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GREAT LAKES SHIPPING, TRADE, AND AQUATIC INVASIVE SPECIES

Vectors and Pathways for Nonindigenous Aquatic Species in the Great Lakes

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The Laurentian Great Lakes have an extensive history of human-mediated biological invasions, beginning at least 150 years ago. During this interval, a number of transitions have occurred both with respect to the types of non-indigenous species (NIS) that established and in the mechanisms that vectored them to the lakes. The number of reported invaders established in the lakes has increased from the early nineteenth century to modern times. Fish and plants were the most common invaders prior to the 20th century, with most introductions resulting from human releases. Algae and invertebrates became more common invaders to the lakes after transoceanic shipping converted to use of liquid ballast prior to 1900. Although the ship ballast vector appears to have become dominant during much of the 20th century, alternative vectors have received less attention. I reassessed the vectors and pathways for all species that unequivocally invaded the Great Lakes since the expanded seaway was opened in 1959. I utilized a conservative approach that required that NIS meet at least 3 of the ten criteria proposed for introduced status by Chapman and Carlton (1991). Fifty-nine species were confirmed as NIS, with an additional 21 species (mainly algae) classified as cryptogenic. Of the confirmed NIS, ships' ballast water was the leading vector for 55% of species, and remained the dominant (47% of species) when alternative vectors were prioritized. Deliberate releases, unauthorized introductions, range extensions, hull fouling and recreational boating were all of lesser importance (<10% of species). A clear vector could not be established for 11% of NIS. Eurasia was the source of 67% of established NIS, followed by North America (14%) and Palearctic/Nearctic (7%). Europe was the source of 94% of ballast-mediated invasions, including 15 species from western and central Europe, 12 from the Ponto-Caspian region, and 3 from the Baltic Sea. Invasions continued to be reported in the basin as recently as 2006, despite implementation of regulations requiring mandatory ballast water exchange (BWE) in 1993. Determination of the efficacy of BWE is encumbered by time lags between introduction and reports of establishment, and by possible contributions by similar vectors, including no-ballast-on-board and coastal domestic shipping, which could introduce NIS.

INTRODUCTION

The Great Lakes are among the most heavily utilized water bodies in the world. They provide more than 40 million residents with access to drinking and industrial water, hydro-electric supplies, recreation, food and transportation. Humans facilitated international commerce via construction of a the Welland Canal, linking Lakes Erie and Ontario, in 1829. Subsequent development of the lock system between Lake Ontario and the Saint Lawrence River in 1847 and between Lakes Superior and Huron in 1855 allowed through passage from the Atlantic Ocean to Lake Superior (Mills *et al*. 1993). Canals were expanded and the modern Seaway opened in 1959. This important development allowed larger vessels, with large loads of ballast water, into the Great Lakes. The development of a navigable water network has opened the Great Lakes region both to international trade and introduction of non-indigenous species (NIS).

Determination of the vector (i.e. mode of introduction) and pathway (i.e. source) of species invasions is a valuable tool to management and control efforts (Ruiz and Carlton, 2003). Invasion histories and vulnerability of ecosystems to future invasions can be recreated through examination of putative vectors (Mills *et. al.,* 1993) including international shipping (e.g. Colautti *et al*., 2003; Drake and Lodge, 2003), or by phylogeographic assessments of genetic structure of native and introduced populations (e.g. Cristescu *et al*., 2001; Kelly *et al*., 2006).

This is particularly relevant to the Laurentian Great Lakes where the introduction of NIS has involved a variety of vectors and pathways that have changed over time.

In Mills *et. al.'s* (1993) ground-breaking retrospective study of the invasion history of the Great Lakes, clear patterns emerge with respect to the nature of NIS that invaded during different time periods. The initial phase of invasion began in the early 1830s with the introduction of sea lamprey (*Petromyzon marinus*) to Lake Ontario. A comparatively low number (8) of other NIS established prior to 1850, and all were marsh-dwelling plants likely released through cultivation (Mills *et. al.,* 1993). Between 1850 and 1900, apparent invasion rate increased and included a wider variety of species such as trees, invertebrates and fishes. However with 18 recognized species, marsh plants were again dominant NIS introduced during this period (Mills *et. al.,* 1993) with ships' solid ballast, accidental releases or cultivation escapees the main vectors of introduction.

Between 1900 through 1958 an additional 54 species were added to the NIS inventory of the Great Lakes (Mills *et. al.,* 1993). The composition of NIS changed during this period, with the first reports (6 species) of algae and growing importance of invertebrates (14 species) and fishes (11 species). However, 15 additional marsh plants invaded, as did 4 species of each of submerged macrophytes and shoreline trees (Mills *et. al.,* 1993). This period marked the first appearance of planktonic invertebrates, including accidental releases of the hydrozoans *Craspedacusta sowerbyi* (1933) and *Cordylophora caspia*, and ballast water release of the copepod *Eurytemora affinis* (1958). In summary, the early phase of invasion in the Great Lakes was dominated by wetland plants, while algae, invertebrates and fishes became far more common additions to the lakes' biota following 1900 in conjunction with switch over from solid to liquid ballast by transoceanic vessels.

A number of studies have explored invasion patterns in the lakes following the opening of the expanded, modern St. Lawrence Seaway in 1959. Grigorovich *et al.* (2003) and Ricciardi (2006) attributed 67% and 65% of introductions, respectively, to ships' ballast water. Ballast water that is loaded in regions outside of the Great Lakes may entrain large numbers of viable freshwater species which are discharged during cargo loading in Great Lakes ports. BOB ships were recognized as a major vector of NIS introduction to the Great Lakes and between 1989 and 1993, the United States and Canada introduced ballast water control policies aimed at reducing further introductions (Locke *et. al.,* 1991; US Coast Guard, 1993). Ships were effectively required to conduct ballast water exchange (BWE) in marine waters to purge most freshwater NIS from tanks and kill those that remained by exposure to open-ocean water. Despite these management efforts, recent studies indicated that the invasion rate of NIS in the Great Lakes has not declined (Grigorovich *et. al.,* 2003; Holeck *et. al.,* 2004; Ricciardi, 2006). A change in species composition was also reported in these studies where an increasing number of species had origins in the Black and Caspian Sea basins of Eastern Europe - hereafter referred to as the Ponto-Caspian region.

Several factors could account for continuing invasions of the Great Lakes. Until the early 1980's, a large number of Russian ships entered the Great Lakes to collect grain (Ivan Lantz, Shipping Federation of Canada, personal communication). Most of these vessels are believed to have carried ballast water of a Baltic Sea origin. Although they have since declined, they may have introduced many NIS. During the 1980's, the characteristics of transoceanic ships also changed. An increasing proportion of ships declared no-ballast-on-board; these "NOBOBs" carried cargo and were exempt from ballast control but carried large volumes of residual water and sediment. Studies have shown that ballast residuals harbor large numbers of viable NIS, which pose a risk of discharge to the Great Lakes during multi-port operations (Colautti *et al*., 2003; Bailey *et. al.,* 2005; Duggan *et. al.,* 2005). Although recent regulations were introduced in the United States and Canada to manage NOBOB residuals (U.S. Coast Guard, 2005; Canada Shipping Act, 2006), it is too early to gauge the efficacy of these policies. A second problem affecting determination of BWE efficiency for ballasted vessels is time lags (Costello *et al*., 2007). Two lags may occur: first, species may not be detected in the lakes until well after they were introduced; secondly, there may exist a gap between when species are first detected and when they are first reported.

The high profile of ballast-mediated invasions may also have distracted researchers from consideration of alternative vectors, leading to uncertainty in evaluations. For example, large numbers of fouling organisms have been found on ships, a sub-vector that is dominant in global introductions in marine environments (Ruiz *et. al*., 2000; Gollasch, 2002). Also, the live fish market, aquarium trade and aquaculture have received less attention, but recent research has indicated that these vectors pose a significant risk to the Great Lakes (Kolar and Lodge, 2002; Rixon *et. al.,* 2004). These alternatives were recognized in previous vector and pathway analyses for the Great Lakes (e.g. Grigorovich *et. al.,* 2003; Holeck *et. al.,* 2004), but were not prioritized.

In the following section we review, on a case by case basis, the most likely mode of introduction of NIS to the Great Lakes since 1959, prioritize alternative vectors, and map the invasion pathways by vector and geographic origin/donor region.

METHODS

Prior to vector and pathway analysis, an initial list of 85 NIS discovered in the Great Lakes drainage since 1959 was compiled using the comprehensive reports of Mills *et. al.,* (1993) and Ricciardi (2006) (Table 1). For the purposes of this paper, the Great Lakes drainage included the St. Lawrence River downstream to the Seaway locks at Montreal. To facilitate vector identification and site and year of discovery, I reviewed the original reports for all NIS when discoveries were initially reported. Two problems influenced whether a species was included or excluded from vector and pathway analysis. First, in several original reports there was evidence of a pre-1959 introduction. For example, 1959 was the year of first discovery of the clam *Lasmigona subviridis*, as reported in Ricciardi (2006). However, in the original report of Clarke and Berg (1959), *L. subviridus* was collected in surveys conducted between 1955 and 1957. European frog-bit, *Hydrocharis morsus-ranae*, reported by Ricciardi (2006) as first occurring in eastern Lake Ontario in 1972, was already established in the St. Lawrence river by 1958 (Mills *et. al.,* 1993).

Secondly, the non-indigenous status of several species was indeterminate, or, there was no reference to a species non-indigenous status in the original report. In such cases, the likelihood that a species was non-indigenous was assessed by comparison with six criteria predicted for NIS as outlined in Chapman and Carlton (1991), and adapted by Ricciardi (2006) (see Appendix 1). Ricciardi (2006) considered a species non-indigenous if it met at least three of the six criteria. Ricciardi (personal communication) recognized that this approach was arbitrary, but that a requirement to meet all six criteria would be impractical, resulting in the rejection of non-indigenous status for most species. In contrast, the use of more than one criterion avoided over-reliance on a single criterion that was less compelling. A species' ability to meet these criteria was assessed using available historical records, bio-geographic surveys, consultations with taxonomic experts, molecular studies, and information on vector associations (see Ruiz *et. al.,* 2000). If a species failed to meet a minimum of three criteria it was classified as 'cryptogenic' (i.e. it was difficult to confidently ascribe it as native or introduced; *sensu* Carlton, 1996), and excluded from further analysis. As an example, the diatom *Thallassiosira weissflogii* was considered an NIS by Mills *et. al.* (1993), who referred to its discovery in the Detroit River in 1962-63 by Wujek (1967). In the original report of Wujek (1967), *T. weissflogii* was catalogued together with over 80 additional diatom species but was not referred to as non-indigenous. An assessment of Appendix 1 criteria was made as follows: Attribute 1 could not be assessed as diatoms of the Detroit River were not studied previously (Wujek, 1967; Table 2). Attribute 2 could not be assessed as extensive diatom surveys of the Great Lakes were conducted only in the late 1970's (Stoermer, 1978). For attribute 3, *Thalassiosira* spp. occurred in the ballast tanks of ships entering the Great Lakes (EPS, 1981) and so the attribute was consistent with predictions for a NIS. *T. weissflogii* was widespread in the Great Lakes diatom surveys of Stoermer (1978), which was inconsistent with attribute 4 for a NIS. *T. weissflogii* was widespread in North American freshwaters on the east and west coasts as well as inland streams (Lowe and Busch, 1975; Hasle, 1978), which was inconsistent with attribute 5. The latter observations also were inconsistent with attribute 6. In summary, only one attribute was consistent with NIS status, and so this species was considered cryptogenic (Table 2).

Figure 1 summarizes the decision rule flowchart used to ascertain whether a species from the initial list was included in vector and pathway analysis. The first query - year of first discovery - led to the exclusion of 5 species from further analysis (Figure 1; Table 1). After assessing attribute criteria for 22 species with indeterminate status, 21 were considered cryptogenic and excluded from further analysis (Figure 1; Tables 1 & 2). Therefore 26 species out of the original 85 were excluded from vector and pathway analysis.

The remaining 59 species were assigned to one or more of the following geographic regions of origin: Eurasia - including the sub-regions East Asia, Baltic Sea, Ponto-Caspian and Europe; North America - including the North-West Atlantic, Pacific, Mississippi and widespread; Australasia; Africa; widespread, including the Palearctic and Nearctic regions; and unknown, with insufficient information to determine geographic origin. Where possible, the true origin for species with 'widespread' native distributions was ascertained using data on previous invasion histories, molecular studies, and from patterns of probable vector activity. For example, the native range of the invading cladoceran *Cercopagis pengoi* is the Ponto-Caspian basin, but the species has an invasion history in the Baltic Sea. Molecular data indicate that the Great Lakes distribution likely resulted from a secondary introduction of propagules from the Baltic Sea (Cristescu *et. al.,* 2001).

I then determined the most likely vector(s) of introduction using a modified version of the Vector Assignment Protocol (VAP) outlined in Holeck *et. al.* (2004) and Lodge *et al.* (2006) (see Figure 2). In the VAP, a series of queries considers all possible vectors until an endpoint is reached. Species were assigned to any of the following vector(s) and/ or associated sub-vectors: 1) Shipping, including all sub-vectors [BOB/ NONBOB water active (live in water); BOB/ NOBOB sediment active (live in sediment); BOB/ NOBOB sediment resting (resting stages in sediment); ship fouling, including hull, anchor chain, sea-chest]; 2) recreational boating (fouling or discharge from live-well water); 3) unauthorized intentional introduction (live bait or aquarium); 4) aquaculture escape; 5) deliberate release (stocking/ cultivation); 6) natural dispersal (e.g. wind/ air); 7) range extension (passive or active movement by canals or hydrologic connections); and 8) unknown (no supporting information).

Assignment was determined using a suite of information including: site of first occurrence in the Great Lakes; life-history; source region; known invasion history in North American freshwaters; presence in North American freshwaters outside of the Great Lakes drainage; associations with aquaculture, intentional stocking, live food markets, aquaria or bait stores; physico-chemical tolerance; fouling ability; resting stage production; reports of association with a specific vector; discovery in an area of shipping activity - shipping records were obtained for de-ballasting activity for each of the Great Lakes and for specific ports from Colautti *et. al.* (2003) and Grigorovich *et. al.* (2003); discovery at or near a "hotspot" associated with de-ballast trimming, for example, where ships may "lighten the load" prior to entering shallow navigational channels such as St. Marys, St. Clair or Detroit Rivers, Welland Canal (see Grigorovich *et. al.,* 2003). Year of discovery was used to further refine assignment to ship sub-vectors. For example, if the NIS was discovered prior to the implementation of ballast exchange policies in 1989, it could be assigned to both BOB and NOBOB vectors. If the species arrived after 1989, and it was intolerant to raised salinity, then it would be assigned only to a NOBOB vector (see Figure 2). For the same period, a species could be assigned to BOB and NOBOB vectors if it was euryhaline. In the latter case, confidence in assignment is based upon an assumed high level of BWE compliance by BOB ships but with the caveat that BWE may not be 100% effective, and that some ships may be unable to comply with guidelines (see Locke *et. al.,* 1991). Parasites and epibionts of NIS were ascribed to the vector of their host species.

The green alga *Enteromorpha flexuosa* provides a working example of the VAP. *E. flexuosa* is native to coastal areas of the North-west Atlantic and Europe and was discovered in 2003 in Muskegon Lake, a water body contiguous with Lake Michigan. *E. flexuosa* is euryhaline and the genus is commonly observed fouling ship hulls (Finlay *et. al.,* 2002; Lougheed and Stevenson, 2004). The VAP indicated BOB or NOBOB ship water and sediment, and ship fouling, as probable vectors. In similar cases of multiple vector assignments, the most likely primary vector was determined from additional supporting information. For example, historical shipping records indicated that transoceanic BOB and NOBOB ships de-ballast in Lake Michigan (Colautti *et. al.,* 2003), and although ships visited the port of Muskegon, none discharged ballast water. Therefore, given the fouling ability and wide salinity tolerance of *E. flexusosa*, coupled with visits by BOB and NOBOB ships, it is more plausible that hull, sea-chest or anchor fouling were the primary vectors, while ships' ballast is the next most likely vector. Therefore, to account for multiple vector assignments, and also to prioritize alternative vectors, data on vector composition were summarized based on the primary (i.e. most likely) vector, as well as based on the secondary vector (i.e. the next most likely vector). Pathways of invasion to the Great Lakes were mapped using information on geographic origin and vector assignment. Pathways of introduction were based only on the most likely vector.

RESULTS AND DISCUSSION

Eurasia was the dominant donor region, accounting for 67% of NIS in the Great Lakes since 1959 (Figure 3). Within Eurasia, Europe and the Ponto-Caspian basin contributed most of the species, with South-East Asia and the Baltic Sea of lesser importance. North America was the next strongest donor region, accounting for 13.5% of NIS, and was dominated by species from the North-West Atlantic coastal region. Of the remaining species, 15% had unknown or widespread origins, while Australasia and Africa each contributed a single species.

Regardless of whether primary or secondary vectors were prioritized, ship-ballast was the strongest vector and accounted for 47-55% of all NIS introductions; ship fouling was a minor vector (Figures 4a,b). Almost 12% of introductions had unknown vectors, that is, there were no available data to support any vector. Deliberate releases, unauthorized intentional introductions, range extensions, and aquaculture accounted individually for between 5 and 10% of introductions depending on whether primary or secondary vectors were prioritized. Both recreational boating and natural dispersal were of minor importance.

Ninety-four percent (31/33 species) of ship-ballast invasions originated in Eurasia (Figure 5). This figure includes the New Zealand mud-snail (*Potomopyrgus antipodarum)*, which was likely introduced as a secondary invasion from Europe after its primary introduction there from Australasia. Europe and the Ponto-Caspian basin were the main donor regions. Only two ballast-mediated introductions had an origin outside of Eurasia: the amphipod *Gammarus tigrinus* and the fourspine stickleback (*Apeltes quadracus*) were of North-West Atlantic origin. Introductions via canals, and one via recreational boating, are shown in Figure 6. The Mississippi Basin has donated two species. Shortnose gar (*Lepisosteus platostomus*) was likely introduced to the Lake Michigan drainage via the Portage canal in 1962 (Priegel, 1963). Carp viremia, native to Eurasia, most likely infected common carp in the Lake Michigan drainage in 2003 after contact with infected Asian carp in the Calumet-Sag canal (Nelson, 2003). The Hudson River drainage was the source of blueback herring (*Alosa aestivalis*), which entered Lake Ontario in 1995 via the Erie and Oswego canals (Owens *et. al.,* 1998). The most likely pathway of introduction for the waterflea *Daphnia lumholtzi* was secondary dispersal through recreational boating after a primary invasion in the Southern United States (Dziabowski *et. al.,* 2000; Fig. 6). A lack of data on site of entry precluded mapping of pathways of introduction for species assigned to any of the remaining vectors.

Unlike previous vector and pathway analyses (see Mills *et. al.,* 1993; Grigorovich *et. al.,* 2003; Ricciardi, 2006), the current study used a decision rule process to ascertain whether assumed NIS were included or excluded from analysis. The final dataset comprised 59 species from an initial list of 85 species, thus it should be noted that the results may not be directly comparable with previous studies. Since 1959, the majority of NIS originated in Eurasia (67%) and the Atlantic coast of North America (10%). It is likely that the proportion of invasions with an origin in Eurasia and the Atlantic coast of North America is higher. For instance, four species had widespread origins that precluded precise assignment to one or the other region. These patterns in geographic origin are similar to that reported by Mills *et. al.* (1993) despite the latter analysis also accounting for invasions since the 1800's. However, identifying the importance of each pathway also requires identification of vectors and their relative strength in relation to each donor region. In previous studies in the Great Lakes, alternative vectors received less attention and so some mechanisms of introduction may have been under-appreciated. The Vector Assignment Protocol (see Holeck *et. al.,* 2004) used here identified multiple probable vectors which allowed the prioritization of alternative vectors. However, even when alternative vectors were considered, ship ballast remained the dominant vector, accounting for 47-55% of all introductions since 1959. This dominance is consistent with Grigorovich *et. al.* (2003) and Ricciardi (2006), though these studies each reported a higher proportion (65-67%) of ship-ballast introductions. The difference is best explained by exclusion from the current study of numerous microscopic species - such as diatoms, rhizopods and a copepod - which previously were assigned to ship-ballast introductions in Ricciardi (2006) and Grigorovich *et. al.* (2003) (see Table 2). Although ship fouling is considered an important vector of introduction for marine species (Gollasch, 2002), it was of minor importance in the current study. Specific physico-chemical tolerances and ecological traits of NIS could explain this. For example, only two species, the algae *Bangia atropurpurea* and *Enteromorpha flexuosa*, were likely introduced on the surface of ships. Both are fouling species and could survive the fully saline conditions of an ocean vessel, unlike the majority of Great Lakes invaders which are mainly benthic and /or intolerant to raised salinity (Sheath and Cole, 1980; Finlay *et. al.,* 2002; Lougheed and Stevenson, 2004). Individually, deliberate release, aquaculture, range extensions and unauthorized intentional vectors were of minor importance, but collectively represented 26-32% of all NIS introductions.

That ship-ballast from Europe and the Ponto-Caspian region was the main vector and pathway of introduction, is consistent with coarse measures of propagule pressure to the Great Lakes. For example, Colautti *et. al.* (2003) and Grigorovich *et. al.* (2003) showed that between 1983 and 1998, 75-88% of commercial ships that entered the Great Lakes had a last port-of-call in Europe. Only a small percentage of ships originated in the Black Sea basin (see Grigorovich *et. al.,* 2003), but this does not weaken the likelihood that ship-ballast was the primary vector. For instance, most Ponto-Caspian species that established in the Great Lakes had a previous invasion history in Western Europe (Ricciardi and MacIsaac, 2000). Indeed, the opening of the Main canal in 1992, which connects the Danube with the Rhine system, provided a new westward colonization pathway from the Black and Caspian Sea basins (Bij de Vaate *et al.,* 2002).

The only non-Eurasian species likely introduced to the Great Lakes in ship-ballast were of North-West Atlantic origin. Both species, *G. tigrinus* and *A. quadracus*, were likely introduced from the Gulf of St. Lawrence. Whether “salties” - ships transiting the Seaway to conduct international trade - or “lakers” - ships that trade solely within the Great Lakes basin - were responsible for these introductions is difficult to discern. For example, lakers may occasionally transit the Seaway to offload cargo at ports downstream of Montreal (Eakins 1999-2000). NOBOB vessels also may offload cargo at ports such as Port-Cartier and Port-Noire - which are downstream of the Seaway - before taking on ballast and proceeding to Great Lakes ports for cargo collection (Colautti *et. al.,* 2003).

Canal-mediated introductions have contributed a small proportion to the total introductions in the Great Lakes, a finding consistent with previous works (see Mills *et. al.,* 1993; Ricciardi, 2003). However, the main pathways from the Mississippi and Hudson River basins are well defined and could pose a risk of future introductions. This is highlighted by the recent construction of an electric fish barrier on the Chicago Sanitary and Ship Canal to prevent further dispersal of Asian carp (Stokstad, 2003). The identification of carp viremia on Asian carp, and the recent infection of common carp in Chicago canals, reinforces the risk of future invasions by this pathway (Nelson, 2003). Prior to 1959 the Erie Canal was of minor relative importance for Great Lakes NIS, but provided a pathway for several North-Atlantic species that had substantial impacts (Mills *et. al.,* 1993). Although only a single species, blueback herring, invaded via this pathway since 1959, its recent (1995) discovery suggests that the Erie Canal could be an entrance mechanism in future. The vector for almost 12% of NIS was unknown but is unsurprising since most of these species could not be ascribed to a donor region. Indeed, Mills *et. al.* (1993) and Ricciardi (2006) reported a similar proportion of unknown vectors.

In summary, despite a focus in this study on alternative vectors, ship ballast was considered the dominant vector since 1959. However, it is difficult to interpret ship ballast-mediated invasions in light of the efficacy of ballast water control policies. For example, there remains a knowledge gap on lags that occur between actual invasion time, discovery, and reporting time. There is also the possibility that greater research effort has led to recent discoveries of NIS that remained undetected for many years. What is clear is that NIS continue to be discovered in the Great Lakes, the majority of which have a European or Ponto-Caspian origin, with ship ballast as the likely vector. The Great Lakes remain at risk of ballast-mediated invasions from these main donor regions. This is illustrated by the most recent invader, the Ponto-Caspian mysid shrimp *Hemimysis anomala*, which was discovered in the Great Lakes in 2006, and was predicted to do so in recent risk assessment models (Ricciardi and Rasmussen, 1998; Griogrovich *et. al.,* 2003). The current study suggests that if resources are limited, future management efforts should focus on preventing ballast mediated introductions from Europe and the Ponto-Caspian region.

REFERENCES

Albert A., Vetemaa, M., and Saat, T. (2006). Laboratory-based reproduction success of ruffe, *Gymnocephalus cernuus* (L.), in brackish water is determined by maternal properties. Ecology of Freshwater Fish, 15, 105-110.

Bailey, S.A., Duggan, I.C., Jenkins, P.T., and MacIsaac, H.J. (2005). Invertebrate resting stages in residual ballast sediment of transoceanic ships. Canadian Journal of Fisheries and Aquatic Sciences, 62, 1090–1103.

Ball, I. R. (1969). *Dugesia lugubris* (Tricladida: Paludicola). A European immigrant into North American freshwaters. Journal of the Fisheries Research Board of Canada, 26, 221-228.

Belcher, J.H. (1960). Culture Studies of *Bangia atropurpurea* (Roth) Ag. New Phytologist, 59, 367-373.

Bij de Vaate, A., Jazdzewski, K., Ketelaars, H.A.M., Gollasch, S., and Van der Velde, G. (2002). Geographical patterns in the range extension of Ponto-Caspian macroinvertebrate species in Europe. Canadian Journal of Fisheries and Aquatic Sciences, 59, 1159–1174.

Brinkhurst, R.O., and Cook, D. G. (1966). Studies on the North American aquatic Oligochaeta III: Lumbriculidae and additional notes and records of other families. Proceedings of the Academy of Natural Sciences of Philadelphia., 118, 1-33.

Bronte, C.R., Ebener, M.P., Schreiner, D.R., DeVault, D.S., Petzold, M.M., Jensen, D.A., Richards, C., and Lozano, S.J. (2003). Fish community change in Lake Superior, 1970–2000. Canadian Journal of Fisheries and Aquatic Sciences, 60, 1552–1574.

Bur, M.T., Klarer, D.M., and Krieger, K.A. (1986). First records of a European cladoceran, *Bythotrephes cederstroemi*, in Lakes Huron and Erie. Journal of Great Lakes Research, 12, 144-146.

Canada Shipping Act (2006). Ballast water control and management regulations, SOR 2006-129.

Carlton, J.T. (1996). Biological invasions and cryptogenic species. Ecology, 77, 1653–1655.

Catling, P.M., and McKay, S.M. (1980). Halophytic plants in southern Ontario. Canadian Field-Naturalist, 94, 248–258.

Chapman, J.W., and Carlton, J.T. (1991). A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). Journal of Crustacean Biology, 11, 386–400.

Clarke, A. H. (1981). The freshwater mollusks of Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Canada.

Clarke, A. H., and Berg, C. O. (1959). The freshwater mussels of central New York. Memoirs of Cornell University, Agricultural Experimental Station, Ithaca, New York, 367, 1-79.

Colautti, R. I., Niimi, A. J., van Overdijk, C. D. A., Mills, E. L., Holeck, K., and MacIsaac, H. J. (2003). Spatial and temporal analysis of transoceanic shipping vectors to the Great Lakes. In: Ruiz G. M., Carlton J. T. (Eds.) Invasive species: vectors and management strategies. Island Press, Washington, DC, p 227–246.

Colautti, R.I., Manca, M., Viljanen, M., Ketelaars, H.A.M., Bürgi, H., MacIsaac, H.J., and Heath, D.D. (2005). Invasion genetics of the Eurasian spiny waterflea: evidence for bottlenecks and gene flow using microsatellites. Molecular Ecology, 14, 1869-1879.

Costello, C., Drake, J.M., and Lodge, D.M. (2007). Evaluating an invasive species policy: ballast water exchange in the Great Lakes. Ecological Applications, 17, 655–662.

Cristescu, M.E.A., Hebert, P.D.N., Witt, J.D.S., MacIsaac, H.J., and Grigorovich, I.A. (2001). An invasion history for *Cercopagis pengoi* based on mitochondrial gene sequences. Limnology and Oceanography, 46, 224–229.

Crossman, E.J., Holm, E., Cholmondeley, R., and Tuininga, T. (1992). First record for Canada of the Rudd, Sca*rdinius erythrophthalmus*, and notes on the introduced round goby, *Neogobius melanostomus*. Canadian Field-Naturalist, 106, 206-209.

Czaika, S.C. (1978). Crustacean zooplankton of southwestern Lake Ontario in spring 1973 and at the Niagara and Genesee river mouth areas in 1972 and spring 1973. Journal of Great Lakes Research, 4, 1-9.

Deevey, S. Jr., and Deevey, G.B. (1970). The American species of *Eubosmina seligo* (Crustacea, Cladocera) Edward. Limnology and Oceanography, 16, 201-218.

De Melo, R., and P.D.N. Hebert. (1994a). A taxonomic re-evaluation of North American. Bosminidae. Canadian Journal of Zoology, 72, 1808-1825

De Melo, R., and P.D.N. Hebert. (1994b). Founder effects and geographical variation in the invading cladoceran *Bosmina* (*Eubosmina*) *coregoni* Baird 1857 in North America. Heredity, 73, 490-499.

Drake, J.M., and Lodge, D.M. (2003). Global hot spots of biological invasions: evaluating options for ballast-water management. Proceedings of the Royal Society of London, B, 271, 575-580.

Duggan, I.C., Bailey, S.A., Colautti, R.I., Gray, D.K., Makarewicz, J.C., and MacIsaac, H.J. (2003). Biological invasions in Lake Ontario: past, present and future. State of Lake Ontario: past, present and future (ed. by M. Munawar), pp. 541–558. Backhuys Publishing, Leiden, the Netherlands.

Duggan, I.C., van Overdijk, C.D.A., Bailey, S.A., Jenkins, P.T., Limén, H., and MacIsaac, H.J. (2005). Invertebrates associated with residual ballast water and sediments of cargo carrying ships entering the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences, 62, 2463–2464.

Duggan, I.C., Bailey, S.A. van Overdijk, C.D.A., and MacIsaac, H.J. (2006). Invasion risk of active and diapausing invertebrates from residual ballast in ships entering Chesapeake Bay. Marine Ecology Progress Series, 324, 57-66.

Dzialowski, A.R., O' Brien, W.J., and Swaffar, S.M. (2000). Range expansion and potential dispersal mechanisms of the exotic cladoceran *Daphnia lumholtzi*. Journal of Plankton Research, 22, 2205-2223.

Eakins, N. (1995). Ships on the Great Lakes in 1994. Canadian Coast Guard.

Eakins, N. (1996). Seaway lakers and salties 1995. Canadian Coast Guard.

Eakins, N. (1997). Seaway lakers and salties 1996. Canadian Coast Guard.

Eakins, N. (1998). Lakers and salties 1997-1998. Canadian Coast Guard.

Eakins, N. (1999). Lakers and salties 1998-1999. Canadian Coast Guard.

Eakins, N. (2000). Lakers and salties 1999-2000. Canadian Coast Guard.

Edlund, M.B., Taylor, C.M., Schelske, C. L., and Stoermer E.F. (2000). *Thalassiosira baltica* (Grunow) Ostenfeld (Bacillariophyta), a new exotic species in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences, 57, 610-615.

Emery, K.M., Beuselinck P., and English, J.T. (1999). Evaluation of the population dynamics of the forage legume *Lotus corniculatus* using matrix population models.New Phytologist, 144, 549-560.

EPS, Environmental Protection Service Environment Canada (1981). The presence and implication of foreign organisms in ship ballast waters discharged into the Great Lakes. Volume 2, Bio-Environmental Services Ltd.

Farara, D. G., and C. Erseus. (1991). *Phallodrilus aquaedulcis* Hrabe, 1960, a meiobenthic freshwater oligochaete (Tubificidae) previously known only from Europe, recorded from the Niagara River, North America. Canadian Journal of Zoology, 69, 291-294.

Finlay, J.A., Callow, M.E., Schultz, M.P., Swain, G.W., and Callow, JA. (2002). Adhesion Strength of Settled Spores of the Green Alga Enteromorpha, Biofouling, 18, 251–256.

Galarowicz, T, and Cochran, PA. (1991). Response by the parasitic crustacean *Argulus japonicus* to host chemical cues. Journal of Freshwater Ecology, 6, 455-456.

Geis, J.W., Schumacher, G.J., Raynal, D.J., and Hydulee N.P. (1981). Distribution of *Nitellopsis obtusa* (Charophyceae, Characeae) in the St. Lawrence River: a new record for North America. Phycologia, 20, 211-214.

Gollasch, S., Macdonald, E., Belson, S., Botnen, H., Christensen, J.T., Hamer, J.P., Houvenaghel, G., Jelmert, A. Lucas, I., Masson, D., McCollin, T., Olenin, S. J. Persson, A. Wallentinus, I., Wetsteyn, L.P., and Wittling, M.J.T. (2002). Life in ballast tanks. In: Invasive Aquatic Species of Europe Distribution, Impacts and Management, Leppäkoski, E., Gollasch, S., Olenin, S. (Eds.) 600 p.

Gollasch, S. (2002). The importance of ship hull fouling as a vector of species introductions into the North Sea. Biofouling, 18, 105-121.

Grigorovich, I.A., Dovgal, I.V., MacIsaac H.J., and Monchenko, V.I. (2001). *Acineta nitocrae*: A new suctorian epizooic on nonindigenous harpacticoid copepods, *Nitocra hibernica* and *N. incerta*, in the Laurentian Great Lakes. Archiv für Hydrobiologie, 152, 161-176.

Grigorovich, I.A., Korniushin, A.V., Gray, D.K., Duggan, I.C., Colautti, R.I., and MacIsaac, H.J. (2003). Lake Superior: an invasion coldspot. Hydrobiologia, 499, 191-210.

Grigorovich, I.A., Colautti, R.I, Mills, E.L., Holeck, K., Ballert, A., and H.J. MacIsaac. (2003). Ballast-mediated animal introductions in the Laurentian Great Lakes: retrospective and prospective analyses. Canadian Journal of Fisheries and Aquatic Sciences, 60, 740–756.

Grigorovich, I.A., Kang, M., and Ciborowski, J.J.H. (2005). Colonization of the Laurentian Great Lakes by the amphipod *Gammarus tigrinus*, a native of the North American Atlantic coast. Journal of Great Lakes Research, 31, 333–342.

Groth, A. T., Lovett-Doust, L., and Lovett-Doust, J. (1996). Population density and module demography in *Trapa natans* (Trapaceae), an annual, clonal aquatic macrophyte. American Journal of Botany, 83, 1406-1415.

Hammer, U. T., Shamess, J., and Haynes, R. C. (1983). The distribution and abundance of algae in saline lakes of Saskatchewan, Canada. Hydrobiologia, 105, 1-26.

Haney, R.A., and Taylor, D.J. (2003). Testing paleolimnological predictions with molecular data: the origins of Holarctic *Eubosmina*, Journal of Evolutionary Biology, 16, 871–882.

Hasle, G.R., and Evensen, D.L. (1975). Brackish-water and fresh-water species of the diatom genus *Skeletonma* Grev. I. *Skeletonema subsalsum* (A. Cleve) Bethge. Phycologia, 12, 283-297.

Hasle, G.E. (1978). Some freshwater and brackish water species of the. diatom genus *Thalassiosira* Cleve. Phycologia 17, 263–92.

Havel, J.E., Colbourne, J.K., and Hebert, P.D.N. (2000). Reconstructing the history of intercontinental dispersal in *Daphnia lumholtzi* by use of genetic markers. Limnology and Oceanography, 45, 1414-1419.

Hayden, K.J., and Rogers, W.A. (1998). *Neoergasilus japonicus* (Poecilostomatoida: Ergasilidae), a parasitic copepod new to North America. The Journal of Parasitology, 84, 88-93.

Hebert, P.D.N., Muncaster, B.W., and Mackie, G.L. (1989). Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences, 46, 1587-1591.

Hirsch, A., and Palmer, C.M. (1958). Some algae from the Ohio River drainage basin. The Ohio Journal of Science, 58, 375-382.

Holeck, K., Mills, E.L., MacIsaac, H.J., Dochoda, M., Colautti, R.I., and Ricciardi, A. (2004). Bridging troubled waters: understanding links between biological invasions, transoceanic shipping, and other entry vectors in the Laurentian Great Lakes. BioScience, 10, 919–929.

Holm, E., and G.A. Coker (1981). First Canadian records of the ghost shiner (*Notropis buchanani*) and the orangespotted sun-fish (*Lepomis humilis*). Canadian Field-Naturalist, 95, 210–211.

Holm, E., and Hamilton, J.G. (1988). Range extension for the fourspine stickleback, Apeltes quadracus, to Thunder Bay, Lake Superior. Canadian Field-Naturalist, 102, 653-656.

Holm, E., and Houston, J. (1993). Status of the ghost shiner, *Notropis buchanani*, in Canada. Canadian Field-Naturalist, 107, 440-445.

Horvath, T.G., Whitman, R.L., and Last, L.L. (2001). Establishment of two exotic crustaceans (Copepoda: Harpacticoida) in the near shore sands of Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences, 58, 1261–1264.

Hoyle, J.A., and Stewart, T.J. (2001). Occurrence of the fish parasite *Heterosporis* sp. (Microsporidea: Pleistophoridae) in Eastern Lake Ontario yellow perch. Ontario Ministry of Natural Resources, Internal Report. 3 p.

Hudson, P.L., Reid, J.W., Lesko, L.T., and Selgeby, J.H. (1998). Cyclopoid and harpactacoid copepods of the Laurentian Great Lakes. Ohio Biological Survey Bulletin (New Series), 12, 1–50.

Hudson, P. L., and Bowen, C. A. (2002). First record of *Neoergasilus japonicus* (Poecilostomatoida: Ergasilidae), a parasitic copepod new to the Laurentian Great Lakes. Journal of Parasitology, 88, 657-663.

Hudson, P.L., and Lesko, L.T. (2003). Free-living and parasitic copepods of the Laurentian Great Lakes: Keys and details on individual species. Ann Arbor, MI. www.glsc.usgs.gov/greatlakescopepods/.

Indiana DNR (2005) Largemouth bass virus. www.in.gov/dnr/invasivespecies/LMBV

Ishida, S., and Taylor, D.J. (2006). Quaternary diversification in a sexual Holarctic zooplankter, *Daphnia galeata*. Molecular Ecology, 14, 569-582.

Janas, U., and Wysocki, P. (2005) *Hemimysis anomala* G. O. Sars, 1907 (Crustacea, Mysidacea) – first record in the Gulf of Gdańsk. Oceanologia, 47, 405–408.

Jude, D. J., Reider, R. H., and Smith, G. R. (1992). Establishment of Gobiidae in the Great Lakes Basin. Canadian Journal of Fisheries and Aquatic Sciences, 49, 416–421.

Kelly, D.W., Muirhead, J.R., Heath, D.D., and MacIsaac, H.J. (2006). Contrasting patterns in genetic diversity following multiple invasions of fresh and brackish waters. Molecular Ecology, 15, 3641–3653.

Kociolek, J.P., Lamb, M.A., and Lowe, R.I. (1983). Notes on the growth and ultrastructure of *Biddulphia laevis* Ehr. (Bacillariophyceae) in the Maumee River, Ohio. Ohio Journal of Science, 83, 125-130.

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

Kott, E., and Fitzgerald, D. (2000). Comparative morphology and taxonomic status of the ghost shiner, *Notropis buchanani*, in Canada. Environmental Biology of Fishes, 59, 385–392.

Lackey, J.B., Wattie, E., Kachmar, J.F., and Placak, O.R. (1943). Some plankton relationships in a small unpolluted stream. American Midland Naturalist, 30, 403-425.

LaMarre, E, and Cochran, PA (1992). Lack of host species selection by the exotic parasitic crustacean, *Argulus japonicus*. Journal of Freshwater Ecology, 7, 77-80.

Lasee, B.A., Sutherland, D.R., and Moubry, M.E. (1988). Host-parasite relationships between burbot (*Lota lota*) and adult *Salmincola lotae* (Copepoda). Canadian Journal of Zoology, 66, 2459-2463.

Leach, J.H. (1980). Limnological sampling intensity in Lake St. Clair in relation to distribution of water masses. Journal of Great Lakes Research, 6, 141-145.

Locke, A., Reid, D.M., Sprules, W.G., Carlton, J.T., and van Leeuwen, H.C. (1991). Effectiveness of mid-ocean exchange in controlling freshwater and coastal zooplankton in ballast water. Canadian Technical Report of Fisheries and Aquatic Sciences 1822, 93 p.

Locke, A., Reid, D.M., van Leeuwen, H.C., Sprules, W.G., and Carlton, J.T. (1993) Ballast water exchange as a means of controlling dispersal of freshwater organisms by ships. Canadian Journal of Fisheries and Aquatic Sciences, 50, 2086–2093.

Lougheed, V.L., and R.J. Stevenson. (2004) Exotic marine macroalgae (*Enteromorpha flexuosa*) reaches bloom proportions in a coastal lake of Lake Michigan. Journal of Great Lakes Research, 30, 538-544.

Lodge, D.M., Williams, S., MacIsaac, H.J., hayes, K.R., Leung, B., Reichard, S., Mack, R.N., Moyle, P.B., Smith, M., Andow, D.A., Carlton, J.T., and McMichael, A. (2006). Biological invasions: recommendations for U.S. policy and management. Ecological Applications, 16, 2035-2054.

Lowe, R.L., and Busch, D.E. (1975). Morphological observations on two species of the diatom genus *Thalassiosira* from freshewater habitats in Ohio. Transactions of the American Microscopical Society, 94, 118-123.

MacIsaac, H.J. (1999) Biological invasions in Lake Erie: past, present and future. State of Lake Erie: past, present and future (ed. by M. Munawar and T. Edall), pp. 305–322. Backhuys Publishing, Leiden, the Netherlands.

MacIsaac, H.J., Grigorovich, I.A., Hoyle, J.A., Yan, N.D., and Panov, I.E. (1999). Invasion of Lake Ontario by the Ponto-Caspian predatory cladoceran *Cercopagis pengoi*. Canadian Journal of Fisheries and Aquatic Sciences, 56, 1-5.

May, G.E., Gelembiuk, G.W., Panov, V.E., Orlova, M.I., and Lee, C.E. (2006). Molecular ecology of zebra mussel invasions. Molecular Ecology, 15, 1021-1031.

May, B., and Marsden, J.E. (1992). Genetic identification and implications of another invasive species of dreissenid mussel in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences, 49, 1501-1506.

McMahon, R.F. (1982). The occurrence and spread of the introduced Asiatic freshwater clam, *Corbicula fluminea* (Muller), in North America: 1924–1982. Nautilus, 96, 134–141.

Michigan DNR. (2004a). Largemouth bass virus continues to spread in Michigan waters. http://www.michigan.gov/dnr/0,1607, 7-153-10364_10950-93547--,00.html

Michigan DNR. (2004b). Muskie Piscirickettsia (Muskie Pox) update. http://www.michigandnr.com/PUBLICATIONS/PDFS/fishing/FishDisease/muskiepoxupdate.pdf

Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C. L. (1993). Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research, 19, 1-54.

Mills, E.L., Rosenberg, G., Spidle, A.P., Ludyanskiy, M., Pligin, Y., and May, B. (1996). A review of the biology and ecology of the quagga mussel (*Dreissena bugensis*)., a second species of freshwater dreissenid Introduced to North America. American Zoologist, 36, 271-286.

Muller, K.M., Cole, K.M., and, Sheath, R.G. (2003). Systematics of *Bangia* (Bangiales, Rhodophyta) in North America. II biogeographic trends in karyology: chromosome trees and linkage with gene sequence phylogenetic trees. Phycologia, 42, 209-219.

Muzzall, P.M., Gillilland, M.G., Bowen, C.A., Coady, N.R., and Peebles, C.R. (2003). Parasites of burbot, *Lota lota*, from Lake Huron, Michigan, U.S.A., with a checklist of the North American parasites of burbot. Comparative Parasitology, 70, 182-195.

Muzinic, C. J. (2000). First record of *Daphnia lumholtzi* Sars in the Great Lakes. Journal of Great Lakes Research, 26, 352-354.

Nicholls, K.H., and MacIsaac, H.J. (2004). Euryhaline, sand-dwelling, testate rhizopods in the Great Lakes. Journal of Great Lakes Research, 30, 123–132.

Nicholls, K.H. (2005). *Psammonobiotus dziwnowi* and *Corythionella georgiana*, two new freshwater sand-dwelling testate amoebae (Phisopoda: Filosea). Acta Protozoologica, 44, 271-278.

Nelson, R. (2003). Exotic Spring Viremia of Carp Virus confirmed in common carp taken from the Calumet-Sag channel near Chicago, Illinois, USFAW. http://news.fws.gov/newsrelease/r3/E5DE11CB-EF51-49E8-A147A9955185C7C9.html.

Owens, R. W., O'Gorman, R., Mills, E.L., Rudstam, L.G., Hasse, J.J., Kulik, B.H., and MacNeill, D.R. (1998). Blueback herring (*Alosa aestivalis*) in Lake Ontario: First record, entry route, and colonization potential. Journal of Great Lakes Research, 24, 723-730.

Patalas, K. (1969). Composition and horizontal distribution of crustacean plankton in Lake Ontario. Journal of the Fisheries Research Board of Canada, 26, 2136-2164.

Priegel, G. (1963). Dispersal of the shortnose gar, *Lepisosteus platostomus*, into the Great Lakes drainage. Transactions of the American Fisheries Society, 92, 178.

Pronin, N.M., Fleischer, G.W., Baldanova, D.R. and Pronina, S.V. (1997). Parasites of the recently established round goby (*Neogobius melanostomus*) and tubenose goby (*Proterorhinus marmoratus*) (Cottidae) from the St. Clair River and Lake St. Clair, Michigan, USA. Folia Parasitologica, 44, 1–6.
Pueschel, C.M., and Stein, J.R. (1983). Ultrastructure of a freshwater brown alga from western Canada. Journal of Phycology, 19, 209-215.

Purcell, N.J. (1976). *Epilobium parviflorum* Schreb. (Onagraceae) established in North America. Rhodora 78, 785-787.

Ricciardi, A. (2001). Facilitative interactions among aquatic invaders: is an 'invasional meltdown' occurring in the Great Lakes? Canadian Journal of Fisheries and Aquatic Sciences, 58, 2513–2525.
Ricciardi, A. (2006). Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Diversity and Distributions, 12, 425-433.

Ricciardi, A., and MacIsaac, H.J. (2000). Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends in Ecology and Evolution, 15, 62-65.

Ricciardi, A., and Rasmussen, J.B. (1998). Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Canadian Journal of Fisheries and Aquatic Sciences, 55, 1759-1765.

Rixon, C.A.M., Duggan, I.C., Bergeron, N.M.N., Ricciardi, A., and MacIsaac, H.J. (2004). Invasion risks posed by the aquarium trade and live fish markets on the Laurentian Great Lakes. Biodiversity and Conservation, 14, 1365-1381.

Robertson, A., and Gannon, J.E. (1981). Annotated checklist of the free-living copepods of the Great Lakes. Journal of Great Lakes Research, 7, 382-393.

Ruiz, G.M., Fofonoff, P.W., Carlton, J.T., Wonham, M.J., and Hines, A.H. (2000). Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. Annual Review of Ecology and Systematics, 31, 481–531.

Ruiz, G.M., and Carlton, J.T. (2003). Invasion vectors: a conceptual framework for management. Invasive species: vectors and management strategies (ed. by G.M. Ruiz and J.T. Carlton), pp. 459–504. Island Press, Washington, D.C.

Sala, O.E., Chapin, F.S., Armesto, J.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., and Wall, D.H. (2000). Global biodiversity scenarios for the year 2100. Science, 287, 1770–1774.

Schloesser, R. E., and Blum, J. L. (1980). *Sphacelaria lacustris* sp. Nov., a freshwater brown alga from Lake Michigan. Journal of Phycology, 16, 201-207.

Schloesser, D.W., Hudson, P.L., and Nichols, S.J. (1986). Distribution and habitat of *Nitellopsis obtusa* (Characeae) in the Laurentian Great Lakes. Hydrobiologia, 133, 91-96.

Sheath, R.G., and Cole, K.M. (1980). Distributions and salinity adaptations of *Bangia atropurpurea* (Rhodophyta), a putative migrant into the Laurentian Great Lakes. Journal of Phycology, 16, 412-420.

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

Simon, T.P., and Vondruska, J.T. (1991). Larval identification of the ruffe *Gymnocephalus cernuus* (Linnaeus) (Percidae: Percini), in the St. Louis River Estuary, Lake Superior drainage basin, Minnesota. Canadian Journal of Zoology, 69, 436-442.

Simons, J., and Nat, E. (1996). Past and present distribution of stoneworts (Characeae) in the Netherlands. Hydrobiologia, 340, 127-135.

Simpson, K.W., and Abele, L.E. (1984). *Ripestes parasita* (Schmidt) (Oligochaeta: Naididae), a distinctive oligochaete new to North America. Freshwater Invertebrate Biology, 3, 36-41.

Sly, P.G. (1991). The effects of land use and cultural development on the Lake Ontario ecosystem since 1750. Hydrobiologia, 213, l-75.

Sprules, W.G., Riessen, H.P., and Jin, E.H. (1990). Dynamics of the *Bythotrephes* invasion of the St. Lawrence Great Lakes. Journal of Great Lakes Research, 16, 346-351.

Stephenson, S.A., and Momot, W.T. (2000). Threespine, *Gasterosteus aculeatus*, and fourspine, *Apeltes quadracus*, sticklebacks in the Lake Superior Basin. Canadian Field-Naturalist, 114, 211-216.

Stepien, C.A., Brown, J.E., Neilson, M.E., and Tumeo, M.A. (2005). Genetic diversity of invasive species in the Great Lakes versus their Eurasian source populations: Insights for risk analysis. Risk Analysis, 25, 1043-1060.

Stepien, C.A., and Tumeo, M.A. (2006). Invasion genetics of Ponto-Caspian gobies in the Great Lakes: a ‘cryptic’ species, absence of founder effects, and comparative risk analysis. Biological Invasions, 8, 61-78.

Stoermer, E. F., and L. Sicko-Goad. (1977). A new distribution record for *Hymenomonas roseola* Stein (Prymnesiophyceae, Coccolithophoraceae) and *Spiniferomonas trioralis* Takahashi (Chrysophyceae, Synuraceae) in the Laurentian Great Lakes. Phycologia, 16, 355-358.

Stoermer, E.F. (1978). Phytoplankton assemblages as indicators of water quality in the Laurentian Great Lakes. Transactions of the American Microscopical Society, 97, 2-16.

Stoermer, E.F., Kreis, R.G. Jr., and Andresen, N.A. (1999). Checklist of diatoms from the Laurentian Great Lakes. II. Journal of Great Lakes Research, 25, 515-566.

Stoermer, E. F., and Yang, J.J. (1968). A preliminary report of the fossil diatom flora from Lake Huron sediments. Proceedings of the 11th Conference on Great Lakes Research, International Association of Great Lakes Research, pp. 253-267.

Stokstad, E. (2003). Can well-timed jolts keep out unwanted exotic fish? Science 301, 157–158.

Taft, C.E. (1964). New records of algae from the west end of Lake Erie. The Ohio Journal of Science, 64, 43-50.

Taylor, D.J., and Hebert, P.D.N. (1993). Cryptic intercontinental hybridization in *Daphnia* (Crustacea): The ghost of introductions past. Proceedings of the Royal Society of London Biological Sciences, 254, 163-168.

Thompson, R.H. (1975). The freshwater brown alga *Sphacelaria fluviatilis*. Journal of Phycology, 11, (suppl.) 5.

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

United States Coast Guard (2005). Ballast water management practices for NOBOB vessels. Fact Sheet, Code of Federal Regulations 33-CFR Part 151.2035.

USDA, United States Department of Agriculture (2006). Viral hemorrhagic septicemia in the Great Lakes. www.aphis.usda.gov/vs/ceah/cei/taf/emergingdiseasenotice_files/vhsgreatlakes.htm

Ussery, T.A., and McMahon, R.F. (1995). Comparative study of the desiccation resistance of zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*). Technical report, U.S. Army Corps of Engineers, 95-6, p 19.

Weber, C. (1970). A new freshwater centric diatom *Microsiphonia potamos* gen. et sp. Nov., Journal of Phycology, 6, 49-153.

Wells, L. (1970). Effects of alewife predation on zooplankton populations in Lake Michigan. Limnology and Oceanography, 15, 556-565.

Werner, R.G. (1972). Bluespotted Sunfish, *Enneacanthus gloriosus*, in the Lake Ontario Drainage, New York. Copeia, 4, 878-879.

Wilcox, S.J., and Dietz, T.H. (1998). Salinity tolerance of the freshwater bivalave *Dreissena polymorpha* (Pallas, 1771) (Bivalvia, Dreissenidae). The Nautilus, 111, 143-148.

Wilson, J. and Powell, E. (2005). Genetic variability and phylogeography of the invasive zebra mussel, *Dreissena polymorpha* (Pallas). Molecular Ecology, 14, 1655-1666.

Witt, J.D.S., Hebert, P.D.N., and Morton, W.B. (1997). *Echinogammarus ischnus*: another crustacean invader in the Laurentian Great Lakes basin. Canadian Journal of Fisheries and Aquatic Sciences, 54, 264-268.

Wujek, D.E. (1967). Some plankton diatoms from the Detroit River and the western end of Lake Erie adjacent to the Detroit River. The Ohio Journal of Science, 67, 32-35.

Wujek, D.E., and Graebner, M. (1980). A new freshwater. species of *Chaetoceros* from the Great Lakes region. Journal of Great Lakes Research. 6, 260-262

Wujek, D.E., and Welling, M.L. (1981). The occurrence of two centric diatoms new to the Great. Lakes. Journal of Great Lakes Research, 7, 55-56.

Zaranko, D.T., Farara, D.G., and Thompson, F.G. (1997). Another exotic mollusc in the Laurentian Great Lakes: the New Zealand native *Potamopyrgus antipodarum* (Gray 1843) (Gastropoda, Hydrobiidae). Canadian Journal of Fisheries and Aquatic Sciences, 54, 809-814.

TABLE 1 List of Nonindigenous Aquatic Species Reported in the Great Lakes Since 1959

Species	Common name	Year of discovery	Supporting references
Species included in vector & pathway analysis			
Pisidium supinum	humpback pea clam	1959	MacIsaac 1999; Clarke 1981
Trapa natans	water chestnut	1959	Mills et al. 1993; Groth et al. 1996
Persicaria longiseta	lady's thumb	1960	Mills et al. 1993
Glugea hertwigi	protozoan	1960	Mills et al. 1993; Sly 1991
Lepisosteus platostomus	shortnose gar	1962	Mills et al. 1993; Priegel 1963
Bangia atropurpurea	red alga	1964	Belcher 1960; Mills et al. 1993; Sheath & Cole 1980; Muller et al. 2003
Epilobium parviflorum	hairy willow herb	1966	Mills et al. 1993; Purcell 1976
Dugesia lugubris	flatworm	1968	Mills et al. 1993; Ball 1969
Myxobolus cerebralis	whirling disease	1968	Mills et al. 1993
Solidago sempervirens	seaside goldenrod	1969	Catling & McKay 1980; Mills et al. 1993
Enneacanthus gloriosus	bluespotted sunfish	1971	Mills et al. 1993; Werner 1972
Cyclops strenuous	copepod	1972	Locke et al. 1993; Hudson et al. 1998; Duggan et al. 2005
Nitocra hibernica	harpacticoid copepod	1973	Cziaka 1978; Mills et al. 1993; Hudson et al. 1998
Lotus corniculatus	birdsfoot trefoil	1975	Emery et al. 1999; Bronte et al. 2003
Renibacterium salmoninarum	bacterium	1975	Bronte et al. 2003
Nitellopsis obtuse	green alga	1978	Geis et al. 1982; Mills et al. 1993; Simons & Nat 1996
Biddulphia laevis	diatom	1978	Wujeck & Welling 1981; Kociolek et al. 1983; Mills et al. 1993
Enteromorpha prolifera	green alga	1979	Catling & McKay 1980; Mills et al. 1993
Corbicula fluminea	Asiatic clam	1980	McMahon 1982; Mills et al. 1993
Ripistes parasita	oligochaete	1980	Simpson & Abele 1984; Mills et al. 1993
Lupinus polyphyllus	lupine	1982	Bronte et al. 2003; regionhttp://www.nobanis.org/files/factsheets/Lupinus%20polyphyllus.pdf
Phallodrilus aquaedulcis	oligochaete	1983	Farara & Erseus 1991; Mills et al. 1993
Bythotrephes longimanus	spiny waterflea	1984	Bur et al. 1986; Sprules et al. 1990; Thierrault et al. 2002; Coluatti et al. 2005
Gymnocephalus cernuus	Eurasian ruffe	1986	Simon & Vondruska 1991; Mills et al. 1993; Stepien et al. 2005; Albert et. al. 2005
Apeltes quadracus	fourspine stickleback	1986	Holm & Hamilton 1988; Mills et al. 1993; Grigorovich et al. 2003; Colautti et al. 2003
Thalassiosira baltica	diatom	1988	Mills et al. 1993; Edlund et al. 2000; Gollasch et al. 2002
Argulus japonicus	parasitic copepod	1988	Galarowicz & Cochran 1991;LaMarre & Cochran 1992; Mills et al. 1993
Dreissena polymorpha	zebra mussel	1988	Leach 1980; Hebert et al 1989; Mills et al. 1993, 1996; Ussery & McMahon 1995; Wilcox & Dietz 1998; Gollasch et al. 2002; Duggan et al. 2005;
Bosmina maritima	waterflea	1988	EPS 1981; De Melo & Hebert 1994; Bailey et. al. 2005; Duggan et. al. 2005
Scardinius erythrophthalmus	Rudd	1989	Crossman et. al. 1992; Mills et al. 1993

Dreissena bugensis	quagga mussel	1989	May & Marsden 1992; Mills et al. 1993, 1996; Ussery & McMahon 1995; Wilcox & Dietz 1998; Gollasch et al. 2002; Duggan et al. 2005; Stepien et al. 2005
Neogobius melanostomus	round goby	1990	Jude et. Al. 1992;Mills et al. 1993; Gollasch et al. 2002; Stepien & Tumeo 2006
Proterorhinus marmoratus	tubenose goby	1990	Jude et. Al. 1992;Mills et al. 1993; Gollasch et al. 2002; Stepien & Tumeo 2006
Potamopyrgus antipodarum	Mud snail	1991	Zaranko et al. 1997; Gollasch et. al. 2002
Neascus brevicaudatus	digenean fluke	1992	Ricciardi 2001
Dactylogyrus amphibothrium	monogenetic fluke	1992	Riccardi 2001
Acanthostomum sp.	digenean fluke	1992	Pronin et al. 1997; Ricciardi 2001
Trypanosoma acerinae	flagellate	1992	Ricciardi 2001
Dactylogyrus hemiamphibothrium	monogenetic fluke	1992	Ricciardi 2001
Ichthyocotylurus pileatus	digenean fluke	1992	Pronin et al. 1997; Ricciardi 2001
Scolex pleuronectis	cestode	1994	Pronin et al. 1997; Ricciardi 2001
Neoergasilus japonicus	copepod	1994	Hayden & Rogers 1998; Hudson & Bowen 2002
Megacyclops viridis	cyclopoid copepod	1994	Hudson et al. 1998
Sphaeromyxa sevastopoli	mixosporidian	1994	Pronin et al. 1997; Ricciardi 2001
Echinogammarus ischnus	amphipod	1995	Witt et al. 1997; Cristescu et al. 2004
Alosa aestivalis	blueback herring	1995	Owens et al. 1998
Heteropsyllus nr. Nunni	harpacticoid copepod	1996	Horvath et al. 2001
Cercopagis pengoi	fish-hook waterflea	1998	MacIsaac et al. 1999; Cristescu et al. 2001
Schizopera borutzkyi	harpacticoid copepod	1998	Horvath et al. 2001; Duggan et al. 2005
Nitocra incerta	harpacticoid copepod	1999	Grigorovich et al. 2001
Daphnia lumholtzi	waterflea	1999	Dziabowski et al. 2000; Havel et al. 2000; Muzinic 2000
Heterosporis sp.	microsporidian	2000	Hoyle & Stewart 2001
Gammarus tigrinus	amphipod	2001	Locke et. al. 1991; Grigorovich et al. 2005; Kelly et. al. 2006
Piscirickettsia cf. salmonis	muskie pox	2002	Michigan DNR 2004a
Largemouth Bass Virus	iridovirus	2003	Michigan DNR 2004b
Enteromorpha flexuosa	green alga	2003	Finlay et al. 2002; Lougheed & Stevenson 2004
Viral Hemorrhagic Septicemia (VHS).	fish virus	2003	USDA 2006
Rhabdovirus carpio	viremia of carp	2003	Nelson 2003
Hemimysis anomala	oppossum shrimp	2006	Janas & Wysocki 2005

Species present before 1959		
Lasmigona subviridis	mussel	Clarke & Berg 1959; Mills et al. 1993
Chroodactylon ramosum	red alga	Taft 1964; Sheath & Morrison 1982; Mills et al. 1993
Eubosmina coregoni	waterflea	Wells 1970; Deevey & Deevey 1971; Mills et al. 1993; De Melo & Hebert 1994a & b; Haney & Taylor 2003
Hydrocharis morsus-ranae	European frogbit	Mills et al. 1993
Daphnia galeata galeata	waterflea	Taylor & Hebert 1993; Ishida & Taylor 2006
Cryptogenic species		
Thalassiosira weissflogii	Diatom	Wujeck 1967; Lowe & Busch 1975; Hasle 1978; Stoermer 1978; EPS 1981; Mills et al. 1993
Skeletonema potamos	diatom	Weber 1970; Stoermer 1978; Mills et al. 1993; Gollasch et. al. 2002
Cyclotella cryptica	diatom	Stoermer & Yang 1969; Stoermer 1978; EPS 1981; Mills et al. 1993;
Cyclotella atomus	diatom	Stoermer & Yang 1969; Stoermer 1978; EPS 1981; Mills et al. 1993;
Cyclotella woltereki	diatom	Stoermer & Yang 1969; Stoermer 1978; EPS 1981; Mills et al. 1993;
Potamothrix vejdovskyi	oligochaete	Mills et al. 1993; Brinkhurst & Cook 1966
Skistodiaptomus pallidus	calanoid copepod	Robertson & Gannon 1981; Mills et al. 1993; Hudson & Lesko. 2003
Thalassiosira guillardii	diatom	Hasle 1978; Stoermer 1978; EPS 1981; Mills et al. 1993
Thalassiosira pseudonana	diatom	Lowe & Busch 1975; Hasle 1978; Stoermer 1978; EPS 1981; Mills et al. 1993
Skeletonema subsalsum	diatom	Hasle & Evensen 1975; Stoermer 1978; Mills et al. 1993; Gollasch et. al. 2002
Sphacelaria fluviatilis	brown alga	Thompson 1975; Schloesser & Blum 1980; Pueschel & Stein 1983; Mills et al. 1993
Sphacelaria lacustris	brown alga	Schloesser & Blum 1980; Mills et al. 1993
Hymenomonas roseola	cocco-lithophore	Lackey et. al. 1943; Stoermer & Sicko-Goad 1977; Mills et al. 1993
Chaetoceros hohnii	diatom	Wujeck & Graebner 1980; Mills et al. 1993
Thalassiosira lacustris	diatom	Lowe & Busch 1975; Hasle 1978; Stoermer 1978; EPS 1981; Mills et al. 1993
Notropis buchanani	ghost shiner	Holm & Coker 1981; Holm & Houston 1993; Mills et. al. 1993; Kott & Fitzgerald 2000
Salmincola lotae	copepod	Lasee et al. 1988; Muzzall et al. 2003
Acineta nitocrae	suctorian	Grigorovich et al. 2001
Psammonobiotus communis	testate amoeba	Nicholls & MacIsaac 2004
Psammonobiotus dziwnowi	testate amoeba	Nicholls & MacIsaac 2004; Nicholls 2005
Psammonobiotus linearis	testate amoeba	Nicholls & MacIsaac 2004

TABLE 2 Correspondence (Y = Agrees, N = Disagrees and 0 = Unobserved) of Observed Attributes with Those Predicted for Nonindigenous Species (See Appendix 1) for Species Whose Status as NIS in the Great Lakes Was Uncertain (See Text). Attributes That Are Indicated as Unobserved Cannot Be Assessed Due to a Lack of Data. Species Failing to Agree with at Least Three Criteria (i.e. Sum = 3 or More) Were Considered Cryptogenic and Excluded from Vector and Pathway Analysis

		Attributes						
Species	Common name	1	2	3	4	5	6	Sum
Thalassiosira weissflogii	diatom	0	0	y	n	n	n	1
Thalassiosira guillardii	diatom	0	n	y	y	n	0	2
Thalassiosira pseudonana	diatom	0	0	y	n	n	n	1
Thalassiosira lacustris	diatom	0	n	y	0	n	n	1
Skeletonema potamos	diatom	0	0	y	0	n	n	1
Skeletonema subsalsum	diatom	0	0	y	0	n	y	2
Cyclotella cryptica	diatom	0	0	y	n	0	n	1
Cyclotella atomus	diatom	0	0	y	n	n	n	1
Cyclotella woltereki	diatom	0	n	y	y	0	n	2
Biddulphia laevis	diatom	y	0	y	y	n	n	3
Chaetoceros hohnii	diatom	0	0	y	y	0	n	2
Potamothrix vejdovskyi	oligochaete	0	0	0	n	n	n	0
Salmincola lotae	copepod	0	0	0	n	y	n	1
Skistodiaptomus pallidus	copepod	0	n	n	n	n	n	0
Sphacelaria lacustris	algae	0	0	0	n	0	0	0
Sphacelaria fluviatilis	algae	0	0	0	y	0	n	1
Hymenomonas roseola	flagellate	0	0	0	y	n	n	1
Acineta nitocrae	suctorian	0	0	0	0	0	y	1
Psammonobiotus dziwnowi	rhizopod	0	0	0	n	0	y	1
Psammonobiotus linearis	rhizopod	0	0	0	n	o	n	0
Psammonobiotus communis	rhizopod	0	0	0	n	0	y	1
Notropis buchanani	Ghost shiner	0	0	n	y	n	n	1

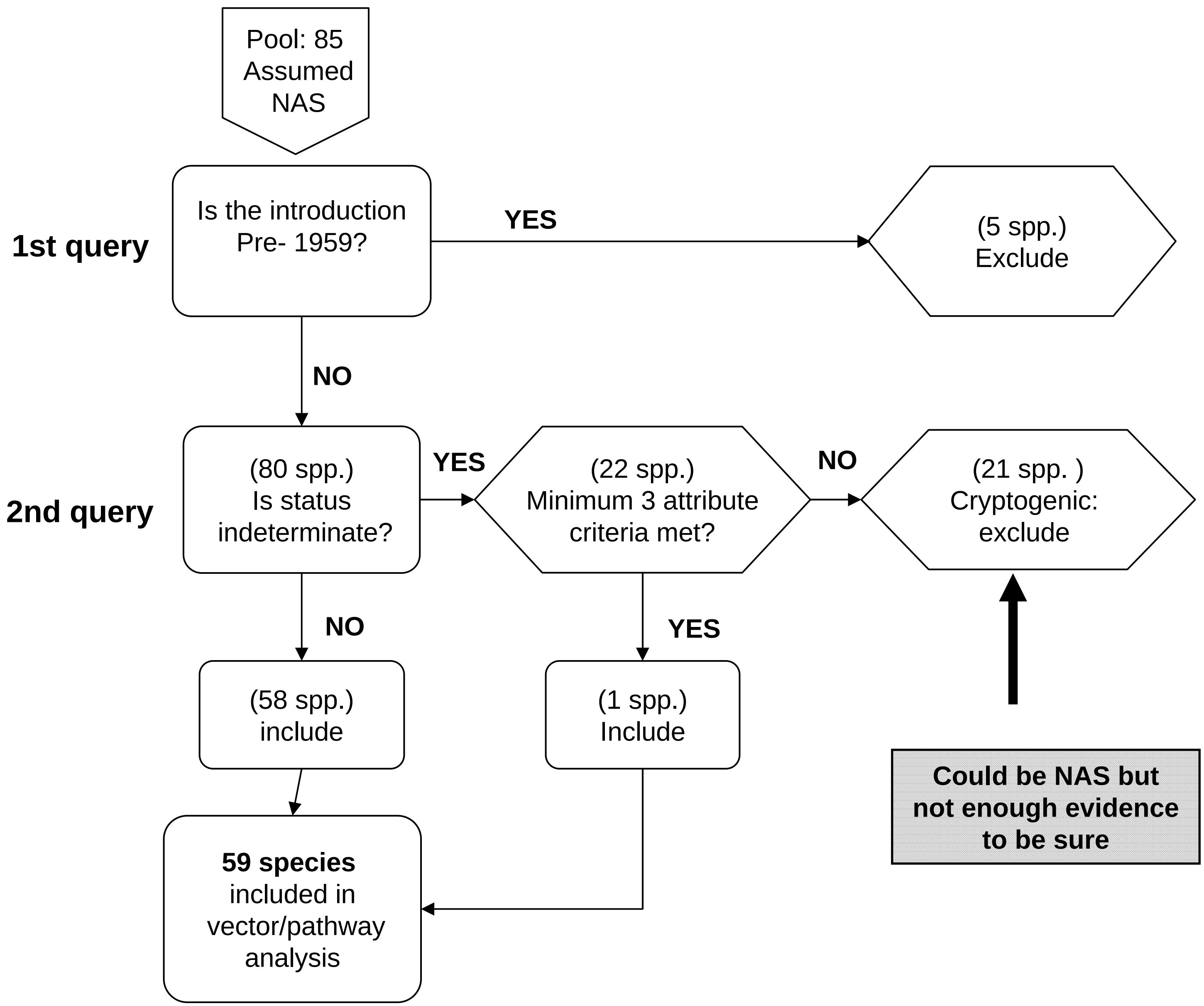

FIGURE 1 Decision-rules used to select species for vector and pathway analysis.
The number of species included or excluded at each step is indicated in parentheses.

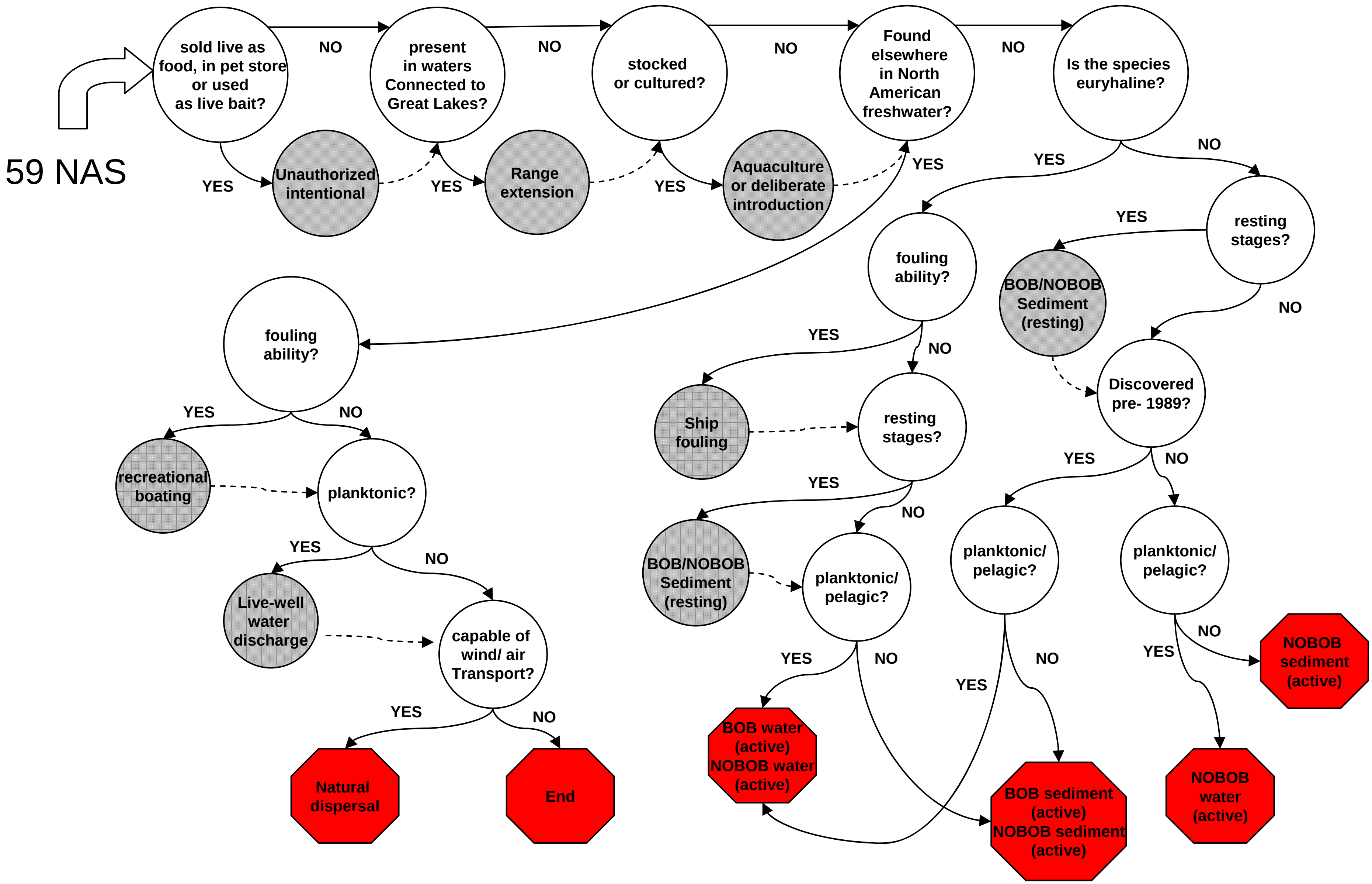

FIGURE 2 Vector assignment protocol (modified from Holeck *et. al.*, 2004).
All probable vectors are considered (shaded circles) until an end-point is reached (hexagons).
After the identification of each probable vector, a dashed line indicates consideration of all other vectors.

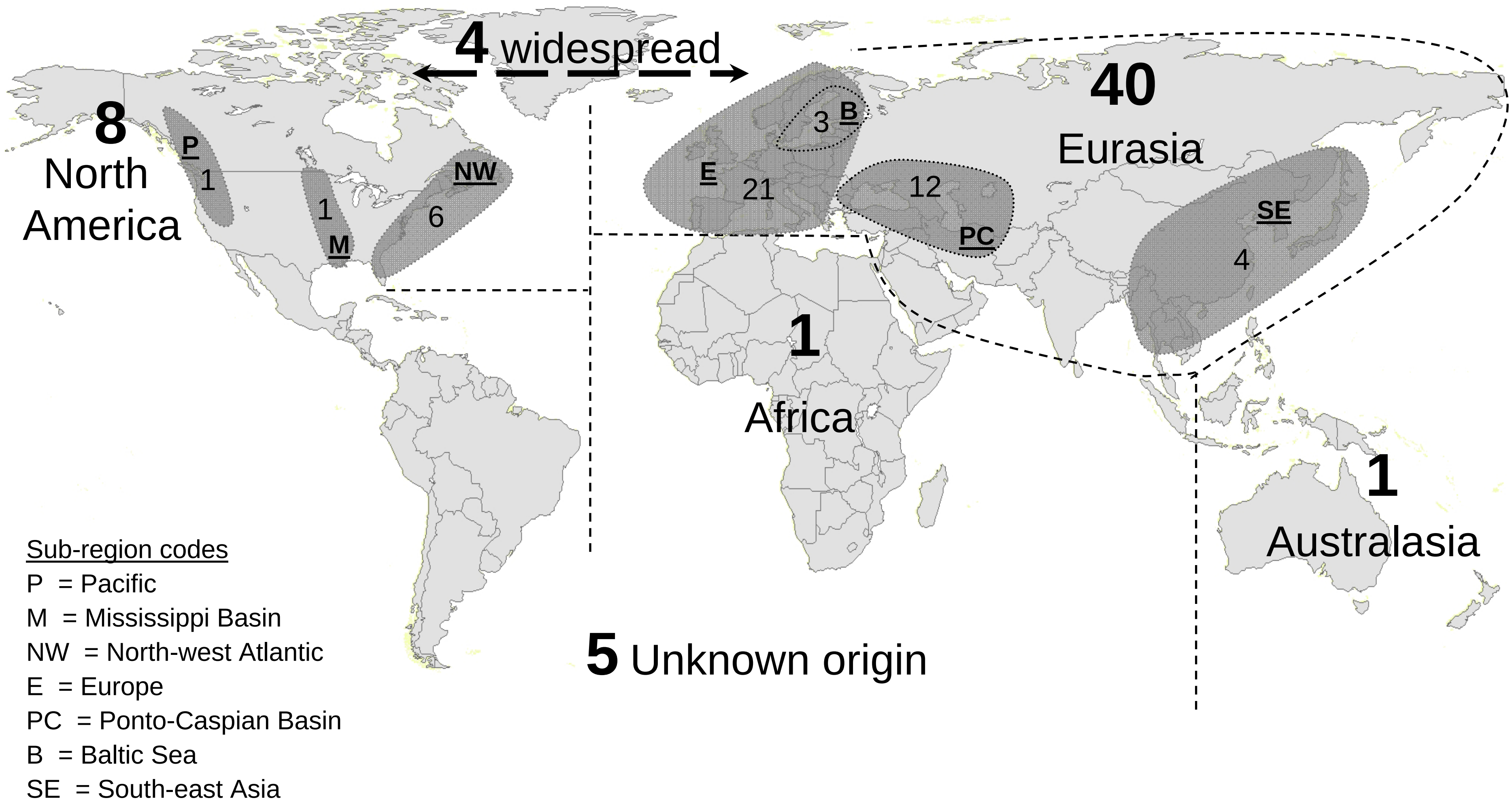

FIGURE 3 Geographic origins of NIS that established in the Great Lakes after 1959.
Numbers in bold indicate the total number of species by region. Shaded areas indicate the number of species by sub-region.
Widespread refers to species whose native range includes North America and Eurasia.

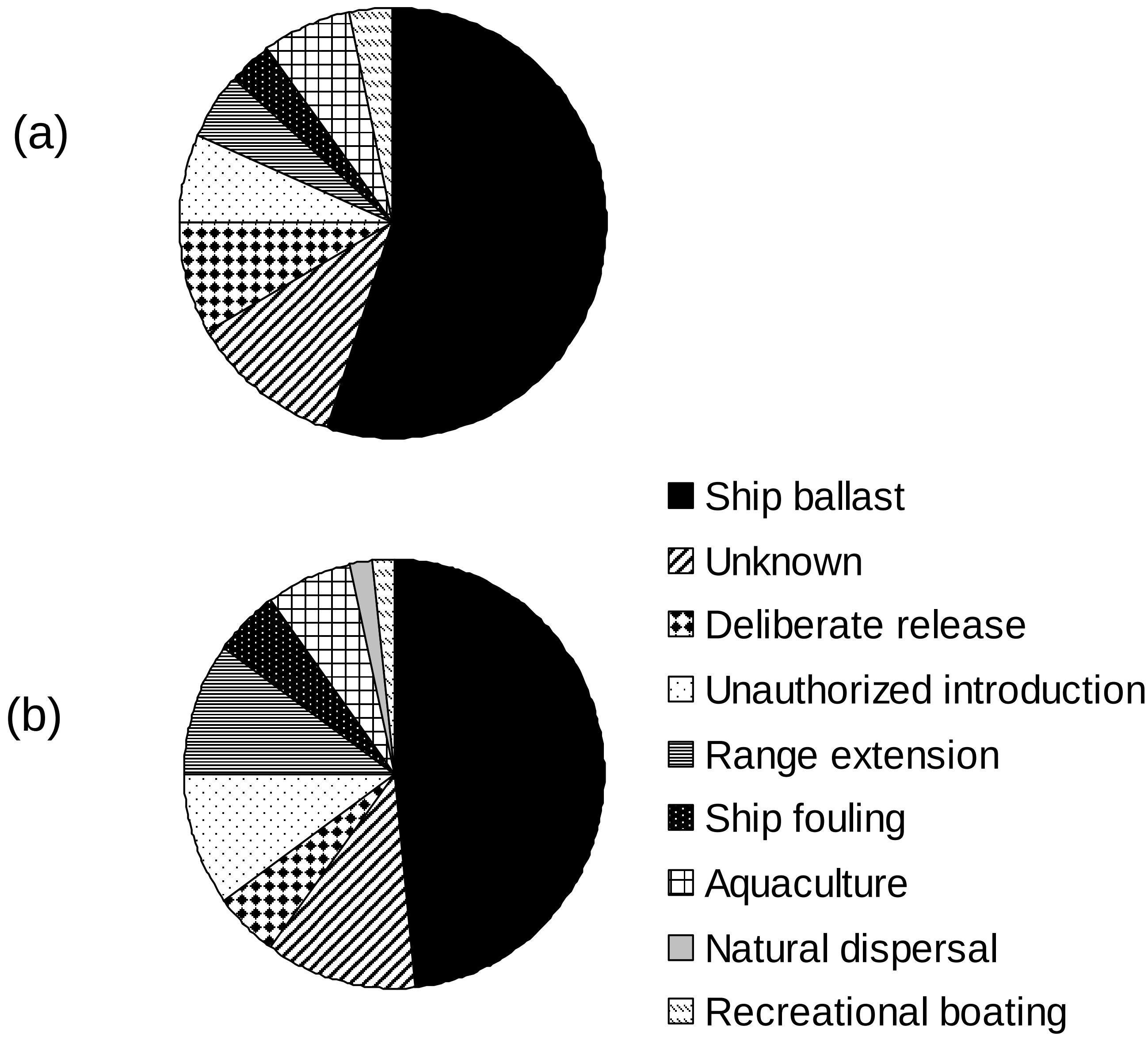

FIGURE 4 Vectors assigned for the introduction of NIS to the Great Lakes since 1959.
(a) Summary based on most likely vector (primary).
(b) Summary based on prioritization of next most likely vector (secondary).

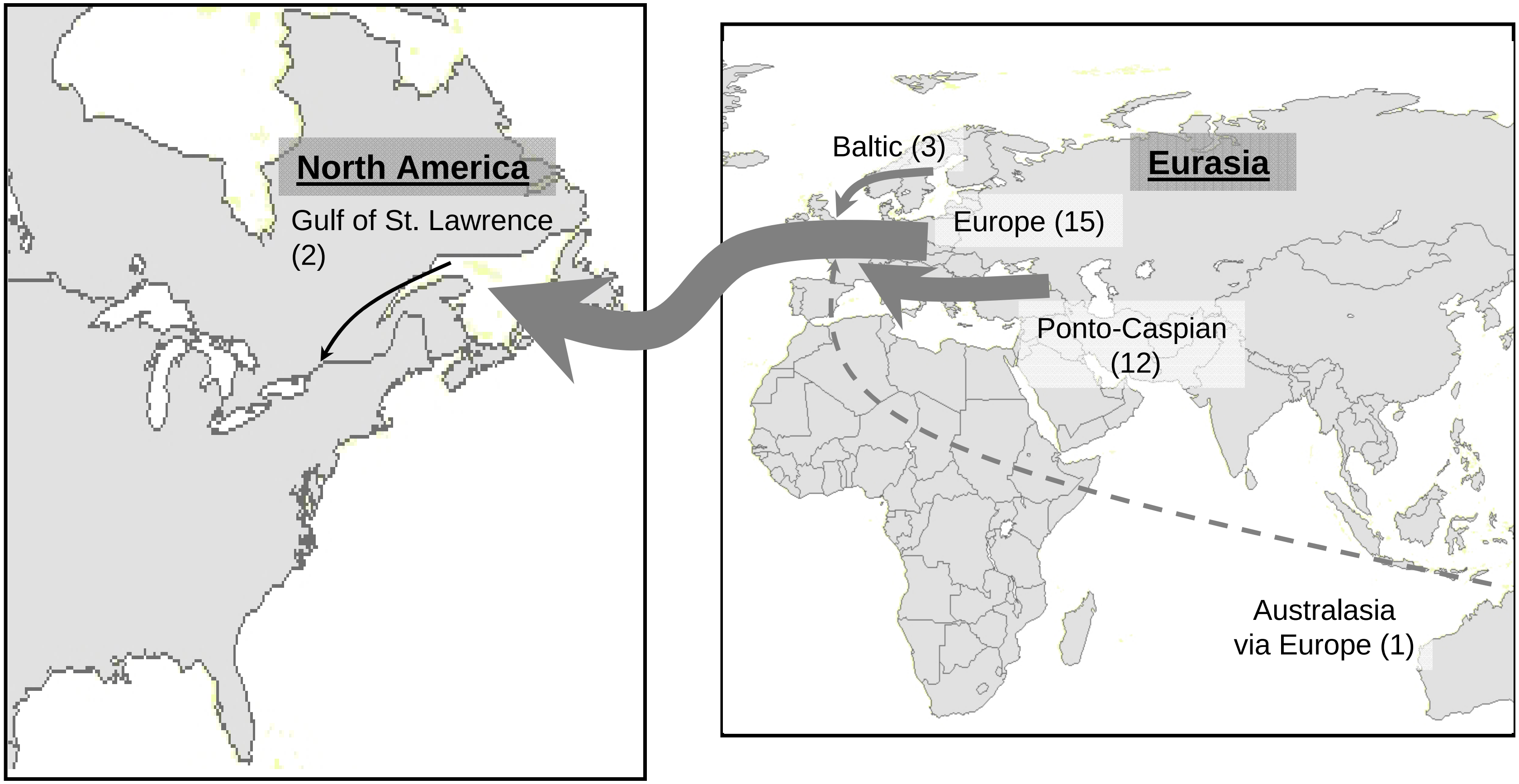

FIGURE 5 Pathways of ship-ballast vectored invasions to the Great Lakes since 1959.
Arrow width is proportional to the strength of each donor sub-region.
Parentheses indicate the number of species originating in each region.

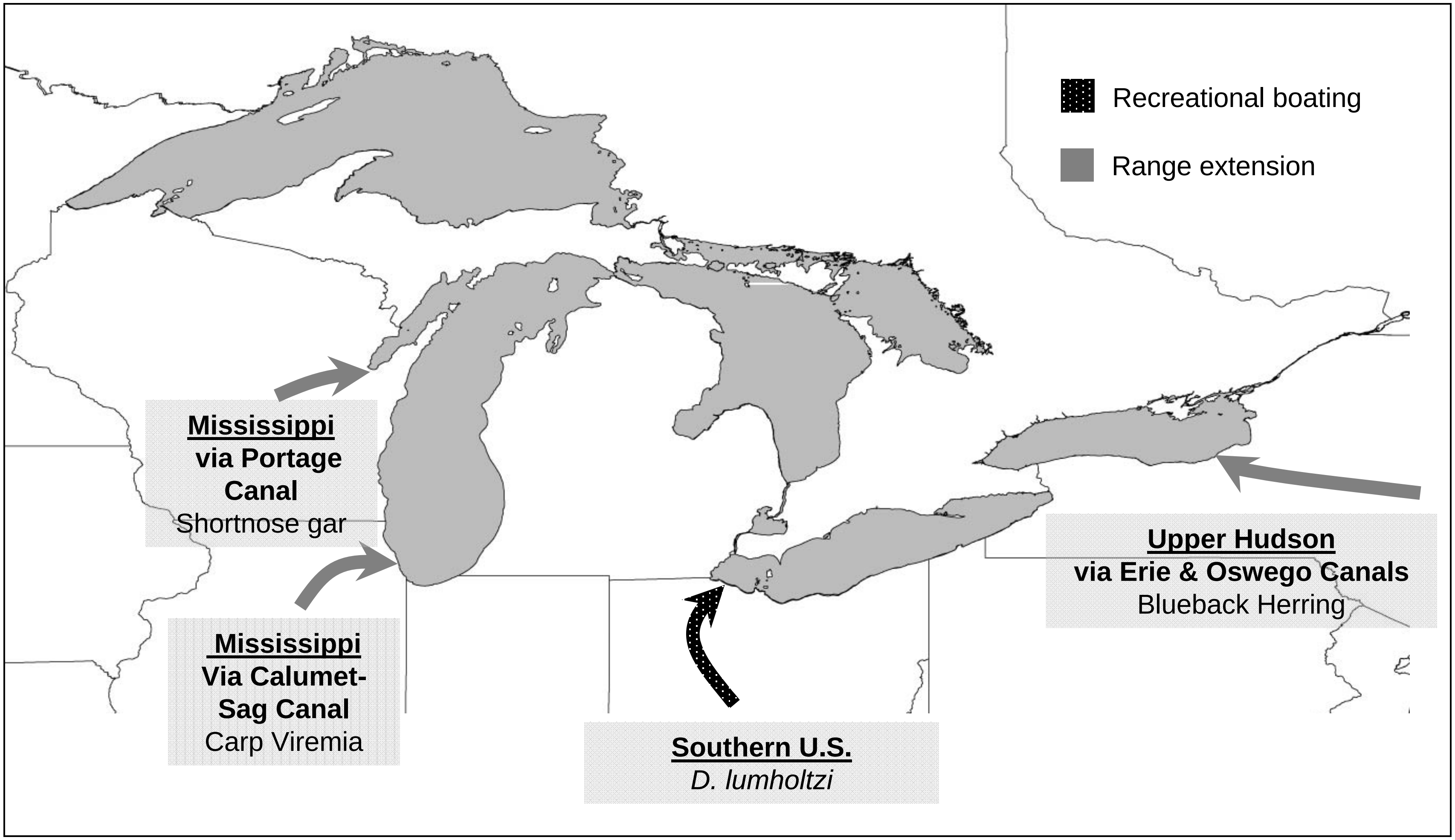

FIGURE 6 Canal and recreational boating pathways of invasion to the Great Lakes since 1959.

APPENDIX 1

Attribute criteria used to assess the likelihood that a species is non-indigenous to the Great Lakes (adapted from Chapman and Carlton, 1991, and Ricciardi, 2006).

1. The species appears in local regions where it was not previously found. Note: this criterion can be assessed only if the Great Lakes region was sufficiently sampled prior to discovery (*sensu* Chapman and Carlton, 1991).
2. The local range expands subsequent to its introduction. Note: this criterion can be assessed only if sufficient surveys were conducted after the introduction.
3. Its global distribution is associated with human mechanisms of dispersal.
4. Its distribution in the Great Lakes basin is restricted as compared with that of ecologically similar species that are native to the Great Lakes.
5. It has a widespread disjunct global distribution where some populations occur as scattered isolates on different continents.
6. It has an exotic evolutionary origin such that those species or groups exhibiting morphological and genetic affinities are distributed elsewhere in the world.