Diversity and Distributions, (Diversity Distrib.) (2006) **12**, 425–433

BIODIVERSITY RESEARCH

Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity

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ABSTRACT

The Laurentian Great Lakes basin has been invaded by at least 182 non-indigenous species. A new invader is discovered every 28 weeks, which is the highest rate recorded for a freshwater ecosystem. Over the past century, invasions have occurred in phases linked to changes in the dominant vectors. The number of ship-vectored invaders recorded per decade is correlated with the intensity of vessel traffic within the basin. Ballast water release from ocean vessels is the putative vector for 65% of all invasions recorded since the opening of the St. Lawrence Seaway in 1959. As a preventive measure, ocean vessels have been required since 1993 to exchange their freshwater or estuarine ballast with highly saline ocean water prior to entering the Great Lakes. However, this procedure has not prevented ship-vectored species introductions. Most ships visiting the Great Lakes declare 'no ballast on board' (NOBOB) and are exempt from the regulation, even though they carry residual water that is discharged into the Great Lakes during their activities of off-loading inbound cargo and loading outbound cargo. Recently introduced species consist predominantly of benthic invertebrates with broad salinity tolerance. Such species are most likely to survive in a ballast tank following ballast water exchange, as well as transport in the residual water and tank sediments of NOBOB ships. Thus, the Great Lakes remain at risk of being invaded by dozens of euryhaline invertebrates that have spread into Eurasian ports from whence originates the bulk of foreign ships visiting the basin.

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Keywords

Ballast water, biological invasions, exotic species, invasion rate, Ponto-Caspian species.

INTRODUCTION

Thousands of non-indigenous species of invertebrates, vertebrates, plants, fungi, and bacteria have invaded most regions of the planet (Vitousek *et al*., 1997). A small fraction but growing number of these invaders threatens biodiversity, ecosystem functioning, natural resources, and human health (Mack *et al*., 2000). The vast majority of recent invasions are attributable to human activities associated with international trade, which is accelerating the spread of organisms into new regions (Mack & Lonsdale, 2001; Levine & D'Antonio, 2003). As a result, invasions are apparently occurring over unprecedented temporal and spatial scales, particularly in large aquatic ecosystems (Cohen & Carlton, 1998; Leppäkoski & Olenin, 2000; Ruiz *et al*., 2000).

To prevent the spread of invasive species, management efforts must aim to control human vectors of dispersal (Ruiz & Carlton, 2003). Apart from exceptional circumstances that permit direct measurement, the only objective method by which we can gauge the efficacy of a vector control strategy is to compare observed patterns and rates of species invasions before and after the strategy's implementation. The documented invasion history of the Great Lakes spans two centuries and implicates a broad array of vectors, including ballast water release from ocean vessels, which is responsible for most invasions in modern times (Mills *et al*., 1993; Ricciardi, 2001; Holeck *et al*., 2004). Since May 1993, ships have been required to exchange their freshwater or estuarine ballast with highly saline oceanic water prior to entering the Great Lakes (United States Coast Guard, 1993), a procedure termed 'ballast water exchange' (BWE); the regulation was preceded by voluntary guidelines issued by Canada in 1989 (Locke *et al*., 1993) and the USA in 1991. In theory, an open-ocean BWE should greatly reduce the risk of invasion as freshwater organisms in ballast tanks would be purged or killed by the highly saline water and be replaced by marine organisms that cannot survive and reproduce if released into the Great Lakes. In practice, open-ocean BWE does not remove all coastal and inland-water taxa from ballast tanks, although it may reduce the numbers of live individuals (Locke *et al*., 1993; Niimi & Reid, 2003; Levings *et al*.,

DOI: 10.1111/j.1366-9516.2006.00262.x

2004). Furthermore, BWE often achieves only brackish salinities because residual freshwater usually remains in the tanks, due to the position of the pump intakes (Locke *et al*., 1993; Niimi & Reid, 2003; Niimi, 2004). Therefore, conditions produced by BWE might not be intolerable to organisms adapted to a broad salinity range.

A further complication is that most ships entering the Great Lakes after 1993 are loaded with cargo and, thus, carry only residual water and tank sediments (Holeck *et al*., 2004); they declare 'no ballast on board' and hence are called NOBOB ships. At the present time, NOBOB ships are not subject to regulation, even though those entering the Great Lakes each year are collectively carrying at least 23,000 m^3 of residual water (Niimi & Reid, 2003) that may contain millions of living invertebrates (Duggan *et al*., 2005). Moreover, NOBOB tank sediments typically harbour cysts, spores, and resting eggs of algae and invertebrates that can hatch or be placed in suspension when the ship re-ballasts, and then are released at another port where the ship discharges water before taking on new cargo (Bailey *et al*., 2003, 2005; Duggan *et al*., 2005). Residual ballast water and sediments have been found to contain crustacean species that have been discovered recently in the Great Lakes, as well as other freshwater invertebrates that have not yet been recorded (Duggan *et al*., 2005). Therefore, NOBOB ships may represent an active vector that plays a role in introducing benthic organisms, especially those with resting stages. Such possibilities call into question the efficacy of BWE in reducing invasions associated with transoceanic shipping.

This paper examines patterns and rates of invasion in the Great Lakes basin in relation to changes in vector activity, particularly shipping. Using a new data set, I evaluate current evidence that BWE has influenced the recent invasion history of the Great Lakes basin. The composition of invaders and their rate of discovery are compared before and after BWE regulation, in order to test the following hypotheses: (1) the rate of invasion in the Great Lakes is correlated with shipping activity; (2) the rate of invasion has been reduced following BWE; and (3) the composition and ecological traits of invaders in the Great Lakes have been altered since the time BWE was implemented.

METHODS

I compiled a comprehensive database of non-indigenous species of vascular plants, algae, invertebrates, and fishes recorded as invaders in the Great Lakes basin (including each of the Great Lakes and their drainages, as well as the upper St. Lawrence River between the outflow of Lake Ontario and the Island of Montreal) from the years 1840–2003. For the purposes of this paper, 'non-indigenous species' are defined as species that have no previous evolutionary history in the Great Lakes basin and were introduced there since the beginning of European colonization. A species whose evolutionary origins are poorly known was considered 'non-indigenous' if it met at least three of the following criteria, adapted from Chapman & Carlton (1991): (1) the species appears suddenly where it has not been recorded previously; (2) it subsequently spreads within the basin; (3) its distribution in the basin is restricted compared with native species; (4) its global distribution is anomalously disjunct (i.e. contains widely scattered and isolated populations); (5) its global distribution is associated with human vectors of dispersal; and (6) the basin is isolated from regions possessing the most genetically and morphologically similar species.

An 'invader' is defined here as an non-indigenous species that has established a reproducing population within the basin, as inferred from multiple discoveries of adult and juvenile life stages over at least two consecutive years (following Ruiz *et al*., 2000). Given that successful establishment often requires multiple introductions of an invader (Kolar & Lodge, 2001), I deliberately excluded records of discoveries of one or a few non-reproducing individuals, whose occurrence may reflect merely transient species or unsuccessful invasions (e.g. Manny *et al*., 1991; Fago, 1993). I have also excluded species that are indigenous to any part of the Great Lakes basin, even though they may have invaded other areas of the basin (e.g. sea lamprey; Waldman *et al*., 2004).

For each invader, I sought to identify the year of its discovery, its endemic region, and the most plausible mechanism of its introduction, which was usually provided in the published report of its discovery. I assigned each invader to one of the following vector categories: (1) shipping — transport by ballast water; (2) shipping — transport by hull fouling; (3) deliberate release (for cultivation and stocking); (4) aquarium release; (5) accidental release (including ornamental escape, research escape, bait bucket release, and unintended release of parasites/pathogens through fish stocking); (6) canals, used as a dispersal corridor; and (7) unknown or other vectors. In the case of multiple implicated vectors, I chose the vector assumed responsible for the initial introduction to the basin. Transoceanic shipping was assumed to be the vector for invertebrate and algal species whose nearest potential source population was located overseas, with the exception of species associated with live trade, e.g. by the aquarium industry. Data were obtained from major reviews by Mills *et al*. (1993), MacIsaac (1999), Cudmore-Vokey & Crossman (2000), Duggan *et al*. (2003), Spencer & Hudson (2003), and Bronte *et al*. (2003), as well as through a search of Internet databases (e.g. Aquatic Sciences and Fisheries Abstracts; http://www.fao.org/fi/asfa/asfa.asp). The complete data set is contained in Appendix S1 in Supplementary Material.

Invasion rates were estimated by dividing the number of established non-indigenous species discovered over a given time interval by the length of that time interval. Two intervals, 'long-term' (1840–2003) and 'modern' (1960–2003), were selected to allow comparison with other aquatic systems that have well-documented invasion histories spanning several decades. Long-term and modern rates in the Great Lakes were also compared to prehistoric rates, which were estimated by calculating the numbers of 'native' species (excluding endemics) that have become naturalized in the basin since glacial recession. The relationship between the discovery rate and shipping activity in the Great Lakes per decade was tested by regression analysis of the net tonnage of cargo ships (both overseas and domestic vessels) averaged over all years within each decade from 1900 to 1999; shipping data were obtained from the Lake Carriers' Association (1999). In order to test whether the rate of discovery has been

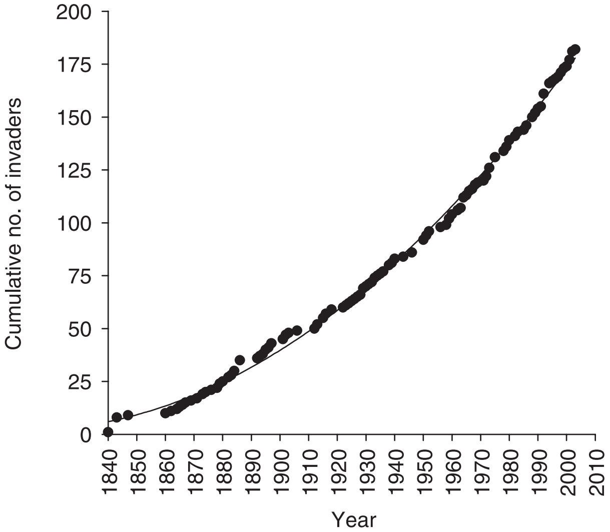

Figure 1 Cumulative number of invaders in the Great Lakes between 1840 and 2003. Line fitted by least-squares regression: $y = 6.02 + 0.27x + 0.005x^2$, where x = years since 1840. The second-order equation ($r^2 = 0.997$) provides a better fit than a straight line ($r^2 = 0.966$).

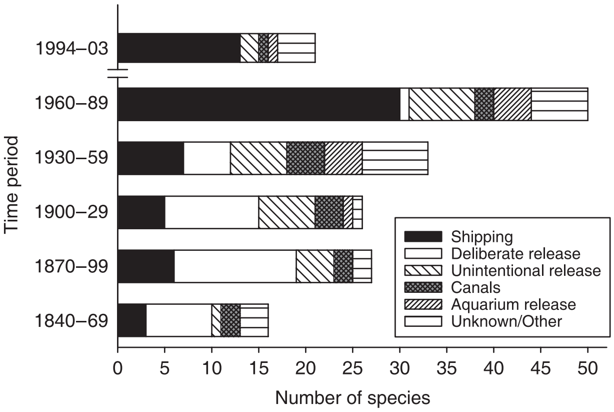

Figure 2 Vectors attributed to Great Lakes invasions since the year 1840. Data are in 30-year time intervals, except for the top bar that corresponds to the decade following ballast water regulation.

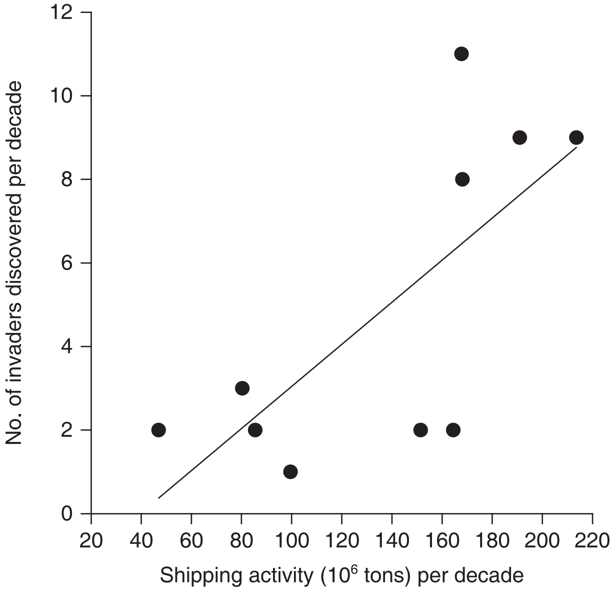

Figure 3 Number of free-living invaders presumed introduced by ships vs. shipping activity in the Great Lakes. Shipping activity is measured in net tonnage (1 ton (Imperial) = 0.9842 t) of cargo ships (both overseas and domestic vessels) averaged over all years within each decade. Line fitted by least-squares regression: $y = 0.05x$; $r^2 = 0.516$, $P < 0.019$. Shipping data are from the Lake Carriers' Association (1999).

altered by the implementation of BWE, I used piecewise regression (Toms & Lesperance, 2003) to identify any significant break points (sharp transitions) in the discovery record during the 1980s and 1990s; the significance of any apparent break point was determined by the Chow test using Proc AUTOREG in SAS version 8.02 (SAS Institute, Cary, NC, USA).

Ecological characteristics of free-living (i.e. non-parasitic, non-pathogenic, non-commensal) invaders assumed to have been transported to the Great Lakes basin by ships were compared before (1960–88) and after (1994–2003) BWE regulation. These characteristics included (1) the invader's endemic origin; (2) whether the adult stage and juvenile stage are benthic or pelagic; (3) whether the species possesses a resting stage; and (4) whether the species is euryhaline, as determined by its occurrence in both brackish-water and freshwater habitats. Fisher's exact tests on categorical data were used to evaluate whether BWE and the increasing prevalence of NOBOB ships have imposed filters that are permeable to euryhaline benthic organisms with resting stages. Because voluntary guidelines were issued by Canada in 1989, although with reportedly high levels of compliance (Locke *et al.*, 1993), I excluded the period 1989–93 from this analysis.

RESULTS

At least 182 non-indigenous species have invaded the Great Lakes basin since the year 1840. Over 40% of these invaders were discovered since the opening of the St. Lawrence Seaway. Consequently, there has been a nonlinear accumulation of non-indigenous species in the Great Lakes over the past two centuries (Fig. 1). The long-term rate of invasion (inferred from the rate of discovery since 1840) is 1.1 species year^{-1}, whereas the modern rate (since 1960) is 1.8 species year^{-1} — i.e. one new invader discovered every 28 weeks. The relative abundance of invading plants, algae, invertebrates, and fishes has changed markedly with time, largely in concordance with changes in vector activity. Over the past 100 years, invasions caused by mechanisms of deliberate release (e.g. via fish stocking or plant cultivation) have declined, whereas shipping-related invasions and modes of unintended release have increased (Fig. 2; see also Mills *et al.*, 1993). Invasions attributable to shipping vectors have increased with shipping activity during the 20th century (Fig. 3). Shipping activity peaked during the latter half of the century, and during this time invasions by vascular plants diminished, while those of

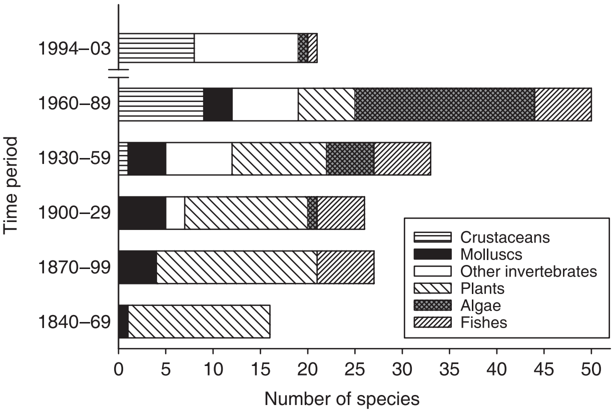

Figure 4 Changes in the taxonomic composition of Great Lakes invaders since the year 1840. Data are in 30-year time intervals, except for the top bar which corresponds to the decade following ballast water regulation.

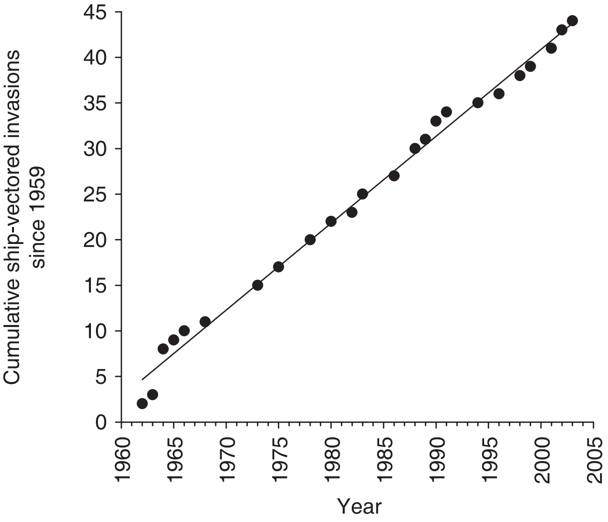

Figure 5 Cumulative number of ship-vectored, free-living invaders discovered in the Great Lakes since 1960. Line fitted by least-squares regression: $y = 0.95x + 2.75$, where x = years since 1960 ($r^2 = 0.992$).

aquatic invertebrates and algae increased (Fig. 4); 65% of all invasions recorded since the opening of the St. Lawrence Seaway in 1959 are attributable to ballast water release. A linear accumulation of ship-vectored invaders is recorded from 1960 onwards (Fig. 5).

From 1960 to 1988, prior to the implementation of BWE, the mean rate of discovery of invaders attributable to shipping was 1.0 species year^{-1}. Since 1993, the mean rate has been 1.2 species year^{-1} (0.9 species year^{-1} for free-living species), suggesting that mandatory BWE has not prevented ship-vectored invasions. There is no significant change in the discovery rate after BWE was implemented; piecewise regression found no break points in the cumulative discovery curve for free-living species during the late-1980s or 1990s (Chow tests, $P > 0.1$ in all cases). Shipping remains the most plausible vector responsible for 62% of non-indigenous species (84% of free-living species) discovered after 1993.

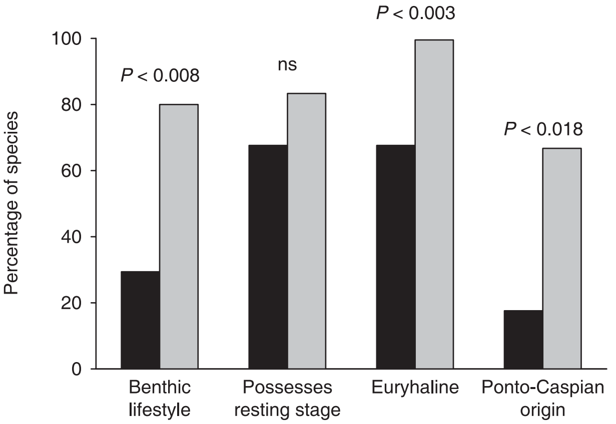

Figure 6 Proportions of Great Lakes invaders possessing attributes hypothesized to affect their introduction under ballast water regulation. Results are shown for free-living species whose introduction is attributed to shipping from 1960 to 1988 (black bars) and 1994–2003 (grey bars), respectively. Two-tailed *P*-values from Fisher's exact tests are shown. ns, not significant.

The composition of invaders appears to have changed after BWE regulation (Fig. 6), but the results must be interpreted with caution because of the relatively small number of invaders in the post-1993 comparison. There is no significant difference in the proportion of invaders with resting stages. However, invaders attributable to shipping after 1993 are more likely to be euryhaline organisms with benthic adult and juvenile lifestyles. Recent invaders are also more likely to be Ponto-Caspian in origin. Ponto-Caspian organisms comprise 10% (3/29) of all ballast-water-vectored invaders recorded between 1960 and 1988, but 69% (9/13) of all such invaders from 1994 to 2003. The percentages remain virtually unchanged if we consider only free-living species: 10% for 1960–88 vs. 70% for 1994–2003.

DISCUSSION

Apparent rates of invasion: modern, long-term, and prehistoric

The long-term rates of invasion (since 1840) estimated for fishes and molluscs are nearly one order of magnitude higher than the prehistoric rates of invasion for these groups over the past 11,000 years since the formation of the Great Lakes: 0.15 species year^{-1} vs. 0.017 species year^{-1} for fishes (Mandrak, 1989; Cudmore-Vokey & Crossman, 2000), and 0.1 species year^{-1} vs. 0.011 species year^{-1} for molluscs (Clarke, 1981). Genetic divergence can also be used to estimate the natural incidence of biotic exchange; this method reveals that modern rates of establishment of European freshwater crustaceans (Cladocera) in the Great Lakes are *c.* 50,000 times higher than prehistoric rates (Hebert & Cristescu, 2002). The modern discovery rate of 1.8 species year^{-1} is higher than that recorded for any other freshwater ecosystem for which long-term data exist (cf. Biró, 1997; Mills *et al.*, 1997; García-Berthou & Moreno-Amich, 2000; Sytsma *et al.*, 2004). A comparison of

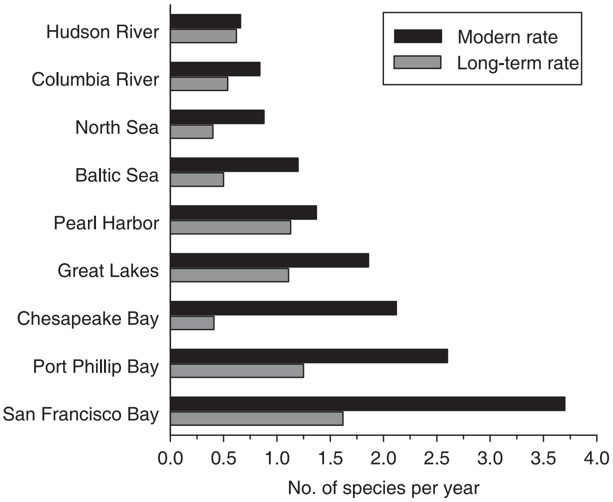

Figure 7 Comparison of invasion rates for large aquatic systems. The modern rate is the rate of discovery of all non-indigenous plants, algae, invertebrates, and fishes since 1960. The long-term rate is the rate of discovery since the earliest recorded introduction (*c.* 150–200 years ago). Sources of data for systems other than the Great Lakes: Mills *et al.* (1997); Cohen & Carlton (1998); Thresher *et al.* (1999); Reise *et al.* (1999); Leppäkoski & Olenin (2000); Fofonoff *et al.* (2003); Sytsma *et al.* (2004).

discovery rates suggests that the Great Lakes basin is among the most highly invaded aquatic ecosystems on the planet (Fig. 7).

The absolute number of Great Lakes invaders cannot be precisely known because almost certainly there have been undetected invasions (Taylor & Hebert, 1993; Kerfoot *et al.*, 2004). The basin contains numerous Holarctic or cosmopolitan species whose endemic origins are unverifiable ('cryptogenic species' *sensu* Carlton, 1996) and represent possible invaders (e.g. *Onychocamptus mohammed*, *Daphnia retrocurva, Potamothrix bavaricus*; Hudson *et al.*, 1998; Spencer & Hudson, 2003; Kerfoot *et al.*, 2004), which were excluded from this study. There are also several introduced species whose establishment could not be verified by multiple records of collection, including the red alga *Compsopogon* cf. *coeruleus* (Manny *et al.*, 1991), the green algae *Monostroma wittrockii* and *Monostroma bullosum* (Taft, 1964), skipjack herring *Alosa chrysochloris* (Fago, 1993), red shiner *Cyprinella lutrensis* (Fuller *et al.*, 1999), and the oligochaete *Psammoryctides barbatus* (Spencer & Hudson, 2003).

Factors affecting the apparent rate of invasion

The invasion rate is normally inferred from the rate of discovery of non-indigenous species, and an increasing discovery rate is interpreted to indicate that a region is becoming more invaded. Multiple factors, environmental and artefactual, may generate a pattern of increasing discovery of invaders. Environmental disturbance, increased propagule pressure, and facilitation among non-indigenous species might render an ecosystem more susceptible to invasion (Mack *et al.*, 2000; Kolar & Lodge, 2001; Ricciardi, 2005). Disturbance (e.g. through habitat alteration) is thought to promote invasion by reducing competition and other forms of community resistance; it appears to be important for the success of introduced plants, but less so for animals (Lozon & MacIsaac, 1997). Much of the large-scale disturbance in the Great Lakes occurred during initial phases of channelization and canal building from the late 19th to the mid-20th centuries (Mills *et al.*, 1993), and plant invaders were more prevalent during this period than at any other time. But vectors of plant introduction were also more prevalent during this period, creating unprecedented opportunities for invasion (Mills *et al.*, 1993).

Arguably, the most important factor contributing to the invasion rate is the frequency in which life-history stages capable of establishing a population are delivered to the basin, i.e. propagule pressure (Kolar & Lodge, 2001). A potential proxy variable for propagule pressure exerted by shipping activity is the net tonnage of cargo ships visiting Great Lakes ports; this variable explains more than half of the variation in the number of invaders (algae, fishes, and free-living invertebrates) presumed introduced by ships. The opening of the St. Lawrence Seaway in 1959 permitted the influx of larger vessels carrying greater volumes of ballast water and tank sediments into the Great Lakes, increasing the abundance and diversity of transported propagules (Holeck *et al.*, 2004). A concomitant increase in domestic vessel traffic has served to spread these propagules between ports and connecting channels throughout the Great Lakes, thereby giving introduced species more opportunities to encounter hospitable habitat and become established. Connecting channels, in particular, offer a great diversity of lentic and lotic habitats as well as shallow areas where incipient populations are more focused and their gametes and larvae are less likely to be diluted in the water column (Holeck *et al.*, 2004).

It has been hypothesized that facilitation between non-indigenous species may also drive an increasing invasion rate. Through direct and indirect positive (mutualistic and commensalistic) interactions, one introduced species may facilitate the establishment of another introduced species by enhancing their survival and population growth upon introduction (Simberloff & Von Holle, 1999). Direct positive interactions are at least as common as direct negative interactions among non-indigenous species in the Great Lakes (Ricciardi, 2001). While it seems plausible that some co-evolved Eurasian species contributed to each other's establishment, or have contributed to an invader's rapid spread within the basin, there is little evidence that facilitative interactions have increased the rate of invasion in the Great Lakes. Facilitation more commonly enhances the abundance and ecological impact of aquatic invaders rather than their establishment (Ricciardi, 2005), which supports the view that aquatic invasions are governed more by dispersal opportunity and physical habitat conditions than by the composition of the recipient community (Moyle & Light, 1996).

Additional factors may have confounded the results of this analysis. Variation and bias in detection effort affect both the rate and the taxonomic composition of invaders discovered (Duggan *et al.*, 2003). For example, the discovery rate was increased by studies of the parasite fauna of two introduced fishes (round goby and Eurasian ruffe) in the early 1990s; the studies identified eight new non-indigenous parasites that were likely introduced with their hosts (United States Department of the Interior, 1993; Pronin *et al*., 1997). In fact, since 1992 there has been a series of discoveries of parasites and pathogens from taxonomic groups that were not previously recorded in the basin. It is not clear whether these species represent a new phase in the Great Lakes' invasion history, or are more easily detected now because of advances in study methods; therefore, to reduce this potential bias, my analysis considers only free-living species. While the discovery rate could also have been enhanced by greater awareness of invasion vectors in recent years, most major floral and faunal surveys were conducted decades ago (see References in Mills *et al*., 1993) and there is no coordinated monitoring system in place to detect new invasions. And even if monitoring efforts were greater in recent years, there is no reason why they should suddenly reveal a conspicuous group of mussels, crustaceans, and fishes sharing a unique biogeographical origin; the unprecedented wave of Ponto-Caspian invasions recorded since the 1980s is probably not an artefact of detection bias, but instead may be a consequence of increasing opportunities to be vectored by ships originating from European ports (see succeeding text).

Were recently discovered invaders introduced by ships prior to BWE?

For less-conspicuous species, there may be a substantial time lag before detection. Time lags between introduction, population growth, and subsequent detection can generate an increasing rate of discovery, even when the actual rate of introduction and detection effort are held constant (Costello & Solow, 2003). It is not possible to determine the extent to which this phenomenon has contributed to discovery rates in the Great Lakes and other highly invaded systems. The question considered here is whether all ship-vectored invaders recorded during the past decade were introduced before BWE regulation. A few species, namely, the amphipod *Gammarus tigrinus* and three rhizopods discovered in 2001 and 2002, may have remained undiscovered in the Great Lakes for several years because of taxonomic difficulties in distinguishing them from closely related native species (Nicholls & MacIsaac, 2004; Grigorovich *et al*., 2005). Time lags might also be extensive for species with resting stages that can remain dormant in sediments for decades (e.g. diatoms). Conversely, the biological attributes and life history of certain species may predispose them to be detected early in their invasion — one example is the fish-hook water flea *Cercopagis pengoi*, a Ponto-Caspian crustacean introduced by transoceanic shipping. *Cercopagis* was discovered in Lake Ontario in 1998 (MacIsaac *et al*., 1999). Given its unique morphology, conspicuous behaviour in the open water, and its rapid rate of reproduction, *Cercopagis* is unlikely to have resided in the Great Lakes for several years prior to being detected; it probably represents a ship-vectored invasion that occurred well after BWE regulation. Two additional crustaceans discovered in nearshore sediments of Lake Michigan in the late-1990s, the Ponto-Caspian copepod *Schizopera borutzki* and another copepod *Heteropsyllus* sp., are also considered to be recent invaders because they dominated the areas in which they were found but did not appear in previous intensive surveys of benthic crustaceans in the lake (Hudson *et al*., 1998; Horvath *et al*., 2001).

Another line of evidence: records of introduced species that failed to invade

Since 1959, there have been multiple discoveries of brackish-water benthic organisms that have failed to establish reproducing populations in the Great Lakes. These discoveries have continued after BWE regulation, and include adult Chinese mitten crab *Eriocheir sinensis* in 1994, 1996, and 2005 (Leach, 2003; V. Lee, Ontario Ministry of Natural Resources, pers. comm.; P. Fuller, http://nas.er.usgs.gov/), European flounder *Platichthys flesus* in 1994, 1996, and 2000 (Leach, 2003; A. Niimi, Canada Centre for Inland Waters, pers. comm.), and the Ponto-Caspian amphipod crustacean *Corophium mucronatum* in 1997 (Grigorovich & MacIsaac, 1999). The most plausible vector responsible for the introduction of each of these species is ballast water release from overseas shipping. European flounder and mitten crab are incapable of establishing reproducing populations in freshwater (Gutt, 1985; Anger, 1991) and, indeed, no young-of-the-year individuals for either species have ever been reported from the Great Lakes. A European flounder collected from Lake Erie in the year 2000 was estimated to be *c.* 7 years old (A. Niimi, pers. comm.), suggesting that it was introduced at the time BWE became mandatory. The lifespan of mitten crabs is < 5 years (Jin *et al*., 2002; Rudnick *et al*., 2005), so at least some of these occurrences — such as in Lake Erie in March 2005 and in Lake Superior in December 2005 — result from recent ship-vectored introductions rather than an extensive time lag between introduction and detection.

Composition of invaders in relation to prevailing vectors

Changes in the type and volume of ship ballast have produced distinct phases in the Great Lakes' invasion history. Before 1900, ships generally carried solid ballast such as rock, sand, or mud, which was unloaded at the destination port where the ships were to receive cargo (Mills *et al*., 1993); most of the invaders recorded during this period were plants that may have been transported as seeds or stem fragments in soil ballast. After ballast water became widely used in the 20th century, particularly after the opening of St. Lawrence Seaway, numerous non-indigenous species of phytoplankton and zooplankton became established. A more recent phenomenon is the influx of Ponto-Caspian organisms that began in the mid-1980s and possibly reflects changes in the European donor region. Dozens of Ponto-Caspian species have invaded western European ports and these range expansions are providing increased opportunities for transport to the Great Lakes (Ricciardi & MacIsaac, 2000; Bij de Vaate *et al*., 2002), as has occurred most recently with *C. pengoi* (Cristescu *et al*. 2001). This influx apparently continues after BWE regulation, possibly because many Ponto-Caspian species have evolved a broad tolerance to salinity and to varying environmental conditions (Reid & Orlova, 2002) and thus may survive an incomplete BWE or transport in the residual ballast of NOBOB vessels. The increasing rate of discovery of Ponto-Caspian species may have biased our comparison of euryhaline invaders pre- and post-1993. Regardless of the cause, the Great Lakes basin has entered a new phase in its invasion history characterized by euryhaline benthic invertebrates.

Surprisingly, invaders discovered after 1993 were not more predisposed to possessing a resting stage than invaders discovered in the period 1960–88 (Fig. 6). Resting stages (diapausing eggs) of several species of zooplankton have been found to survive exposure to seawater (Gray *et al*., 2005). Conversely, a severely reduced hatching rate under brackish-water conditions has been observed for some species collected from tank sediments of ships entering the Great Lakes (Bailey *et al*., 2004), indicating that the possession of a resting stage does not necessarily confer resistance to the broad salinities produced by BWE.

Implications for vector management

With regards to my original hypotheses, these results suggest that (1) the apparent rate of invasion in the Great Lakes is correlated with shipping activity; (2) the rate of invasion due to shipping has not declined following BWE regulation; and (3) the composition of new invaders in the Great Lakes has shifted to euryhaline benthic organisms following BWE regulation. The effectiveness of BWE has been undermined by the increasing proportion of inbound foreign vessels that are not subject to regulation. Rather than eliminating the risk of invasion via transoceanic shipping, BWE, combined with the predominance of NOBOB ships, has apparently altered the composition of new invaders in the Great Lakes by imposing a semipermeable filter. Consequently, unless management strategies are adopted to treat residual water and sediments in ballast tanks, the Great Lakes basin remains susceptible to future ship-vectored invasions, particularly by Ponto-Caspian invertebrates (Ricciardi & Rasmussen, 1998). This is significant because ports in western Europe continue to be invaded by Ponto-Caspian species (e.g. Janas & Wysocki, 2005; Rodionova *et al*., 2005) and because previous Ponto-Caspian invaders (such as dreissenid mussels, the fish-hook water flea *C. pengoi*, and the round goby *Neogobius melanostomus*) have demonstrated a propensity for causing substantial ecological impacts in the Great Lakes and elsewhere (Ojaveer *et al*., 2002; Vanderploeg *et al*., 2002).

Finally, it is remarkable that not a single non-indigenous species ever established in the Great Lakes basin is known to have subsequently disappeared. Thus, there has been an accumulation, rather than a turnover, of non-indigenous species in the basin. Because non-indigenous species can interact in ways that exacerbate each other's impacts (e.g. interactions between quagga mussels and round gobies have caused recurring outbreaks of avian botulism in Lake Erie; see Ricciardi, 2005), an accumulation of invaders may lead to a greater frequency of synergistic disruption.

ACKNOWLEDGEMENTS

I thank Greg Ruiz, Dave Reid, and Hugh MacIsaac for their valuable comments on earlier versions of the manuscript. Funding provided by the Natural Sciences and Engineering Research Council of Canada and by FQRNT Quebec is gratefully acknowledged.

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SUPPLEMENTARY MATERIAL

The following material is available online at http://www.blackwell-synergy.com/loi/ddi.

Appendix S1 List of non-indigenous species recorded in the Great Lakes, and their vectors of introduction.