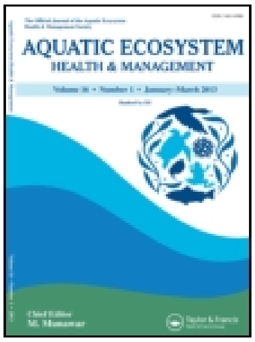

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Relative comparison and perspective on invasive species in the Laurentian and Swedish Great Lakes

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The Laurentian Great Lakes and the Swedish Great Lakes both have a long history of being invaded by non-native species, although the total number reported in the former system far exceeds that in the latter. Until about the 1980s, non-native species that had the greatest ecosystem and/or socioeconomic impacts in both systems were controlled, or their negative impacts ameliorated by management actions; most prominent of these species were the Sea Lamprey and Alewife in the Laurentian Great Lakes, and Crayfish plague in the Swedish Great Lakes. In the 1980s, a number of species native to the Ponto-Caspian region were introduced into the Laurentian Great Lakes via the ballast water of transoceanic ships, and these species had significant ecosystem impacts, could not be controlled by management actions, and changed the way these lake resources were managed. Similar introductions have not occurred in the Swedish Great Lakes, but many of the same species that have impacted the Laurentian Great Lakes are spreading in European systems and in the Baltic Sea, and thus could pose an invasion risk to lakes in Sweden. Based on experiences in the Laurentian Great Lakes, it seems prudent to conduct a thorough assessment of these invaders relative to potential vectors of introduction for the Swedish Great Lakes. Also, an assessment of long-term monitoring programs is in order. Long-term data provides baseline information of the ecosystem and tracks ecosystem responses if indeed an invader becomes established.

Keywords: non-native species, ballast-water introductions, large lake systems, socio-economic impacts

Introduction

Of the various threats to the ecosystem integrity of large freshwater lakes around the world, including nutrient enrichment, habitat modification, and contaminant inputs, perhaps the threat most likely to impact and modify entire lake ecosystems and cause significant socioeconomic hardships is the introduction of an invasive species. An invasive species can be defined as a species that is not native to any part of a given lake basin and, when introduced and established, has the potential to reach

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high densities, spread, and significantly impact ecosystem form and function. There are many documented instances where an invasive species was introduced into a large lake, disrupted ecosystem function, and shifted entire food webs with ensuing socioeconomic consequences (Hall and Mills, 2000; Kelley et al., 2009; Strayer, 2010).

While introductions of non-native species considered invasive have been ongoing since before the 19th century, the incidence and extent of these introductions has increased on a global scale in the past few decades. Reasons are varied, but one major reason is the expansion of world markets and global trade. Ships carrying goods between and within continents have become major vectors for the spread as these species via ship ballast water and/or hull biofouling (Holeck et al., 2004; Ricciardi, 2006). Also contributing to unintentional introductions have been the aquarium, bait, and water-garden trades (Rixon et al., 2005).

The Laurentian Great Lakes (Lakes Superior, Michigan, Huron, Erie and Ontario) have an extensive record of being invaded by non-native species. Since the 1840s, over 180 species have been identified in these lakes that were introduced from outside the system (Ricciardi, 2006; National Oceanic and Atmospheric Administration, 2013). While some species were intentionally introduced, most entered unintentionally, and often the vector for introduction was a direct result of infrastructures designed to facilitate trade and commerce. Examples of such infrastructures include the Erie Canal, which connected the Great Lakes to the Atlantic Ocean via the Hudson River (in 1830), the Welland Canal, which connected the Great Lakes to the Atlantic Ocean via the St. Lawrence River (in 1833), and the St. Lawrence Seaway, which allowed large, transoceanic ships from around the world to enter the lakes (in 1959). In particular, the rate of new introductions increased notably after the St. Lawrence Seaway was constructed. Of all documented non-native species in the Great Lakes, 45% became established after Seaway construction in 1959. Moreover, while 20% of new introductions could be attributed to ballast water release before 1959, this percentage increased to approximately 55% after 1959 (Kelly et al., 2009). Increased transoceanic ship traffic in the Laurentian Great Lakes not only led to increased inoculation rates and hence invasion risks, it also increased the probability that species from other continents would be introduced and become established. In particular, a high proportion of non-native species recently established in the Laurentian Great Lakes are native to the Ponto-Caspian region (Ricciardi and MacIsaac, 2000).

The Swedish Great Lakes (Lakes Mälaren, Hjälmaren, Vättern, and Vänern), on the other hand, have just 20 species that are considered to be non-native (Josefsson and Andersson, 2001). This number, however, is deceiving since it includes pathogens/parasites, invertebrates, fish, and mammals, but does not include algae, bacteria, viruses, and other "microscopic" organisms. Nonetheless, even if these microscopic organisms were not considered for the Laurentian Great Lakes, the number of non-native species in the Laurentian Great lakes would be 5 times greater than the number found in the Swedish Great Lakes (Table 1). Relative vectors of introduction are also different in the two systems. As noted, ballast

Table 1. Number of invasive species present in the Laurentian and Swedish Great Lakes as arranged by major taxanomic group. NI = Not included. Sources: GLANSIS (2013) for the Laurentian Great Lakes and Josefsson and Andersen (2001; see Table 1 in their paper) for the Swedish Great Lakes. Although Josefsson and Andersen (2001) stated that 20 non-native species occur in the Swedish Great Lakes, the taxonomic status of only 18 were provided.

Major Groups of Invasive Taxa	Laurentian Great Lakes	Swedish Great Lakes
Plants	61	5
Invertebrates	52	5
Fish	26	4
Algae (Pelagic and Benthic)	26	NI
Bacteria, Virus, Flukes, Fungi, etc.	20	2
Mammals	0	1
Birds	0	1

water is the primary vector for recent introductions of non-native species in the Laurentian Great Lakes, but this vector accounts for just 14% of introductions in the Swedish Great Lakes (Josefsson and Andersson, 2001). While both systems are open to transoceanic ship traffic (via the St. Lawrence Seaway for the Laurentian Great Lakes and via the Gotä Canal system for the Swedish Great Lakes), ships entering the Swedish Great Lakes are limited to a draft of <6 m, and ocean-ship cargo entering these lakes (i.e. Lake Vänern; http://www.mariterm.se/download/Rapporter/Vanerradet/Summary.pdf) is only about 15% that entering the Laurentian Great Lakes. More important vectors of introduction are the ornamental plant trade (26%) and intentional stocking (21%) (Josefsson and Andersson, 2001).

In this article, some invasive species that have had the greatest impacts on both the Laurentian and Swedish Great Lakes are reviewed. These species can be defined as those having at least several of the following consequences: Caused broad changes in ecosystem form and function, caused socio-economic hardships, or forced response measures by lake managers and policy-makers. Further, evidence is presented that shows the Laurentian Great Lakes are presently in a state of unprecedented change as a result of invasive species. While a similar situation does not presently exist in the Swedish Great Lakes, the current state of the Great Lakes does provide a perspective on how invasive species can disrupt entire lake ecosystems, force managers to reconsider management strategies, and potentially serve as a warning that similar state-changes can occur in large-lake systems open to ocean-going vessels such as the Swedish Great Lakes.

Invasive species in the Laurentian and Swedish Great Lakes

As noted, there are over 180 non-native species in the Laurentian Great Lakes, but aside from those intentionally introduced, very few of these species have had major impacts on ecosystem function, or had severe socioeconomic consequences. With an appreciation that any introduced species may cause direct or indirect changes, Mills et al. (1994) listed 13 non-native species (deemed nuisance species) that have had substantial impacts on resources of the Laurentian Great Lakes: *Petromyzon marinus* (Sea Lamprey), *Lythrum salicaria* (Purple Loosestrife), *Alosa pseudoharengus* (Alewife), *Oncorhynchus tshawytscha* (Chinook Salmon), *Oncorhynchus kisutch* (Coho Salmon), *Cyprinus* carpio (Common Carp), *Salmo trutta* (Brown Trout), *Aeromonas salmonicida* (Furunculosis), *Morone americana* (White Perch), *Myriophyllum spicatum* (Eurasian Milfoil), *Glugea hertwigi* (Protozoan), *Gymnocephalus cernuus* (Eurasian Ruffe) and *Dreissena polymorpha* (Zebra Mussel). Leach et al. (2002) added to this list *Neogobius meanostomus* (Round Goby) and *Osmerus mordax* (Rainbow Smelt), whereas this author would add *Dreissena rostriformis bugensis* (Quagga Mussel), *Bythotrephes longimanus* (Spiny Water Flea), and *Cercopagis pengoi* (Fishhook Water Flea). If the above list of species only focused on those that negatively impacted resources (directly or indirectly) as defined by water quality/water use and fish production over broad areas (nearshore and offshore in most of the lakes), then the number of species would be narrowed considerably. Based on these criteria, it could be argued that the list would then include only Sea Lamprey, Alewife and Dreissenid Mussels. The Sea Lamprey was first reported in Lake Ontario in the 1830s but was confined to this lake until early in the 20th century. At that time, improvements in the Welland Canal allowed this species to spread upstream to all the lakes in the 1930s and 1940s. This fish parasite decimated populations of important commercial and sport fish such as Lake Trout, Lake Whitefish, Chub, and Lake Herring. The decrease in Lake Trout, which was the top piscivore in the Great Lakes at the time, allowed populations of another invader, the Alewife, to increase dramatically. Similar to the Sea Lamprey, the planktivorous Alewife was originally confined to Lake Ontario but gained access to the rest of the lakes when the Welland Canal was improved. It spread to all the lakes by the 1950s and, with the loss of major fish predators because of the Sea Lamprey, Alewife populations increased to nuisance levels in the 1960s. Besides changing the structure of the lower food web and complicating interpretations of water quality problems associated with eutrophication (Kitchell et al., 1988), annual die-offs of Alewife littered beaches with decaying fish.

Usually when an invasive species becomes established in a large lake ecosystem, there are few or no management options for control.

However, in the case of Sea Lamprey and Alewife, lake managers were able to successfully control populations and, in the specific case for Alewife, were able to provide socio-economic benefits from control measures. For Sea Lamprey, a chemical biocide that specifically targeted this species was discovered in the 1950s and, ever since, this biocide is routinely applied to streams where adults spawn and juveniles spend time in developmental stages. Other control methods have since been developed and are now being used (i.e. weirs, male sterilization, etc.). With Sea Lamprey populations under control, Pacific Salmon (*Oncorhynchus* spp.) were intentionally introduced in the late 1960s to serve as a major predator of Alewife. Subsequently, Salmon stocking programs have kept Alewife populations in check and at the same time have provided a popular sport fishery.

In the late 1980s, Dreissenid Mussels (Zebra Mussels and Quagga Mussels) were introduced into the Laurentian Great Lakes via ballast water of transoceanic ships. The spread of both species across the lakes was rapid; Zebra Mussels were found in all five lakes by 1990, and Quagga Mussels were found in all lakes by 2005. Zebra Mussels became most abundant in nearshore regions within a few years of establishment, but Quagga Mussels have now displaced Zebra Mussels in the nearshore, and are proliferating in deep, offshore regions where Zebra Mussels were rarely found (Mills et al., 1999; Nalepa et al., 2010). Except for Lake Superior, Dreissenids have now colonized most depths in all the lakes.

While other invasive species in the Laurentian Great Lakes have caused limited impacts, had few socioeconomic consequences, or could be controlled through management actions (i.e. Sea Lamprey, Alewife), the introduction and establishment of Dreissenid Mussels has caused ecological changes and socio-economic hardships that are unprecedented. Dreissenids are efficient filter-feeders and, because of high abundances, high filtration rates, and broad distributions, they have directly or indirectly altered most aspects of ecosystem function (Vanderploeg et al., 2002). Mussels have changed pathways of nutrient and energy flow (Hecky et al., 2004), caused declines of native species (Nalepa et al., 1998, 2009; Pothoven et al., 2010), and created conditions that promote growth of nuisance algae such as the toxic cyanophyte *Microcystis* (Vanderploeg et al., 2001) and *Cladophora* (Auer et al., 2010). By filtering seston from the water column, Dreissenids have diminished food available for both pelagic and benthic invertebrates. This has led to a cascading effect, and fish dependent on these invertebrates have declined or exhibited a loss of condition (Mohr and Nalepa, 2005; Hondorp et al., 2005; Riley et al., 2008). Preyfish populations, including Alewife, have reached such low levels in Lakes Huron and Michigan that salmon stocking rates have been reduced.

Certainly, not all invertebrates and fish species have been negatively affected by Dreissenids. For instance, some benthic invertebrates have benefitted from increased amounts of detrital food on the bottom in the form of mussel biodeposits, and some fish species in nearshore areas are doing well (Vanderploeg et al., 2002). Yet it is generally believed that the capacity of some of the lakes to support fish production has been greatly diminished. In essence, energy that once efficiently passed from lower to upper trophic levels is now being diverted to support large standing stocks of Dreissenids (Nalepa et al., 2009). Further, it has been estimated that 37% of carbon assimilated by Dreissenids is used for shell production (Chase and Bailey, 1999). Shells can comprise up to 80% of Dreissenid mass (Nalepa et al., 2009) but have no energetic value and therefore represent energy lost to upper trophic levels. Although a few studies indicate at least some energy may be transferred to upper trophic levels (Madenjian et al., 2010), overall, Dreissenid standing stocks represent an energy sink. As an indication that the capacity of the Great Lakes to support fish production has decreased, a recent study found that non-native species introduced via ship-borne ballast water have caused a median annual loss of 5.3 million (U.S. $) to the commercial fishery, and 106 million to the sport fishery (Rothlisberger et al., 2012). While this study did not provide a breakdown by species, Dreissenids were the likely cause of most of these losses.

In the Swedish Great lakes, the only invasive species to cause ecological changes and have socio-economic impacts has been the crayfish plague, *Aphanomyces astaci* (Josefsson and Andersson, 2001). This fungus was likely introduced into Europe in 1860 via ballast water, and the first record of this species in Sweden was in Lake Mälaren in 1907. The crayfish plague decimated populations of the Noble Crayfish (*Astacus astacus*), which is an important native species of considerable economic and cultural value as it is commercially harvested and widely used as a food item. It is estimated that Noble Crayfish populations declined by 95% after the crayfish plague was introduced (Bohman and Edsman, 2011). To compensate for the loss of the Noble Crayfish, a program to stock Signal Crayfish (*Pacifastacus leniusculus*), a native to western North America, was initiated in the 1960s to basically restore a crayfish fishery in regions where the Noble Crayfish was lost. The model basically followed the successful introduction of Signal Crayfish to Lake Tahoe between 1895 and 1916. Presently, the status of Signal Crayfish populations in the Swedish Great Lakes is still evolving. For instance, the Signal Crayfish was introduced into Lake Vänern in 1969, but it was not until 2009 that populations reached a state where a commercial harvest was possible (Andersson et al., 2012). Although the Signal Crayfish is resistant to the crayfish plague, it is a carrier of this fungus, and introductions are strictly regulated to protect remnant populations of the Noble Crayfish.

One invasive species that has been long established in both Lakes Vänern and Mälaren but has recently increased (in the mid-2000s), is the Chinese Mitten Crab (*Eriocheir sinensis)* (Drotz et al., 2010, 2012). This species may reach great abundances and can outcompete native species, clog water intakes, and cause bank erosion through burrowing activities. It has been suggested that the increase of Mitten Crab in Lake Vänern is a result of ballast water discharges from ships entering the lake through the Gota River (Drotz et al., 2010). Although several Chinese Mitten Crabs have been reported from the Great Lakes, presumably introduced by the ballast water of transoceanic ships (Nepsky and Leach, 1973), a reproducing population has never become established.

Given the dramatic changes that Dreissenid Mussels have caused in the Laurentian Great Lakes, the status of Dreissenids in the Swedish Great Lakes is worth noting. The Zebra Mussel was first reported in Lake Mälaren in 1926, and is now mostly found in low numbers in the northern and eastern portions of this lake, and in the western portion of Lake Häjlmaren (Josefsson and Andersson, 2001; Hallstan et al., 2010). While present in these two lakes, it is not abundant enough to cause problems as severe as in the Laurentian Great Lakes. Most likely, population growth is limited by low calcium levels, although magnesium seems a better predictor of Zebra Mussel distributions throughout Sweden (Hallstan et al., 2010). In general, Zebra Mussel populations are stressed/limited when calcium concentrations are <15 mg l^{-1} (Cohen and Weinstein, 2001). In the Swedish Great Lakes, calcium concentrations are <10 mg l^{-1} and, while Zebra Mussels may survive at these concentrations, they seemingly cannot reach densities that would create severe ecosystem disruptions. This seems analogous to the situation found in Lake Superior. While Zebra Mussels are present in this lake, they are mostly confined to the western end (Duluth Harbor region) where calcium concentrations are higher than the rest of the lake (13–23 mg l^{-1} vs. <12 mg l^{-1}). Quagga Mussels have recently been found in Lake Superior (Grigorovich et al., 2008) but have not been reported from the Swedish Great Lakes. While distributions of Quagga Mussels will likely be different than Zebra Mussels in these two systems (i.e. occur at deeper depths), calcium requirements are generally similar to those for Zebra Mussels and hence, like Zebra Mussels, would not attain high enough densities in the Swedish Great Lakes to disrupt ecosystems.

Potential new invaders in the Laurentian and Swedish Great Lakes

The most recent and disruptive invaders in the Laurentian Great Lakes originated from the Ponto-Caspian region and were introduced via the ballast water of transoceanic ships (Ricciardi 2006). Besides those species already introduced, Ricciardi and Rasmussen (1998) identified 17 other species that were native to the Ponto-Caspian region and had high potential for being introduced into the Laurentian Great Lakes via ballast water. Indeed, one of these species, *Hemimysis anomala*, has already become established. These 17 species had an invasive history in Eurasia and possessed life habits and/or morphological traits that characterized them as invasion threats. While a detailed assessment of species that could potentially be introduced into the Swedish Great Lakes has not been performed, a similar assessment was made for Finnish lakes (Pienimäki and Leppäkoski, 2004). Species considered an invasion risk for lakes in Finland can also be considered an invasion risk for the Swedish Great Lakes since: (1) both systems are open to the Baltic Sea for cargo-carrying ships (Gottä Canal in Sweden, Saimaa Canal in Finland); (2) both systems have similar geology and hence generally similar ionic composition of waters (i.e. low calcium content); (3) lakes in the two countries have a similar invasion history; that is, as in Sweden there are about 20 non-native species established in Finland with the most significant invader being the crayfish plague. Species in the study by Pienimäki and Leppäkoski (2004) were categorized by relative probability of being introduced. Of the total number listed, 6 species were considered to have a high probability of being introduced into Finnish lakes: *Anguilla crassus* (Nematode), *Potamothrix heschui* (Oligochaete), *Potamothrix vejdovski* (Oligochaete), *Hemimysis anomala* (Bloody Red Shrimp), *Cercopagis pengoi* (Spiny Water Flea) and *Gmelinoides fasciatus* (Amphipod). All species are invertebrates, and the authors deemed ballast water as the likely vector for introduction into Finland. Of these, Cer*copagis* and *Gmelinoides* can have substantial ecological impacts if introduced (Vanderploeg et al., 2002; Berezina and Strelnikova, 2010). Another 10 species in the study by Pienimäki and Leppäkoski (2004) were considered to have an intermediate probability of introduction. Two have already been introduced into the Laurentian Great Lakes in the 1990s: *Neogobius meanostomus* (Round Goby) and *Chaetogammarus ischnus* (Amphipod). As noted, the Round Goby has had substantial ecological impacts in nearshore areas (Vanderploeg et al., 2002). It is noteworthy that two of the species considered to have a low probability of introduction into Finland, the Quagga Mussel and *Corbicula fluminea* (Asian Clam), are currently spreading in both Eurasia and North America and are having major ecological and socio-economic impacts. While naturally low calcium levels in lakes of both Sweden and Finland would likely prevent the Quagga Mussel from becoming abundant, the Asian Clam does well at low calcium levels (calcium threshold of 6 mg l^{-1}; Whittman et al., 2008). For example, this species is rapidly increasing and causing ecologic changes in Lake Tahoe in the western U.S. (Wittman et al., 2008). Calcium levels in Lake Tahoe (mean = 9 mg l^{-1}) are similar to those found in the Swedish Great Lakes. In addition, there is concern that locally high levels of calcium associated within Asian Clam beds may promote the establishment of Quagga Mussels (Whittman et al., 2008).

While certain species can be targeted as an invasion risk, it is far more difficult to predict impacts of an invader on the recipient ecosystem (Ricciardi and MacIsaac, 2011). For instance, although extreme densities achieved by Dreissenids (particularly Quagga Mussels) in the Laurentian Great Lakes were perhaps somewhat unexpected, it could have been predicted that they would do well in these lakes if introduced. They had a history of spread in Eurasia, had colonized various habitats (rivers, lakes, canals, etc.), possessed life habits of a r-strategist (high reproductive capacity, short time to maturity, etc.), and had a planktonic larval stage and a byssate adult stage that facilitated spread. While some ecosystem impacts were indeed predictable (increased water clarity, decrease in chlorophyll), others were totally unforeseen. Examples of the latter include the near total loss of the native amphipod *Diporeia* (Nalepa et al., 2009), blooms of the toxic cyanophyte *Microcystis* (Vanderpleog et al., 2001), and outbreaks of type-E botulism in waterfowl (Pérez-Fuentetaja et al., 2011). Also unexpected was the disappearance of the spring diatom bloom in deep, offshore waters (Fahnenstiel et al., 2010). The point is that while some species can be considered an invasion risk, ecosystems are complex and ultimate impacts of an invader can often be unexpected.

A lesson from the Laurentian Great Lakes

In the past, managers of the Laurentian and Swedish Great Lakes have faced similar problems as related to anthropogenic stressors. For instance, in the 1950s and 1960s, nutrient enrichment was a problem in both systems, and some lakes (particularly Lake Erie and Lake Mälaren) showed signs of advanced eutrophication. When phosphorus loads and algal biomass (chlorophyll) in the 1960s were examined and compared across individual lakes in the two lake systems, the relationship was highly significant (see Figure 1 in Wilander and Persson, 2001). Hence, it could be predicted that responses to nutrient reductions would be similar. Nutrient abatement programs were initiated in the 1970s and indeed reductions in nuisance algal blooms and improvements in water quality occurred in both systems (Evans et al., 2011; Willén 2001a,b). Another common stressor in both systems was the accumulation of persistent organic contaminants in the 1950s and 1960s. These contaminants were banned in the 1970s which led to lower levels in many species of fish (Lindell et al., 2001).

In terms of introductions of non-native species as a stressor, historically both systems have been subjected to invaders that had ecosystem impacts and socioeconomic consequences–Sea Lamprey and alewifc in the Laurentian Great lakes, and crayfish plague in the Swedish Great lakes. For the most part, these invaders were subject to managerial control, or negative consequences were ameliorated with management actions. However, the role of invasive species in the two systems diverged dramatically beginning in the 1980s. In the Laurentian Great Lakes, a number of invasive species introduced via the ballast water of ships (i.e. Dreissenid Mussels, Round Goby, Spiny Water Flea) have permanently changed the character of the ecosystem, while similar introductions over the same time period were not apparent in the Swedish Great Lakes. Unlike past invaders, these recent invaders, and particularly Dreissenids, cannot be controlled by management actions, and hence these species have added a permanent level of complexity in the way managers must deal with other issues such as nutrient control and fish sustainability. With invasive species now being the primary driver of change in the Laurentian Great Lakes, ecosystem responses to management actions are less predictable; that is, responses are more subject to density-dependent, feed-back loops involving the invader. A good example is the relationship between phosphorus loads and phytoplankton biomass (chlorophyll). As noted, this close linear relationship was the basis for abatement programs in the 1970s to reduce loads and reverse the negative effects of eutrophication. After Dreissenids invaded, this relationship is no longer valid (Nicholls et al., 2001; Evans et al., 2011), and any new paradigm for nutrient management must consider the dynamics of Dreissenid populations.

Control of recent invaders such as Dreissenid Mussels in the Laurentian Great Lakes is not a possibility, therefore the best management actions must focus on preventing or minimizing further unwanted introductions. In 1993, regulations were enacted that required ballasted ships to exchange their water in the open ocean before entry into the Great Lakes, and beginning in 2006 ships with only residual ballast water were required to do the same. While not without risk (Bailey et al., 2011), these regulations have been generally successful as no new introductions via ballast water have been documented since 2006. No doubt the disruptive role of species already introduced have partly motivated efforts to keep the Asian carp (Cyprinidae) from entering the Great Lakes via a connective canal that links the Mississippi River basin to Lake Michigan (Rasmussen et al., 2011).

Based on recent developments in the Laurentian Great Lakes, it seems that risks associated with unintentional introductions should be closely examined for the Swedish Great Lakes. While all vectors relative to probable invaders should be assessed, including the aquarium and garden pond industry (Adebayo et al., 2011), vectors associated with shipping activities need to be closely examined. Historically, the ballast-water vector has not been as important as other vectors as a means of new introductions in the Swedish Great Lakes. However, nuisance invasive species already introduced into the Laurentian Great Lakes via ballast water are spreading in the Baltic Sea and pose an invasion risk for the Swedish Great Lakes (Leppäkoski et al., 2002). Early warnings of introductions via ballast water were provided for the Laurentian Great Lakes, and these warnings of impending introductions soon became realities. Similar warnings are now being given for the Swedish Great Lakes (Degerman et al., 2001).

As argued by Kelly et al. (2009), although systematic studies/risk assessments of all likely vectors and pathways are a key element of a comprehensive program to prevent unplanned invasions, such efforts cannot be expected to prevent all invasions. Monitoring programs in the Swedish Great Lakes should be evaluated for consistency and completeness so that all important ecosystem components are assessed at appropriate temporal and spatial scales in case a nuisance species indeed becomes established. One key aspect of determining ecosystem impacts of an invader is having dependable long-term data. Such data provides baseline information of the ecosystem prior to any introduction, and subsequently tracks ecosystem responses after an introduction (Nalepa et al., 1998; Riley et al., 2008; Fahnenstiel et al., 2010). Further, such data is valuable in assessing impacts relative to other stressors (Evans et al., 2011).

Finally, perhaps the single most important lesson from the Laurentian Great Lakes as relevant to the Swedish Great Lakes is that, even though both lake systems are large, even a single invasive species has the potential to permanently change the way these lake ecosystems are managed.

Conclusions

In conclusion, both the Laurentian and the Swedish Great Lakes have been subjected to invasive species that have caused significant socio-economic hardships. With increased global trade and the expansion of world markets, both of these lake systems, because they are open to trans-oceanic shipping, remain at risk for further invasions. The Laurentian Great Lakes have a far greater number of invasive species compared to the Swedish Great Lakes, yet many of the same species that have impacted the former system are spreading through the Baltic region and hence poise a risk of being introduced into the latter system. In the Laurentian Great Lakes, recent regulations have reduced invasion risk. For the Swedish Great Lakes, a necessary first step for the prevention of new introductions should include a thorough analysis of pathways and vectors relative to the species most likely to invade.

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