Nonindigenous species in Lake Erie: A chronicle of established and projected aquatic invaders

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Introduction

By limiting the dispersal of species, natural barriers and climatic conditions have been paramount in shaping the evolution of biotas of the world's biogeographical regions (Elton, 1958; Vermeij, 1991; Lodge, 1993; Johnson and Taylor, 2004). However, global biodiversity has undergone massive and unprecedented change in the last 500 years, mainly as a result of anthropogenic activity (Everett, 2000; Mack et al., 2000). Humans have initiated the breakdown of ecological barriers through habitat destruction and deliberate and accidental introduction of nonindigenous species (NIS); when combined with the extirpation of native species, a dramatic homogenization of the world's biotas is presently well underway (Rahel, 2002; Sax and Gaines, 2003; Olden

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et al., 2004). This mixing of species across continents, oceans and lakes threatens the integrity of native communities by altering food web patterns, ecosystem processes, and, in some cases, causing species extinctions (Rahel, 2002; Olden et al., 2004; Ricciardi, 2005 and Atkinson, 2004). Many ecosystem changes associated with NIS are predictable based upon the species' performance in its native range, or in other invaded systems; however, synergisms between native species and NIS or between different established NIS may render prediction of some ecological impacts difficult or impossible (Ricciardi, 2004).

The combination of historical and contemporary anthropogenic stresses and NIS introductions threaten recreational and commercial uses of the Great Lakes, as well as their ecological integrity (Ricciardi et al., 1998; Ricciardi and MacIsaac, 2000). Lake Erie, in particular, has been impacted through a combination of habitat loss, additions of toxic chemicals and nutrients, overfishing, and introduction of NIS. Recent increases in total phosphorus, coupled with blooms of toxic cyanobacteria and development of extensive hypoxic zones indicate that the lake continues to evolve (see State of Lake Erie below). While Lake Erie's invasion history was reviewed by MacIsaac (1999), he only considered species whose establishment in Lake Erie represented the first record of invasion in the Great Lakes basin and his list of future invaders was based primarily on potential transport in ballast water. This review is more comprehensive, including all NIS recorded from the lake, regardless of whether the invasion was primary or secondary. We discuss some of the biotic and abiotic trends in the lake that have occurred over the past five years, as well as trends in the composition of NIS established in the lake and pathways of introduction. Our aim is to provide a thorough review of the status of aquatic NIS in Lake Erie, while minimizing overlap with earlier efforts. Finally, we review studies of various pathways that may be responsible for introduction of NIS to the Great Lakes in an attempt to forecast possible invaders to Lake Erie.

State of Lake Erie

Of all the Great Lakes, Lake Erie arguably has been exposed to the greatest level of anthropogenic stressors. Lake Erie is both the

shallowest of the Great Lakes and the smallest by volume; because it supports the largest human population, Lake Erie is exposed to the greatest effects from urbanization and agriculture (Lake Erie LaMP, 2004). The increased importance of these stressors roughly coincides with development of the human population in the lake's basin. For example, between 1910 and 1960, the human population in the Lake Erie basin grew from 3.8 million to 11.2 million (USPHS, 1965). Concomitant with human development along its shorelines, the lake suffered early-on from wetland destruction and habitat alteration (Regier and Hartman, 1973). Subsequent stressors included overfishing, inputs of nutrients (effluent) and organic and metal contaminants to the lake, as well as introduction of NIS (Regier and Hartman, 1973; Koonce et al., 1996; Lake Erie LaMP, 2004). The lake suffered a number of dramatic biological changes concurrent with cultural eutrophication, including massive growth of the nuisance alga *Cladophora glomerata* in some nearshore areas, changes in fish community composition, and a reduction or loss of oxygen-sensitive invertebrates (Regier and Hartman, 1973; Shear and Konasewich, 1975; Koonce et al., 1996). These effects were most pronounced in the western and central basins, although species composition changes occurred in all three basins.

Owing to concerns regarding water quality and health of the lake, phosphorus abatement programs were implemented in 1972 under the Canada-US Great Lakes Water Quality Agreement (IJC, 1988). These programs fostered dramatically improved water quality, and organic contaminant loads have declined in recent years (Makarewicz and Bertram, 1991; Dolan, 1993; Marvin et al., 2004). Reductions in turbidity and increased dissolved oxygen concentrations in the western basin, and increased oxygen levels and enhanced cold water habitat in the central basin, appear to have benefited species intolerant of enriched conditions (Ludsin et al., 2001). For example, oligotrophication of the lake led to increased abundance and diversity of the fish community, and a return of anoxia-sensitive mayflies, *Hexagenia limbata*, to the western basin (Krieger et al., 1996). Most recently, however, the lake has suffered a number of serious setbacks. An alarming increase in total phosphorus concentration in the western basin has been observed, beginning in 1993, which cannot be accounted for by identified loadings from anthropogenic sources (Nicholls et al., 2001; Pelley, 2003; Marvin et al., 2004). At the same time, a toxic strain of the cyanobacterium *Microcystis aureginosa* has formed mid-summer 'blooms' in the southern half of the western basin over the past seven years (Makarewicz et al., 1999; Vanderploeg et al., 2001; Budd et al., 2001). In the central basin, hypoxic zones, influenced by stratification and bacterial respiration both in sediments and the water column, have become more severe and more frequent (Pelley, 2003). These changes appear to be linked to the phenomena occurring in the western basin. It is not yet clear whether the development of extensive hypoxic zones are sufficient to cause fish and invertebrate 'die offs' similar to those observed during the 1960's-70s (Regier and Hartman, 1973; Reynoldson and Hamilton, 1993). Finally, mass mortalities of diving waterbirds, such as common loons (*Gavia immer*) and red-breasted mergansers (*Mergus serrator*), in the eastern basin of the lake have been observed since 1999 (see Holeck et al., 2004). It has been hypothesized that quagga mussels and zebra mussels (*Dreissena rostriformis bugensis* and *D. polymorpha*, respectively), facilitate growth of *Clostridium botulinum* bacteria, which the mussels then filter from the water (Holeck et al., 2004). The contaminated mussels are consumed by round gobies, which, after becoming ill and disoriented, are in turn preyed upon by diving waterbirds. These very troubling developments indicate a clear need for additional study to confirm the etiology of waterbird mortalities and the role(s), if any, played by NIS.

The dramatic physicochemical changes in Lake Erie highlight the continuing anthropomorphic stresses to which the lake has been exposed. Although the role of disturbance in facilitating invasion success is highly contentious (see Lozon and MacIsaac, 1997; Colautti et al., 2005), the possibility that physicochemical changes may contribute, in part, to past or future invasions cannot be dismissed outright.

Superimposed on ecological changes wrought by habitat loss, overfishing and contaminant loadings are those associated with introduction of NIS. Establishment of NIS can drive complex interactions that influence current and future distributions of both native and nonindigenous species within Lake Erie. One of the most damaging invaders to the Great Lakes has been the sea lamprey (*Petromyzon marinus*), whose introduction, facilitated by the construction of the Welland Canal, was instrumental in the decline of lake trout (*Salvelinus namaycush*). In Lake Erie, the development

of intensive control programs using lampricide reduced sea lamprey populations and enhanced lake trout survival in the mid-1990's (Page et al., 2004; Sullivan et al., 2003). However, suppression of treatment has seen a recent surge in sea lamprey populations in the lake together with the occurrence of trout skin lesions equivalent to that in pre-control times; this development may hinder conservation efforts unless management actions are increased (Sullivan et al., 2003).

Establishment and spread of the zebra mussel has been instrumental in water clarity improvement in the Great Lakes (Vanderploeg et al., 2002). However, selective rejection by dreissenid mussels of *Microcystis aeroginosa* colonies may explain, in part, the increasingly frequent summer blooms of this toxin-producing species in western Lake Erie, as well as in Saginaw Bay, Lake Huron (Vanderploeg et al., 2001). Zebra mussels have promoted macroinvertebrate diversity and density in western Lake Erie through provision of shell-generated habitat and pseudofaeces, but they may also have facilitated abundance and spread of other Ponto-Caspian invaders such as the amphipod *Echinogammarus ischnus* and the round goby *Neogobius melanostomus* (Stewart et al., 1998; Bially and MacIsaac, 2000; Ricciardi, 2001; Vanderploeg et al., 2002).

Although most aquatic NIS appear to impart little ecological or economic harm, the species described above are but a few of the damaging NIS that have become established in Lake Erie. The only reliable way to prevent damage associated with NIS is to prevent their establishment. One method of prevention is to determine current vectors that translocate species, and then identify methods to intercept or kill species in the vector stream. In this manner, we can minimize future invasions by learning from past invasions.

Methods

Following the methods of Duggan et al. (2003), we compiled a list of aquatic NIS established in Lake Erie by cataloguing distributions of NIS known from the Great Lakes basin. Primary references include Mills et al. (1993), Grigorovich et al. (2003a, b) and the references therein. We recorded the first report of each NIS within Lake Erie, acknowledging that for many taxa the date of establishment may precede the date of first report as a result of time lags between establishment and detection. For each species we also recorded the likely pathway(s) of introduction to the Great Lakes basin, native region(s) and whether Lake Erie was the site of first introduction in the basin. The date of first detection in Lake Erie was not documented in the literature for several species currently established in Lake Erie; therefore we could only record year of introduction as being after the first recorded sighting in the Great Lakes. If we could not find published accounts of NIS known from the other Great Lakes in Lake Erie, we assumed that they were not present. As discussed by Duggan et al. (2003), we considered annelid taxa as cryptogenic in origin (see Carlton, 1996), and excluded them from analysis. In addition, we excluded marginal swamp plants and shoreline trees, but included submerged macrophytes. Our estimate of NIS established in Lake Erie is, therefore, likely to be conservative.

For assessment of pathways of introduction, we followed the categories used by Mills et al. (1993). We explored the relationship between invaders and time by plotting the temporal accumulation of recorded NIS using non-linear regression (least squares fit; Statistica 6.0). The taxonomic composition of NIS was examined, as was the origin and dominant pathway of introduction for each. Temporal changes in dominance of taxonomic groups and modes of introduction were examined by classifying invasions into four time intervals: early period (1840-1880); pre-industrial (1881-1920); industrial (1921-1960); and post-opening of the St. Lawrence Seaway (1961-2002). Time intervals were selected for consistency with a comparable study for Lake Ontario (Duggan et al., 2003).

We used data from Colautti et al. (2003) to describe trends in shipping patterns for Lake Erie for the period 1994-2000. Two types of transoceanic vessels operate in Lake Erie: ships without cargo that carry only saltwater ballast on board (BOB) and ships fully loaded with cargo, carrying only residual water on board (NOBOB) (see Colautti et al., 2003). The number of BOB and NOBOB vessels visiting Lake Erie ports were inferred from cargo movements, following Duggan et al. (2003). We assumed uptake of Great Lakes water by NOBOB ships that off-loaded cargo at their first port of call, and discharge of salt water by BOB ships that loaded cargo. We also compiled data on the proportion of Lake Erie ports where NOBOB ships loaded cargo and, thus, where they were assumed to have discharged ballast.

For prediction of new invaders to Lake Erie, we conducted a literature review of the main pathways operating on the Great Lakes. We compiled a list of the species most likely to invade the lake by each pathway, and provide a description of one species predicted by each. Species predicted to invade via international shipping were identified using methods similar to Grigorovich et al. (2003a). Potential invaders were identified based on their presence in important donor regions, presence of an invasion history, tolerance of ambient temperature and water chemistry, and likelihood of uptake and survival in ballast tanks. The resulting list was refined by including only those species found in all three major donor regions identified in Grigorovich et al. (2003a): North Sea basin, Baltic Sea basin, Black Sea – Azov Sea basin. Species predicted to enter Lake Erie via the aquarium trade and live food fish markets were chosen with reference to Rixon et al. (2005), who identified a donor pool of potential invaders to the Great Lakes based on temperature tolerances, invasion history, and frequency of occurrence in aquarium stores or live fish markets. The latter characteristic was selected to serve as a proxy for 'propagule pressure', or introduction effort. Similarly, invaders predicted by introductions associated with aquaculture were chosen with reference to the risk assessment model for fishes developed by Kolar and Lodge (2002) for the Great Lakes. Species placed in the 'higher' and 'medium' risk categories, based on their predicted rate of spread and potential impacts, were included in the list. Finally, by compiling a list of species that have invaded Great Lakes other than Erie, we identified likely invaders resulting from intra-basin transfer by regional shipping or advection. Species not found in the Great Lakes proper (i.e., species present exclusively in the surrounding watershed) were excluded, and the remaining species were evaluated for the presence of characteristics amenable to transport in ships' ballast tanks (e.g., resting stages).

History of Invasions

We tabulated 72 NIS of aquatic vertebrate and invertebrate animals, protists, algae and submerged macrophytes in Lake Erie proper (Table 1). Fishes and algae were represented by the most NIS in the lake, each having 16 established species. For fishes, 28% of established

Table 1. List of species introduced to Lake Erie arranged by date of introduction. Key to pathways of introduction: A – accidental, AQ – aquarium release, BW – ballast water, C – canal, Cu – escape of cultivated plants, D – deliberate, F – unintentional establishment associated with fish release, HF – hull fouling, SB – solid ballast, U – unknown. Multiple vectors are listed in order of importance. Primary source of information was Mills *et al.*, 1993; additional sources listed in reference column.

Taxon	Species	Year of Introduction	Pathway	Additional References
Plant	*Nasturtium officinale*	>1847*	Cu	
Mollusca	*Bithynia tentaculata*	>1871	SB, D	
Pisces	*Oncorhynchus tshawytscha*†	1873	D	
Crustacea	*Gammarus fasciatus*	>1874*	SB, BW	Grigorovich *et al.*, 2003b
Pisces	*Oncorhynchus mykiss*	>1876*	D	
Pisces	*Carassius auratus*	<1878	D, AQ, F, A	
Pisces	*Cyprinus carpio*	1879	D	Van Meter and Trautman, 1970
Mollusca	*Pisidium moitesserianum*‡	1895	SB	Grigorovich *et al.*, 2003b
Plant	*Potamogeton crispus*	<1900	D, F	Stuckey, 1979
Mollusca	*Sphaerium corneum*	1900	U	Mackie, 1995
Mollusca	*Radix auricularia*	1911	AQ, A	
Mollusca	*Valvata piscinalis*	>1913*	SB	Grigorovich *et al.*, 2003b
Mollusca	*Viviparus georgianus*	1914	AQ	
Mollusca	*Pisidium henslowanum*	>1916*	SB	Grigorovich *et al.*, 2003b
Pisces	*Petromyzon marinus*	1921	C, HF	
Pisces	*Lepomis humilis*†	1929	C	
Algae	*Stephanodiscus binderanus*	1930	BW	Stoermer *et al.*, 1996
Plant	*Nymphoides peltata*†	1930	A	
Pisces	*Alosa psuedoharengus*	1931	C, F	
Pisces	*Osmerus mordax*	1932	C, D	Van Meter and Trautman, 1970
Plant	*Najas minor*†	1932	D	
Hydrozoa	*Craspedacusta sowerbyi*†	1933	A	Grigorovich *et al.*, 2003b
Pisces	*Oncorhynchus kisutch*†	1933	D	
Bryozoa	*Lophopodella carteri*†	1934	A	Ricciardi and Reiswig, 1994; Grigorovich *et al.*, 2003b
Pisces	*Salmo trutta*	1939	A, D	Trautman, 1957
Mollusca	*Cipangopaludina chinensis malleata*	1940s	AQ	
Mollusca	*Cipangopaludina japonica*†	1940s	D	
Insecta	*Acentropus niveus*†	1950	A	
Pisces	*Phenacobius mirabilis*†	1950	C, F	
Plant	*Marsilea quadrifolia*	1951	D	
Plant	*Myriophyllum spicatum*†	1952	AQ, HF	
Pisces	*Morone americana*	1953	C	Fuller *et al.*, 1999
Hydrozoa	*Cordylophora caspia*†	1956	A	
Protista	*Glugea hertwigi*†	1960	F	Grigorovich *et al.*, 2003b
Algae	*Actinocyclus normanii* f. *subsala*	1960	BW	Hohn, 1969
Crustacea	*Eurytemora affinis*	1961	BW	Grigorovich *et al.*, 2003b
Mollusca	*Pisidium amnicum*	<1962	SB	Herrington, 1962
Algae	*Thalassiosira weissflogii*	1962	BW	
Algae	*Skeletonema potamos*†	1963	BW	
Algae	*Bangia atropurpurea*†	1964	BW, HF	
Algae	*Chroodactylon ramosum*†	1964	BW	

Table 1. Contd.

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†first recorded sighting for Great Lakes is in Lake Erie proper
‡first record from Lakes Erie and St. Clair
§first record from Lakes Erie and Ontario
*date known only as being after first record for the Great Lakes basin

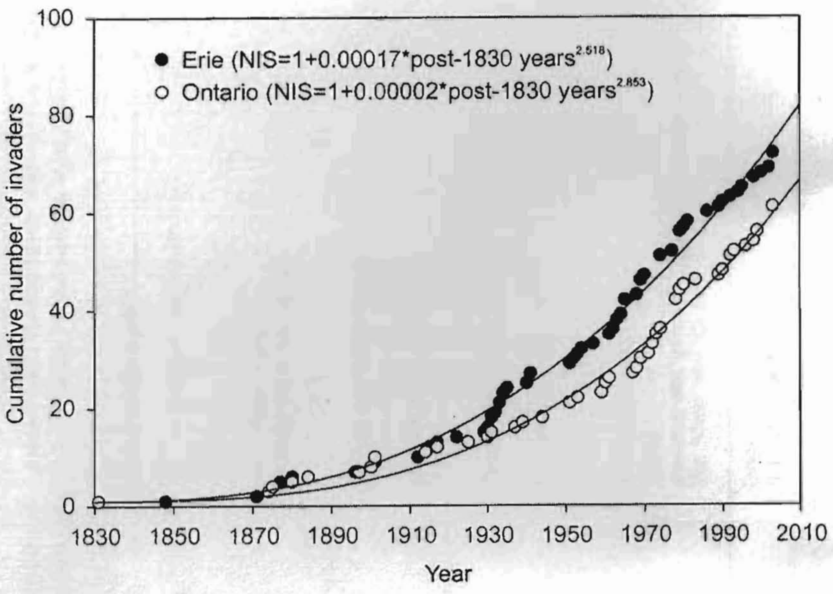

Fig. 1. Cumulative number of NIS established in Lake Erie and Lake Ontario, exclusive of oligochaetes. Solid lines fitted using least-squared non-linear regression.

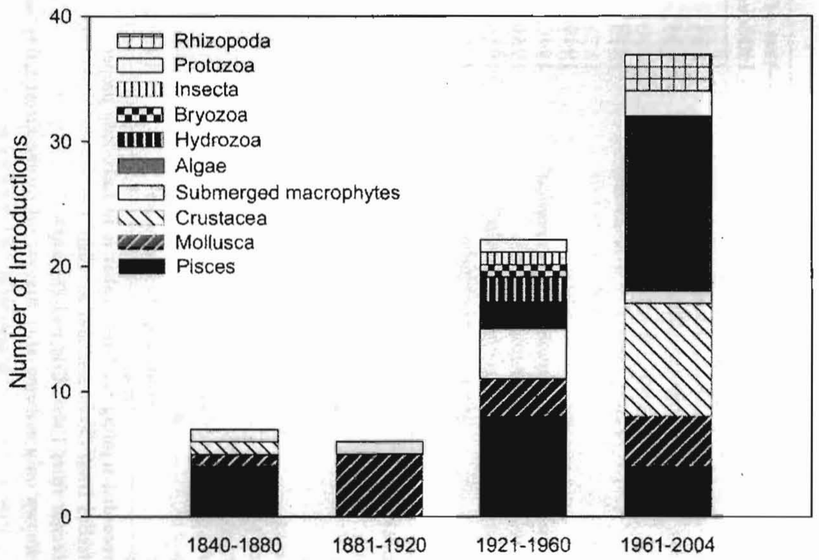

Fig. 2. Temporal sequence of NIS introductions into Lake Erie, by taxon.

NIS resulted from intentional stockings, 28% were intra-basin transfers due to construction of canals, 12% were ballast water releases, and 12% were baitfish releases. In contrast, algal introductions were attributed solely to the shipping vector. Following fishes and algae, the richest groups of NIS in the lake were molluscs (13 species), crustaceans (10 species) and submerged macrophytes (7 species). In addition, small numbers of NIS of protists, bryozoans, hydrozoans and insects were established in the lake (totalling 10 species). The rate of establishment of NIS in Lake Erie was distinctly non-linear since the initial invasion of the watercress, *Nasturtium officinale* (= *Rorippa nasturtium aquaticum*), after 1847. Both the cumulative number of invaders and the rate of invasion are greater than that described from Lake Ontario for the same time period (Fig. 1; see Duggan et al., 2003). While early and pre-industrial invaders were predominantly fishes and molluscs, respectively, recently established NIS consist of a diverse array of fishes, crustaceans, molluscs, algae, protists and plants (Fig. 2). Nearly half of these species (49%) were Eurasian in origin. The majority of the remaining species exhibited either a widespread distribution (17%) or originated from restricted distributions in North America (14%).

Twenty-nine NIS reported from Lake Erie, representing a broad array of taxonomic groups, were new introductions to the Great Lakes. However, as discussed in Duggan et al. (2003), the non-linear model conceals a punctuated pattern of invasion. Biases in taxonomic expertise, temporal effort, and survey location almost certainly affect the retrospective patterns observed today. As an example, two of the first records for Lake Erie, *Pisidium moitesserianum* and *Psammonobiotus linearis*, were recorded simultaneously from other areas in the Great Lakes after multiple-lake surveys were conducted. As most surveys conducted on the Great Lakes have been spatially restricted, usually involving only one lake or basin, only records of physically prominent species are likely to approximate the actual spatial pattern of introduction.

Vector patterns

Although international shipping activities have accounted for 45% of introductions to Lake Erie, ballast water and other ship-associated

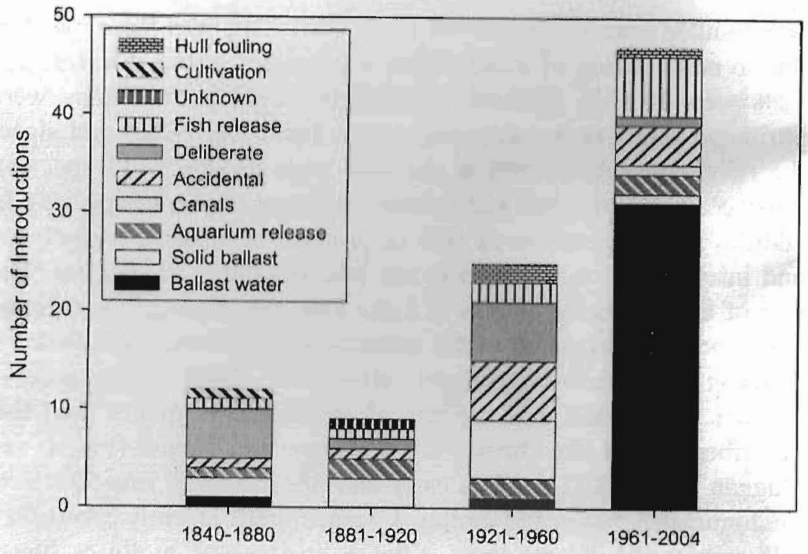

Fig. 3. Temporal sequence of pathways of introduction of NIS into Lake Erie. Note: taxa with multiple vectors were scored for each possible mechanism.

mechanisms have been a dominant pathway only since 1961 (Fig. 3). Prior to that, deliberate release of fishes, unintentional release of taxa associated with baitfish and the aquarium trade, and construction of canals to link previously isolated waterbodies were important pathways of introduction. Although accidental and incidental releases have been relatively minor mechanisms of introduction in recent years, they have remained as persistent vectors.

During the period 1994-2000, Lake Erie received approximately 20% of the total number of saline ballast water discharges into the Great Lakes (Colautti et al., 2003). In addition, Lake Erie received 13% of discharges by NOBOB ships. These discharges would be composed mainly of Great Lakes water mixed with small amounts of ballast residuals from global sources, the latter of which could harbour live and/or dormant NIS (e.g., see Bailey et al. 2003, 2005). Lake Erie was the first port-of-call for more than 40% of international vessels operating on the lakes, providing opportunity for establishment of hull fouling species (e.g., *Bangia atropurpurea*). Hull fouling is a common mode of species transfer in marine systems (e.g., Apte et al., 2000; Gollasch, 2002), and although most investigators feel that that this pathway is not operational for vessels entering the Great Lakes from marine waters, this assumption requires formal testing.

Future Invasions

Previous studies that sought to identify future invaders to Lake Erie and the Great Lakes have focussed primarily on taxa likely to be transported by ship-mediated vectors (Ricciardi and Rasmussen, 1998; MacIsaac, 1999; Grigorovich et al., 2003a). In his review of invasions in Lake Erie, MacIsaac (1999) attempted to identify future invaders by considering global species distributions and information regarding international trade and travel patterns. Ricciardi and Rasmussen (1998) based their predictions of potential invaders to the Great Lakes on life history characteristics, invasion history, and likelihood of uptake in ballast tanks. Although none of the 17 potential invaders listed by Ricciardi and Rasmussen (1998) have been found in Lake Erie[1], two of the 31 species listed by MacIsaac (1999) have since established: the waterflea *Daphnia lumholtzi*, and the fishhook waterflea *Cercopagis pengoi* (Muzinic, 2000; Therriault et al., 2002b). While *D. lumholtzi* probably spread from earlier introductions in the southern United States (Havel and Hebert, 1993), *C. pengoi* was likely transferred to Lake Erie in ballast water from its earlier point of introduction in Lake Ontario (Therriault et al., 2002b). Many of the remaining 29 species predicted by MacIsaac (1999) have also been identified as potential invaders by Grigorovich et al. (2003b), whose risk assessment framework was based predominantly on shipping patterns, history of invasiveness, and environmental matches. The amphipod *Gammarus tigrinus*, a species with a 'moderate' risk of invasion in Grigorovich et al.'s (2003b) analysis, is now established in Saginaw Bay, Lake Huron (D.W. Kelly, unpubl.) and likely will enter Lake Erie via advective dispersal or regional shipping activities.[2]

Future ballast water invaders will likely possess characteristics amenable to uptake and survival in ballast tanks, such as the ability to produce dormant life stages, ability to enter diapause as an adult, and a capability for parthenogenetic reproduction. Given the apparent suitability of the Great Lakes environment for the potential invaders listed by MacIsaac (1999) and Grigorovich et al. (2003b), and the availability of suitable vectors, we expect that additional species listed in these two studies will establish in Lake Erie in the future. Although international shipping has been the dominant vector of introductions to Lake Erie since 1961, it is apparent that other vectors are also operating (Fig. 3). Thus, while we predict similar species via the shipping vector as those listed in MacIsaac (1999) and Grigorovich et al. (2003b), we provide additional insight for four other potentially important pathways (Table 2).

Species valued as ornamental aquarium fish, as live fish sold for human consumption, or those used in aquaculture represent a relatively large pool of potential invaders (Mills et al., 1993; Duggan et al., 2003). Of primary importance for evaluating the probability of successful introduction for these species is their ability to tolerate the temperature and salinity characteristics of the Great Lakes, their past invasion history, and their popularity in pet shops and live fish food markets, both of which serve as proxies for propagule pressure (Rixon et al., 2005). For example, the Oriental weatherfish, *Misgurnus anguillicaudatus*, is native to eastern Asia, but has been introduced to many parts of North America (Fuller et al., 1999). It was found in the Shiawassee River, Lake Huron drainage, in 1958, in the Lake Michigan drainage in 1987, and in the Chicago Sanitary and Shipping Canal in 1994 (Fuller et al., 1999). It has not yet been reported from the Great Lakes proper (Rixon et al., 2005). Based upon its popularity in the aquarium trade, and its temperature tolerances (survival as low as 2°C), Rixon et al. (2005) predicted that the species could spread well beyond its current distribution in the Great Lakes basin. Its ecological impacts are unknown; however, if it becomes abundant and spreads it could reduce the availability of aquatic insects for native fishes (Fuller et al., 1999).

The bighead carp, *Hypophthalmichthys nobilis*, is an important fish species sold live in human food markets, representing an estimated 52% of the weight of all live freshwater fish marketed in Ontario (Goodchild, 1999). The species has been recorded in many U.S. states, and has established breeding populations in the lower and middle Mississippi and Missouri Rivers (Schrank and Guy, 2002). Rixon et al. (2005) identified this species as a potential invader to the Great Lakes based on its popularity in live fish food markets, prior invasion history, and its ability to survive at temperatures as low as 4°C. Individuals of bighead carp have been reported from Lake Erie (Fuller et al., 1999), indicating that releases have taken place. Establishment of bighead carp could have profound effects on Great Lakes habitats, considering that the fish can grow extremely large (>22 kg) and that they can consume up to 50% of their body weight

1. The freshwater shrimp *Hemimysis anomala*, a potential invader listed by Ricciardi and Rasmussen (1998), was recently recorded from Lakes Ontario and Michigan (Kipp and Ricciardi, 2007) and will likely enter Lake Erie via natural or ship-mediated dispersal.
2. In fact, *Gammarus tigrinus* has recently been reported from all of the Great Lakes (see Grigorovich et al. 2005).

Table 2. List of NIS predicted to invade Lake Erie by various vector pathways, arranged taxonomically. See text for source information.

Taxon	Species	Common name	Pathway
Mollusca	*Potamopyrgus antipodarum*	New Zealand mudsnail	Intra-basin transfer
Crustacea	*Dikerogammarus haemobaphes*	Amphipod	Shipping
	Dikerogammarus villosus	Killer shrimp (amphipod)	Shipping
	Gammarus tigrinis[2]	Amphipod	Intra-basin transfer
	Hemimysis anomala	mysid shrimp	Shipping
	Heteropsyllus cf. *nunni*	Harpacticoid copepod	Intra-basin transfer
	Pontogammarus robustoides	Amphipod	Shipping
	Schizopera borutzkyi	Harpacticoid copepod	Intra-basin transfer
Pisces	*Apeltes quadracus*	Fourspine stickleback	Intra-basin transfer
	Ctenopharyngodon idella	Grass carp	Live food fish
	Gymnocephalus cernuus	Ruffe	Intra-basin transfer
	Hypophthalmichthys nobilis	Bighead carp	Live food fish
	Hypopthalmichthys molitrix	Silver carp	Aquaculture
	Ictalurus furcatus	Blue catfish	Aquaculture
	Lepomis microlophus	Redear sunfish	Aquaculture
	Misgurnus anguillicaudatus	Oriental weatherfish	Aquarium trade
	Morone saxatilis	Striped bass	Live food fish
	Tanichthys albonubes	White cloud mountain minnow	Aquarium trade
Plant	*Egeria densa*	Brazilian elodea	Aquarium trade
	Hygrophila polysperma	Indian swampweed	Aquarium trade
	Myriophyllum aquaticum	Parrotfeather	Aquarium trade

2. In fact, *Gammarus tigrinus* has recently been reported from all of the Great Lakes (see Grigorovich et al. 2005).

per day in plankton (Dettmers and Pegg, 2003). However, this species was not among the most likely fish species identified in Kolar and Lodge's (2002) study of possible invaders to the Great Lakes.

Another Asian carp species, the silver carp (*Hypophthalmichthys molitrix*), has the potential to enter Lake Erie owing to aquaculture activities. It has been imported to North America for use as a food fish and as a control for phytoplankton blooms (Shelton and Smitherman, 1984). Silver carp are established in the Mississippi and Ohio rivers in Louisiana, and have been reported from 12 other states (Fuller et al., 1999). According to Kolar and Lodge's (2002) model, this species would spread slowly if it establishes in the Great Lakes, but would not likely become a nuisance species. However, that model did not account for the fish's leaping behaviour (startle response), which can injure boaters (Kolar and Lodge, 2002). Trade and/or live possession restrictions have been placed on Asian carp species in all Great Lakes states and in Ontario, as of summer 2004. These restrictions should dramatically reduce but not eliminate the risk of establishment of carp in the Great Lakes. For example, silver carp remained among the Asian carp species observed in live food stores in Toronto during autumn 2004 (P. Moy, University of Wisconsin Sea Grant Institute, Manitowac, WI, USA, pers. comm.).

Many invaders established in other regions of the Great Lakes could spread to Lake Erie through advective dispersal or interregional movement of ballast water. For example, two species of harpacticoid copepod new to Lake Michigan, *Heteropsyllus* cf. *nunni* and *Schizopera borutzkyi*, represent likely invaders due to their proximity to Lake Erie, and their high abundances within their current range. *S. borutzkyi* has been reported in the Danube River delta in the Black Sea basin, but was discovered at high abundance in Lake Michigan in 1998 (Horvath et al., 2001). *H.* cf. *nunni* was also found at high abundances (55-100% of harpacticoid abundances to 9 m depth) in 1998, although its origin is unknown (Horvath et al., 2001). Because the origin of *H.* cf. *nunni* is unknown, Horvath et al. (2001) did not state a vector of introduction; the establishment of *S. borutzkyi*, however, was likely the result of ballast water discharge. Although the ecological effects of these harpacticoid invaders remain unclear, Horvath et al. (2001) speculated that they could negatively affect native species through resource competition.

Discussion

Five new aquatic NIS have been recorded as established in Lake Erie since the review by MacIsaac (1999), including two species that are first records for the Great Lakes (see Table 1; 1999-2002). Four of the five species were likely introduced via international shipping, which has remained a dominant vector of aquatic NIS despite ballast water exchange regulations implemented in 1993 (USCG, 1993). The remaining species, *Daphnia lumholtzi*, most likely was originally introduced to North America as a contaminant with imported fishes or aquarium plants (Havel and Hebert, 1993). This recent invasion rate - one species per year - is similar to the current rate of invasion for the Great Lakes basin (1 species every 8 months; Ricciardi, 2001). However, the three *Psammonobiotus* testate rhizopod species recently identified (Nicholls and MacIsaac, 2004) are a previously understudied group in the Great Lakes, and may have established long before they were reported. Thus it is difficult to determine the actual introduction rate of NIS. Until the underlying vectors responsible for transfer of NIS are addressed, further invasions by NIS may be anticipated (see Mack et al., 2000).

The region between western Lake Erie and southern Lake Huron has been identified as an invasion 'hotspot' in the Great Lakes, based upon an assessment of post-1959 invaders (Grigorovich et al., 2003a). Since the majority of these invaders were introduced by ballast water, this trend is possibly a result of ship ballasting patterns. In support of this, Lake Erie ports received the second largest number of ballast water discharges since 1959, but discharges here declined over time and were low relative to Lake Superior, which received 75% of discharges (Colautti et al., 2003). Lake Erie also received more than 10% of ballast discharges by NOBOB ships annually, but again, this value was low relative to Lake Superior ports, which received ~70% of all discharges (Colautti et al., 2003). Thus, shipping activity predicts a greater number of NIS in Lake Superior than in Lake Erie. In terms of first reports of NIS in the Great Lakes, many more occurrences were in Lake Erie than in Lake Superior. Various hypotheses have been proposed to account for this discrepancy, including a bias in research effort, differences in physicochemical regimes between lakes, and fewer NIS in Lake Superior that may facilitate invasional meltdown (Ricciardi, 2001; Colautti et al., 2003;

Grigorovich et al. 2003b). It is also possible that hull fouling may play an heretofore unappreciated role in introductions since Lake Erie, together with Lake Ontario, is a principal initial port-of-call for vessels declaring NOBOB status entering the Great Lakes (Colautti et al., 2003).

The accumulation rate of NIS in Lake Erie is similar to that of Lake Ontario (Duggan et al., 2003), except for a surge of eight species introductions in Erie from 1930-1934. This surge of invaders in Erie is a surprising result, considering that Lake Ontario probably received a greater number of ballast water discharges during this time period than did Erie (i.e., as only small ships could access Erie prior to the opening of the St. Lawrence Seaway). In fact, only one of the invaders, the diatom *Stephanodiscus binderanus*, likely entered Lake Erie via ballast water discharge, while five species were introduced via deliberate or accidental introduction. Thus the surge appears to be the result of numerous releases that by choice or by chance did not present similar introduction effort into Lake Ontario; in fact, these five species are still not recorded from Lake Ontario. Otherwise, the two lakes show similar trends in composition of invaders and relative importance of vectors, and are currently subjected to similar shipping activity, although Lake Erie has received more invaders than Ontario since 1959. This pattern may reflect a larger number of unregulated[3] ballast discharges from NOBOB ships in Lake Erie (13% vs. 4%). In addition, the Detroit River and western Lake Erie could receive more ballast discharges than is presently reported owing to draft adjustments, by which ships temporarily reduce ballast volume while travelling through the shallow passages.

This review provides evidence that Lake Erie has been, and continues to be, a 'hotspot' for NIS in the Great Lakes. A large proportion of NIS recorded in the Great Lakes initially established in Lake Erie. Ballast exchange regulations enacted in 1993 have likely reduced the importance of the ballast water introductions, but additional mechanisms (including other ship-associated subvectors) must be addressed to curtail the establishment of future invaders. As an example, the government of Ontario recently amended the Fish and Wildlife Conservation Act to prohibit the sale of live bighead, black, silver and grass carp in the province (Ontario Regulation 113/04, subsection 32.2), as have all other political jurisdictions bordering

Lake Erie, to prevent introductions of live Asian carp species to the lakes. These efforts should serve to reduce the likelihood of invasion by these potentially hazardous species.

Holeck et al. (2004) reviewed all of the recent species additions to the Great Lakes and all of the pathways potentially involved in these introductions. In many instances, multiple pathways were capable of single species introductions, thus careful analyses must be conducted to isolate mechanisms of introduction. In Lake Erie, ballast water has been the dominant mechanism of introduction throughout most of the latter half of the 20th century. However, ballast water exchange regulations currently in place, and best management practises employed by the shipping industry, should curtail the importance of this pathway. Future efforts should focus on alternate pathways that collectively are capable of delivering a wide variety of NIS of plants, animals and microbes to Lake Erie.

Summary

Lake Erie has an extensive history of human-mediated perturbation, ranging from habitat destruction to nutrient and contaminant loadings and introduction of nonindigenous species (NIS). Currently, at least 72 NIS of aquatic vertebrate and invertebrate animals, protists, algae and submerged macrophytes are established in Lake Erie. Fishes and algae are represented by the most NIS (16 species each), followed by molluscs (13 species), crustaceans (10 species) and submerged macrophytes (7 species). In addition, 10 NIS of protists, bryozoans, hydrozoans and insects are established in the lake. Both the taxonomic composition of new NIS and pathway of introduction have varied temporally. Before 1880, aquatic invaders consisted primarily of fishes that were deliberately introduced. Molluscs were the principal invaders between 1881 and 1920, and were introduced by a variety of mechanisms including ships' solid ballast and aquarium releases. After

3. Although NOBOB ships were not regulated at the time of writing this manuscript, Canada became the first country to introduce mandatory ballast water regulations for NOBOB ships in June 2006, requiring vessels to flush tanks at sea or to comply with a code of 'best management practices.'

1920, a wide variety of aquatic NIS were introduced via an array of vectors, although ballast water was the predominant pathway (responsible for 66% of invasions after 1960). NIS continue to establish in Lake Erie at a rate of one invader per year; and until the numerous pathways of introduction are addressed, it is expected that the lake remains at risk of further invasion.

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