammarus fasciatus* in laboratory and field experiments: displacement patterns and mechanisms. Freshwat. Biol. 48, 567-578.

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