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The future of species invasions in the Great Lakes-St. Lawrence River basin

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ABSTRACT

No other freshwater system contains as many non-native species or has been invaded as frequently as the Great Lakes-St. Lawrence River basin. Over 180 non-native species have become established in the basin within the past two centuries. Collectively, these invasions have altered biodiversity, habitat structure, productivity, water quality, contaminant cycling and ecosystem services. The composition and rate of discovery of invaders are correlated with changes in dominant vectors, such as transoceanic shipping. We review the invasion history of the basin and identify future invasion threats by considering trends and potential scenarios in changing vectors and pathways. Whereas most non-native species discovered since the opening of the St. Lawrence Seaway in 1959 were attributable to ballast water discharge from transoceanic vessels, recent regulations have apparently reduced the threat of this vector. Nevertheless, non-native species may continue to be introduced through poorly-regulated vectors, particularly those associated with trade in live organisms. The spread and impact of current and future invaders are expected to be exacerbated by interactions with other anthropogenic stressors that are increasing in frequency and spatial extent. Most notably, the continued warming of surface waters of the Great Lakes basin will lift thermal barriers to invasions by warm-water taxa. Contrary to any perception that the "worst is over" (i.e. most harmful invasions have already occurred), the basin remains vulnerable to further ecological and economic disruptions from non-native species.

Introduction

The Great Lakes-St. Lawrence River basin (hereafter, the Great Lakes basin) is the world's most invaded freshwater system (Ricciardi, 2006). Non-native species have been introduced to the basin through numerous vectors and pathways that operate on multiple spatial scales and are mediated by environmental and socioeconomic factors (Mills et al., 1993, 1994; Ricciardi, 2006). The relative influence of a given vector or pathway evolves as new regulations are implemented and the recipient ecosystem is altered by various stressors (Williams et al., 2013). Therefore, a strategy to address the scope of challenges presented by invasive species (defined here as those non-native species that spread aggressively and cause undesirable impacts) must involve managing vectors, developing risk assessments, monitoring for new non-native populations, and implementing appropriate policy — all in the context of shifting patterns of invasion risk. To this end, resource managers require knowledge of changes in vector activity, the efficacy of current regulations and control strategies, and future invasion threats.

Valuable predictive information can be derived from an analysis of invasion history and vector activity within the Great Lakes basin. Here, we examine patterns of species introductions in the basin over the past 50 years (1963–2013), with consideration given to other drivers including climate change and legislative actions. We then hypothesize three scenarios for the basin over the next 50 years (2013–2063), based on 1) the effectiveness of different governance strategies that have been, or may be, adopted for regulating currently active vectors

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and pathways, and 2) projected rates of warming of surface waters. Under each scenario, we identify probable future invaders entering the Great Lakes basin using a simple algorithm.

A long history of species invasions in the Great Lakes Basin

Over 180 non-native species have been recorded established in the Great Lakes basin within the past two centuries (GLANSIS, 2014; Mills et al., 1993; Ricciardi, 2006). About 40% of these species were introduced via shipping (i.e., ballast water release, dumping of solid ballast, and hull fouling). Ship-mediated invasions have grown in frequency over the past 50 years (Fig. 1), concomitantly with increased visits and greater volumes of ballast water discharged by transoceanic vessels entering the basin since the opening of the St. Lawrence Seaway in 1959 (Ricciardi, 2006). In contrast, hull fouling associated with international shipping has played an unimportant role (likely responsible for only two species introductions – both involving marine algae; Ricciardi, 2006), because of the lack of environmental match between transported species and recipient freshwater habitats (Sylvester and MacIsaac, 2010). Another source of introductions that has grown in recent decades are vectors involving 'live trade' – the commercial importation of live organisms (e.g., ornamental plants, aquarium pets, baitfish, fish and invertebrates for food markets, organisms for scientific research and teaching). Most non-native fish present in the Great Lakes basin were delivered to the region through commercial sale as food, live bait, or stocking for angling and aquaculture (Mandrak and Cudmore, 2010). Some plant and animal invasions have apparently resulted from unauthorized aquarium releases (Mills et al., 1993), which are frequent and involve a diverse range of taxa (Cohen et al., 2007; Leach, 2003). By comparison with shipping and live trade vectors, canals have become less influential as a source of primary introductions in the latter part of the 20th century (Fig. 1), but remain an important vector of secondary spread for species already established in the basin, and may also play an important role in facilitating new invasions mediated by climate change (see *Canals and recreational boating*).

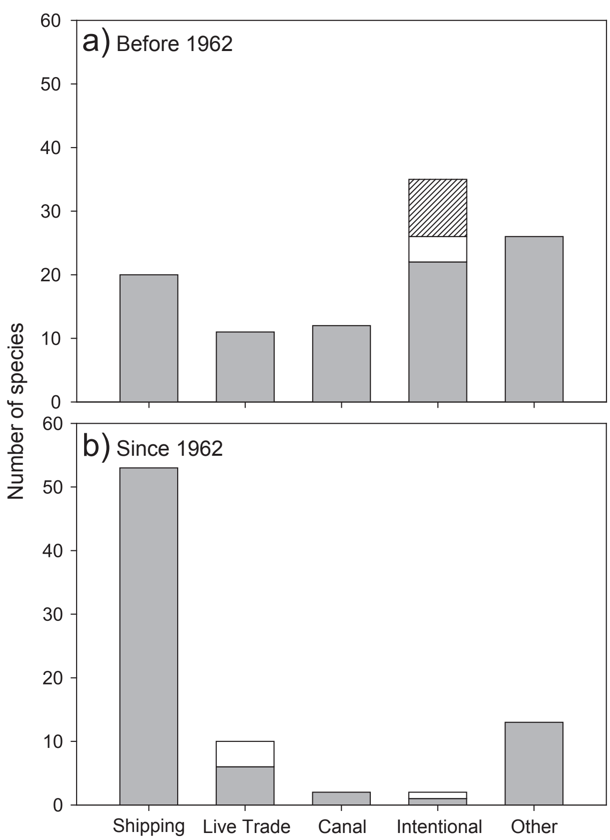

Fig. 1. The number of established non-native species in the Great Lakes distinguished by vector of entry, before and after 1962. 'Shipping' constitutes all activities related to this vector (ballast water, solid ballast, hull fouling), 'Live Trade' includes aquarium/ornamental/pet releases (gray) and bait fish releases (white), whereas 'Intentional' refers to stocked fish (gray) and cultivated plants (white), as well as other methods of intentional release (crosshatched). Data are from Mills et al. (1993), Ricciardi (2006) and GLANSIS (2014).

Nearly half of all non-native species recorded as established in the Great Lakes basin are Eurasian, and most of these were introduced either intentionally or through shipping vectors (Fig. 2). In recent decades, ship-mediated invasions have often involved Ponto-Caspian species — i.e. those originating from the freshwater and brackish margins of the Azov, Black, and Caspian Seas (Ricciardi and MacIsaac, 2000). Invasions associated with live trade most often involve Asian and Eurasian species. Species from a variety of regions have invaded the Great Lakes basin through canals, but the majority is indigenous to the Atlantic and Mississippi drainages (Fig. 2).

Since the opening of the Seaway, one new established non-native species has been discovered every 8 months (82 species since 1960), or 1.52/year, on average (Ricciardi, 2006; Ricciardi, unpubl. data). This well exceeds rates recorded for the Rhine River (0.56/yr; Leuven et al., 2009), the Hudson River (0.66/yr; Mills et al., 1997), Lake Champlain (0.68/yr; Marsden and Hauser, 2009), the Columbia River (0.84/yr; Sytsma et al., 2004) and the Thames River (1.04/yr; Jackson and Grey, 2012). The number of new discoveries peaked between 1959 and 1993, which was a period characterized both by high shipping frequency and unregulated ballast water release. Ballast water carried by ships arriving from foreign ports was regulated for the first time in 1993 and more comprehensively in 2006 (GC, 2006). Virtually all ships entering the seaway since 2008 were inspected for compliance (GLSBWWG, 2014). Perhaps as a result, the number of non-native species discovered in the 2000s is the lowest for any decade since the Second World War. Indeed, no new invasions attributable to shipping have been reported since 2006 (Bailey et al., 2011).

Impacts of species invasions in the Great Lakes basin

The impacts of most non-native species in the Great Lakes basin are poorly known (Mills et al., 1993). Nevertheless, non-native species have been shown to be a driving force of ecological change within the basin, causing native biodiversity declines, food web transformations, altered nutrient and contaminant cycling, and shifts in productivity (Hogan et al., 2007; Mills et al., 1993; Ricciardi, 2001; Vanderploeg et al., 2002). A prominent example is the sea lamprey *Petromyzon marinus*, which spread quickly throughout the Great Lakes basin and contributed to the collapse of native lake trout *Salvelinus namaycush* populations in the late 1940s and 1950s (Mills et al., 1993). Within two decades, the annual commercial yield of lake trout was reduced from 15 million pounds to only 300 000 pounds in the upper Great Lakes, whereas in the lower Great Lakes the lake trout fishery disappeared by 1960 (GLFC, 2010). The loss of this top predator facilitated the expansion of populations of alewife *Alosa pseudoharengus* in the 1950s and 1960s (Ricciardi, 2001), which provoked the declines of native planktivorous fishes (Mills et al., 1994).

High-impact invaders appear to have become more frequent in recent decades (Table 1), but it is not clear whether this trend reflects a reduction in the resilience of ecosystems in the Great Lakes basin or an artifact of better detection methods and increased scientific attention to ecological change. Nearly 20% of all invading species discovered over the past 50 years have had significant impacts on native species populations (Ricciardi, unpubl. data). For example, the Eurasian ruffe *Gymnocephalus cernuus* and the round goby *Neogobius melanostomus* have displaced native fishes (Balshine et al., 2005; Lauer et al., 2004), and predatory waterfleas *Bythotrephes longimanus* and *Cercopagis pengoi* have drastically altered zooplankton communities (Barbiero and Tuchman, 2004a). A variety of introduced pathogens have caused

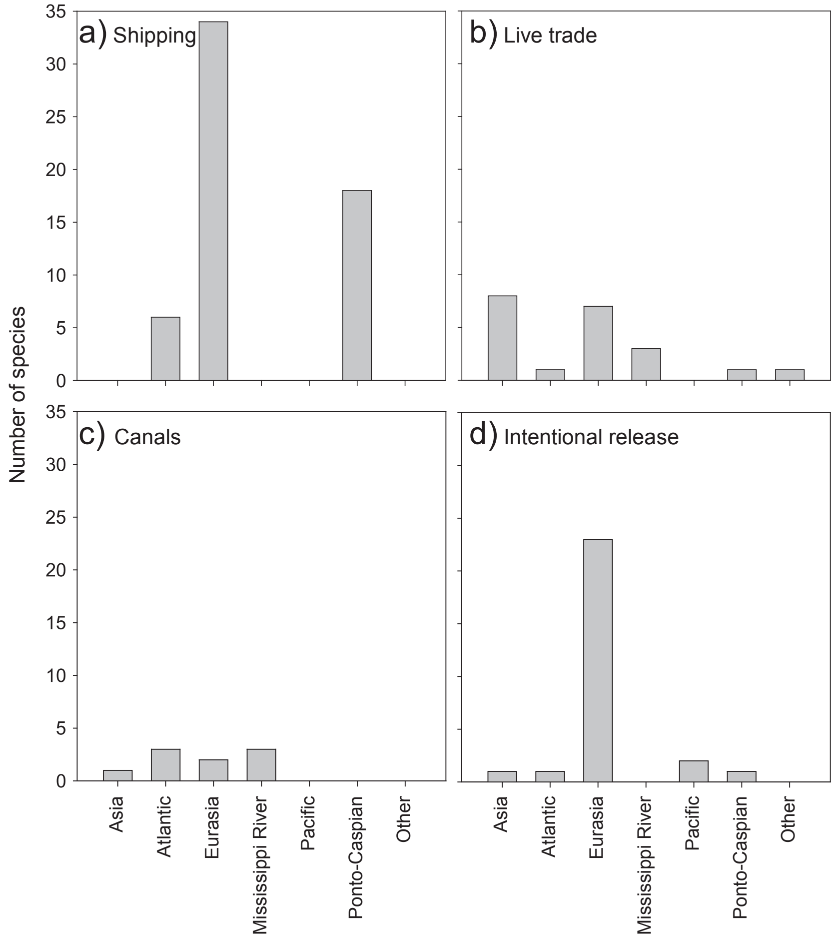

Fig. 2. The number of established, aquatic non-native species in the Great Lakes basin distinguished by vector and location of origin. 'Shipping' constitutes all activities related to shipping (ballast water, solid ballast, hull fouling), 'Live Trade' refers to all activities leading to the unintended release of species through live fish trade, live baitfish release, aquarium release and pet release. 'Intentional' refers to stocked and planted species. Data are from Mills et al. (1993), Ricciardi (2006) and GLANSIS (2014).

mass die-offs of fishes throughout the Great Lakes basin (Table 1), and more were discovered from 2000 to 2005 than in all previous years combined. Myriad, conspicuous, ecosystem-level impacts were associated with the establishment of dense populations of dreissenid mussels (including the zebra mussel *Dreissena polymorpha*, and the quagga mussel *D. rostriformis bugensis*), whose filter-feeding activities have dramatically increased water clarity, reduced phytoplankton biomass, transformed benthic and pelagic invertebrate communities, caused diet shifts in native fishes, altered nutrient and contaminant cycling, and may have also increased the frequency of blue-green algal blooms and botulism outbreaks in fish and waterfowl (Barbiero and Tuchman, 2004b; McNickle et al., 2006; Rennie et al., 2009; Vanderploeg et al., 2002; Yule et al., 2006).

The societal costs of these impacts are difficult to measure, but the economy of the Great Lakes basin has undoubtedly suffered damage as a result of ever-accumulating invasions. This damage includes a loss of revenue in sport and commercial fisheries, recreation and tourism, costs of disruptions to municipal water supplies, industrial facilities and power plants, and the chronic costs of control measures (Rosaen et al., 2012). In a recent study of the impacts of ship-borne invasive species in US waters of the Great Lakes basin (Rothlisberger et al., 2012), median damages aggregated across multiple ecosystem services were estimated to be at least $138 M per year, and maximum damages as high as $800 M annually for the sportfishing industry alone. Investment into prevention and early eradication would likely incur a substantively lower cost than the damage caused by unimpeded invasions (Leung et al., 2002; Vander Zanden et al., 2010).

Regulations and measures to prevent and control invasions

In response to a burgeoning number of ship-borne invaders discovered in the basin, the Canadian and US governments developed regulations requiring transoceanic ships destined for Great Lakes ports to exchange the water in their ballast tanks with seawater obtained 200 nautical miles offshore, prior to entering the seaway. It was expected that freshwater organisms in the ballast tanks would be flushed out or killed by exposure to the high salinity level (>30‰) of the oceanic water, whereas marine organisms taken up in the open ocean would not survive in the Great Lakes basin. This procedure, termed ballast water exchange (BWE), was implemented as a voluntary measure by Canada and the US in 1989 and 1990, respectively. In 1993, BWE became mandatory for all ships that enter the seaway declaring ballast on board (Locke et al., 1993). Subsequent discoveries of new invaders suggested that BWE regulations were inadequate (Ricciardi, 2006; Ricciardi and MacIsaac, 2008; but see Costello et al., 2007). Nearly 90% of ships that entered in the 1990s declared no ballast on board, and thus were not subject to mandatory BWE, even though their ballast tanks contained residual sediments and water (Holeck et al., 2004). Regulations adopted by Canada in 2006 and the US in 2008 required ships with residual ballast to flush their tanks with seawater, through sequential or flow-through exchanges, in order to achieve a minimum salinity of 30‰ (GC, 2006). Furthermore, as of December 2013, the US Environmental Protection Agency has issued a new five-year Vessel General Permit that requires all cargo ships entering US waters of the Great Lakes and the St Lawrence Seaway to carry equipment designed

Table 1
Non-native aquatic species that have had demonstrable community-level and ecosystem-level impacts in the Great Lakes basin. Data from Mills et al. (1993), Ricciardi (2006) and GLANSIS (2014). * = pathogen.

Invasive Species	Year discovered
Sea lamprey (*Petromyzon marinus*)	1835
Purple loosestrife (*Lythrum salicaria*)	1869
Alewife (*Alosa pseudoharengus*)	1873
Chinook salmon (*Oncorhynchus tshawytscha*)	1873
Rainbow trout (*Oncorhynchus mykiss*)	1876
Common carp (*Cyprinus carpio*)	1879
Brown trout (*Salmo trutta*)	1883
Furunculosis (*Aeromonas salmonicida*)*	1902
Flowering rush (*Butomus umbellatus*)	1905
Rainbow smelt (*Osmerus mordax*)	1912
Coho salmon (*Oncorhynchus kisutch*)	1933
White perch (*Morone americana*)	1950
Eurasia milfoil (*Myriophyllum spicatum*)	1952
Glugea (*Glugea hertwigi*)*	1960
Whirling disease (*Myxobolus cerebralis*)*	1968
Bacterial Kidney Disease (*Renibacterium salmoninarum*)*	1975
Spiny waterflea (*Bythotrephes longimanus*)	1982
Eurasian ruffe (*Gymnocephalus cernuus*)	1986
Zebra mussel (*Dreissena polymorpha*)	1988
Quagga mussel (*Dreissena bugensis*)	1989
Round goby (*Neogobius melanostomus*)	1990
Ponto-Caspian amphipod (*Echinogammarus ischnus*)	1994
Fish-hook waterflea (*Cercopagis pengoi*)	1998
Microsporidean (*Heterosporis* sp.)*	2000
Spring Viraemia of Carp (*Rhabdovirus carpio*)*	2001
Muskie pox (*Piscirickettsia* cf. *salmonis*)*	2002
Largemouth Bass Virus (*Ranavirus* sp.)*	2002
Viral Hemorrhagic Septicemia (*Novorhabdovirus* sp.)*	2005

to limit the number of organisms occurring in a cubic meter of ballast water. All ships are expected to be retrofitted with such equipment by 2018. Vessels in violation can have ballast water discharge permission revoked under the US Clean Water Act. Similarly, in 2012 the US Coast Guard mandated the installation of certain technologies (Ballast Water Management Systems) to satisfy treatment standards for live organisms in ballast water prior to discharge.

With the exception of BWE, no regulations of aquatic invasive species exist at the bi-national level, and this gap has likely hindered effective prevention. The bulk of legislation to prevent new species introductions currently resides with individual state and provincial governments (Thomas et al., 2009). The Great Lakes Water Quality Agreement (GLWQA, 2012; annex 5 & 6) includes consideration of invasive species management, which directs Canada and the US to create watch lists, identify priority locations, develop monitoring protocols and management strategies that include the establishment of barriers, and develop bi-national response mechanisms.

The need for a coordinated bi-national response is particularly exemplified by live trade, which is expected to become a significant vector of future invasions (Keller and Lodge, 2007; Rixon et al., 2005). Regulations concerning the commercial importation of living organisms exist in all states and provinces that border the Great Lakes basin (Table 2), but vary in their degree of control across borders, generating a "weakest-link" problem that may result in the spread of non-native species between contiguous regions that encompass weakly protected jurisdictions (Peters and Lodge, 2009). Among provincial, state and federal regulations concerning live trade, aquaculture and live bait are the most regulated, whereas live fish sales and the pet trade are the least regulated industries (Thomas et al., 2009). Only two of the eight states bordering the Great Lakes basin (Illinois and Minnesota) have included provisions that target escapees from aquaculture facilities, indicating a clear lack of preparedness for dealing with potential fish invasions via this vector. The same non-native species may be distributed by multiple vectors that are subject to varying levels of control, ranging from no regulation to complete prohibition (Peters and Lodge, 2009).

In Canada, the federal and provincial governments have long had few regulations for live trade (Mandrak and Cudmore, 2010; Vasarhelyi and Thomas, 2003). In the US, the primary legislation intended to protect non-agricultural systems from animal invasions is the injurious wildlife provision of the Lacey Act, which gives the US Fish and Wildlife Service the authority to prohibit importation and interstate transport of listed animals deemed to be a threat to wildlife resources. This Act is undermined by a lack of effective risk assessment protocols that anticipate impending threats prior to their introduction and establishment (Fowler et al., 2007). In either the US or Canada, virtually no risk assessment is required for the importation of aquatic species.

Control programs can be effective if the biology of the target organism is well known and there is long term commitment to the program by all stakeholders. The best example of this is the collaborative action of the governments of Canada and the US that produced a sustained reduction of sea lamprey populations to 10% of their former levels, through the use of lampricides, barriers and traps (GLFC, 2010). Though controversial, the stocking of non-native salmonids has also been used effectively to manage nuisance forage fish populations including alewife (Mills et al., 1994); however, the salmonids themselves have had some negative ecological impacts (Crawford, 2001). Preventative measures against species introductions are favored over attempted eradication and control, which may not always be successful (Vander Zanden et al., 2010). Removing a widespread and well-established species from an expansive system is an immense challenge, and thus such eradications are rarely attempted.

Increased efforts have been made to educate and engage the public in preventing the spread of invasive species across the Great Lakes basin. Various governmental agencies and non-governmental organizations run educational programs to inform citizens about various mechanisms of dispersal including transport via recreational boats, aquarium release, baitfish release, and illegal transport of live organisms (GLFC, 2010; Rosaen, 2012). The GLWQA (2012) also calls for implementing public education programs to prevent new introductions.

Table 2
The provincial and state legislation and regulation pertaining to the control of non-native fish in the Great Lakes basin. Provisions of the legislation over aquaculture, baitfish, live fish sales and the management of escapees is included shown. Adapted from Thomas et al. (2009) and Legislative Assembly of Ontario (2014). √ = covered, X = not covered.

Province/State	Legislation	Aquaculture	Baitfish	Fish Sales	Escapes
Ontario	Fishing Licensing Regulations; Fish and Wildlife Conservation Act; Invasive Species Act	√	√	√	√
Illinois	Fish and Aquatic Life Code	√	√	√	√
Indiana	Indiana Admin. Code; Indiana Statute	√	√	√	X
Ohio	Ohio Admin. Code	√	√	√	X
Michigan	Michigan Aquaculture Development Act; Natural Resources and Environmental Protection Act	√	√	X	X
Minnesota	Minnesota Statute	√	√	√	√
New York	NY Environmental Conservation Law	√	√	√	X
Pennsylvania	Pennsylvania Admin. Code	√	√	√	X
Wisconsin	Wisconsin Admin. Code; Wisconsin Statute	√	√	√	X

Interactions between invasive species and other anthropogenic drivers

Undoubtedly, invasive species will continue to be one of the most complex drivers of change in the Great Lakes basin over the next 50 years, particularly because of their capacity to interact with other anthropogenic drivers. At least three general categories of drivers are likely to be implicated in these interactions: climate change, biological and chemical contaminants, and socioeconomic drivers.

Climate change

Despite growing pressure for changes in energy policy, both the US and Canada continue to increase fossil fuel production and consumption (Murphy, 2012). Continued CO_2 emissions at current levels are expected to drive a mean global temperature increase of 2.3–4.5 °C by the end of this century (Rogelj et al., 2012). Such changes should benefit at least some non-native species in the Great Lakes basin (Bronte et al., 2003; Magnuson et al., 1997), and be detrimental to others currently established (e.g., Thorp et al., 1998). A likely prospect is the removal of thermal barriers to numerous warm-water species that otherwise could not invade, despite persistent opportunities for their introduction (see *Future scenarios*).

Climatic change will affect water levels, through altered spatial and temporal patterns of precipitation and evaporation. However, there is considerable uncertainty regarding projected changes to Great Lakes water levels, which are not expected to be uniform across the basin (Ehsanzadeh et al., 2013; Lofgren et al., 2011). It is unclear how alterations to seasonal water cycles (e.g. Gronewold and Stow, 2014) will affect invasion risk. In areas subjected to lower water levels, the consequent increase in exposed shoreline is expected to favor invasive macrophytes (Tulbure and Johnston, 2010; Tulbure et al., 2007).

Changes in temperature and the addition of non-native organisms to aquatic food webs can dramatically alter energy flow (Bronte et al., 2003; Kolar et al., 1997). Native zooplankton are threatened by invasive crustacean predators, such as the bloody-red mysid shrimp *Hemimysis anomala* and the subtropical waterflea *Daphnia lumholtzi*, which are expected to benefit from increased temperatures and become more widely distributed in the Great Lakes basin (Ricciardi et al., 2012; Tudorancea et al., 2009). Conversely, some current invaders, such as the spiny waterflea *Bythotrephes longimanus*, thrive in cooler conditions (Kerfoot et al., 2011; Kim and Yan, 2011) and might be negatively affected by climate change. Among the non-native fishes in the Great Lakes that may benefit from warmer temperatures are striped bass *Morone saxatilis*, rainbow smelt *Osmerus mordax*, alewife, and sea lamprey (Bronte et al., 2003; Rixon et al., 2005). A variety of warm-water fishes that are currently restricted to the lower Great Lakes, or that are excluded from the basin, are predicted to expand their ranges through the basin (Mandrak, 1989). Climate change may also exclude native coldwater fishes from formerly hospitable habitat; for example, the survival of lake trout fry declines with increasing temperature (Casselman, 2002), and a significant loss in their recruitment will negatively impact recreational fisheries.

Biological and chemical contaminants

As the Great Lakes basin warms, biological contaminants (organisms or their products that are hazardous to animal health) may also become increasingly problematic (Schindler, 2001). Warmer temperatures may allow disease organisms to complete their life cycle more rapidly, and thus magnify the spread and impact of non-native parasites and pathogens (Marcogliese, 2001). More complex host–pathogen interactions may occur through temperature-driven increases in biological oxygen demand (BOD) and rates of decomposition. A recurring example in the Great Lakes basin is the elevated BOD associated with massive decomposing organic material that produces anoxic conditions favorable to the bacterium *Clostridium botulinum*. A link between alewife boom-and-bust die-offs and botulism outbreaks was identified in the 1960s (Fay, 1966). Another mechanism of such outbreaks has become apparent in recent decades. The filtration activities of dreissenid mussels increase light transparency and thus promote prolific macrophyte growth whose biomass, when decomposed later in the summer, can create periodic anoxic conditions (Vanderploeg et al., 2002). The mussels can also concentrate the cells and toxin of *C. botulinum*, such that molluscivores including the round goby *Neogobius melanostomus* can accumulate the toxin and transfer it to higher trophic levels (e.g., piscivorous waterfowl). This is the presumed cause of annual die-offs of tens of thousands waterfowl in the lower Great Lakes observed since the late 1990s (Hebert et al., 2014; Yule et al., 2006). Selective filtration by dreissenid mussels may also promote cyanobacterial blooms, including that of *Microcystis*, which produces a toxin hazardous to humans (Knoll et al., 2008). Mussels reject *Microcystis* as a food item, but filter out other phytoplankton that compete with it, thereby allowing it to flourish in areas with high mussel densities (Vanderploeg et al., 2002).

The Great Lakes basin has also been afflicted with a variety of fish diseases from non-native sources (Table 1). Among these are viral hemorrhagic septicemia virus (VHSV), spring viraemia of carp virus (SVCV), and muskie pox *Piscirickettsia cf. salmonis*. Originating from cultured salmonids in Europe, VHSV is a deadly virus that has spread to the Atlantic coast and, subsequently, throughout the Great Lakes basin (Bain et al., 2010). It affects nearly 50 species of fish and causes mass die-offs (Kipp et al., 2013), which prompted the US government to enact legislation in 2005 that prohibited interstate transport of live susceptible species from US states and Canadian provinces bordering the Great Lakes basin (Gustafson, 2007). SVCV, originally from Europe, has spread into established populations of carp across North America over the past decade (Dikkeboom et al., 2004; Garver et al., 2007); it also affects other cyprinid species, northern pike *Esox lucius*, and pumpkinseed sunfish *Lepomis gibbosus*. Muskie pox was detected initially in 2002 and threatens the muskellunge *Esox masquinongy* fishery in Lake St. Clair by causing high rates of fingerling mortality (Thomas and Faisal, 2009).

Invasive species also generate new pathways for the transfer of chemical contaminants. Alewife bioaccumulate polychlorinated biphenyls (PCBs) and the insecticide toxaphene and transfer them to higher predators (Stapleton et al., 2002). Dreissenid mussels filter particulate material from water and concentrate pollutants (including PCBs and heavy metals) that can be passed on to molluscivores, like the round goby, and ultimately to sportfishes and waterfowl (Hogan et al., 2007; Kwon et al., 2006).

Socioeconomic drivers

The cost of species invasions to ecosystem services in the Great Lakes basin has been estimated to be at least $138 M per year (Rothlisberger et al., 2012). Through their myriad impacts on ecosystems, ecosystem services and human health, invasions affect many sectors of the economy — including a) fisheries, recreation and tourism; b) utilities and manufacturing; and c) shoreline development. Fisheries employ over ten thousand people in the Great Lakes basin and provide several billion dollars annually in revenue (Allan et al., 2013; Rosaen et al., 2012). Invasive species' impacts on fish diversity and productivity have ramifications that affect commercial fishermen, recreational anglers, charter boat captains, and manufacturers of fishing gear and boats. Tourism is a $30 B per year industry that has likely been negatively affected by beach fouling from die-offs of dreissenid mussels, alewife and macroalgae, as well as encroachment by invasive plants such as Eurasian watermilfoil *Myriophyllum spicatum* (Rosaen et al., 2012).

Invasions have also had significant economic impacts on factories, power plants, and water treatment facilities that draw water from the Great Lakes basin. Impacts of invasive fouling organisms on water intake facilities exceed $40 M per year (Rosaen et al., 2012). On average, Ontario power plants that draw cooling water from the Great Lakes basin spend $1.2 M per plant per year to monitor and control dreissenid mussels. Without such controls, mussel fouling can force plant shutdowns (Park and Hushak, 1999). As a probable consequence of increased water clarity driven by dreissenid filtration activities, prolific growth of *Cladophora* in Lake Ontario forced the shutdown of the James A. Fitzpatrick nuclear power plant in New York on multiple occasions. Another species, the spiny waterflea *Bythotrephes longimanus*, impacts water intake systems indirectly: *Bythotrephes* outcompetes native invertebrate planktivores such as *Leptodora* (Weisz and Yan, 2011), whose prey – including the cladoceran *Holopedium gibberum* – may flourish in the absence of their adapted predator. Owing to its gelatinous sheath, *H. gibberum* can clog filters in water intakes (Thelen, 2012), thereby potentially adding to the impacts of other fouling organisms.

Riparian ecosystems in the Great Lakes basin are also at risk of alteration. Shoreline development has created a system of dikes to control natural seasonal flooding of wetland areas along the Great Lakes basin. Diked wetlands are hotbeds for invasive plants such as the common reed *Phragmites australis*, purple loosestrife *Lythrum salicaria*, and reed canary grass *Phalaris arundinacea* (Herrick and Wolf, 2005; Steen et al., 2006). Such invasive monocultures result in low biodiversity of birds and fishes that rely on wetlands as nursery habitat (Howe et al., 2007; Trebitz et al., 2009)

How will vectors and their invasion risks change in the next 50 years?

Shipping

Ballast water release by transoceanic ships is deemed responsible for most aquatic invasions in the basin (Mills et al., 1993; Ricciardi, 2006). We extrapolated from the modern rate of discovery (Ricciardi, 2006; Ricciardi, unpubl. data) to predict the cumulative number of invaders in the Great Lakes basin introduced via shipping up to the year 2060 under three possible scenarios: (i) 100% of the 1960–2003 rate (98 total invaders); (ii) 50% of the 1960–2003 rate (71 invaders); and (iii) no new invaders (asymptote at 44 invaders; Fig. 3). The inclusion of ships declaring "no ballast on board" in BWE regulations

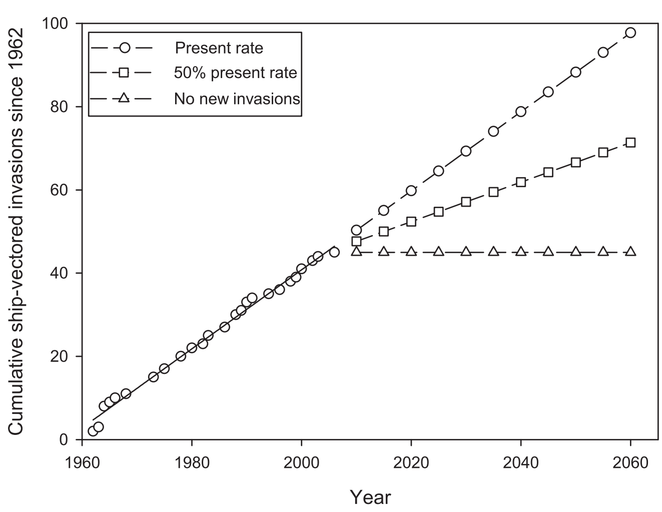

Fig. 3. Cumulative number of ship-vectored, free-living invaders discovered in the Great Lakes since 1962. Line fitted by least-squares regression: $y = 0.95x - 1857.38$, where x = year since 1960 ($r^2 = 0.99$). Data for 1962-2006 from Ricciardi (2006; unpubl. data). Data from 2010-2060 are projected values (denoted by dashed lines) at the current rate of invasion, at 50% of the current rate of invasion, or with future ship-mediated invasions halted. Predicted values for cumulative invaders for the year 2060 are: 98 (current rate), 71 (50% rate), and 44 (no new introductions).

in 2006 appears to have severely lowered the risk of ship-mediated invasions (Bailey et al., 2011).

BWE reduces the number of live organisms from ship ballast tanks through a combination of purging and osmotic stress (Gray et al., 2007), but fails to remove life stages of all taxa (Briski et al., 2011a; b; Ricciardi and MacIsaac, 2008). This procedure may achieve only brackish salinities, owing to residual freshwater remaining in tanks (Locke et al., 1993; Niimi and Reid, 2003), and such conditions are tolerable to organisms with broad salinity tolerance. Perhaps this explains why most non-native invertebrates discovered in the basin since 1993 are euryhaline (Ricciardi, 2006). The new USEPA regulation, if effectively enforced, could ultimately lower invasion risk by limiting the numbers of organisms delivered in ballast tanks; but under favorable conditions for certain taxa even very small numbers of propagules can lead to establishment (e.g., Gertzen et al., 2011). In particular, parthenogenetic species, microorganisms and pathogens require only a few introduced cells or individuals for establishment (Gertzen et al., 2011; Hallegraeff, 1998). Another persistent risk is posed by invertebrate resting eggs, which can withstand harsh physico-chemical conditions and remain viable inside ballast tanks for many months to more than a year (Briski et al., 2011b). BWE and saltwater flushing did not reduce the abundance or species richness of invertebrate resting eggs in ships arriving in the Great Lakes basin between May 2007 and August 2009 (Briski et al., 2011a).

Furthermore, current BWE regulations for the Great Lakes basin target primary introductions associated with transoceanic shipping activities (Rup et al., 2010). Domestic vessels (i.e., those traveling within the continental region) account for ~90% of commercial shipping operations in the basin, but are not regulated at the federal level in Canada or the US. They are perhaps viewed as a low-risk vector for invasion because they typically operate over relatively short distances. However, ballast water transport by domestic vessels can increase the distributional range of invasive species, including pathogens, through secondary spread (Adebayo et al., 2014; Rup et al., 2010). Moreover, zooplankton carried by domestic vessels within the Great Lakes basin are significantly higher in density and species richness compared with those carried by transoceanic vessels (Briski et al., 2012). Some domestic vessels have been found to transport several species that are non-native to large areas of the basin; for example, the fish-hook waterflea *Cercopagis pengoi* was discovered in domestic vessels destined for discharge in Lake Superior, which has not yet been invaded by this high-impact predator (Briski et al., 2012).

Live trade

The relative importance of live trade will increase over the coming decades as BWE regulations limit introductions via transoceanic shipping, and as trade in non-native fish becomes more widespread within Canada and the US. This risk is recognized in the recently amended GLWQA (2012), which calls for bi-nationally coordinated risk assessments on live trade pathways including the aquarium trade, the sale of live bait for angling, live fish imported for food markets, and organisms distributed by biological supply houses.

The live bait trade poses invasion risks through distribution and release of bait and other organisms carried in the holding water by anglers, as well as unintentional escapes of fishes stocked in baitfish holding ponds. Surveys in Ontario indicate that over one-third of anglers release their bait into waters in which they have fished — a proportion that has not improved over the past two decades, despite provincial regulations and significant educational efforts (Ward et al., 2011). This practice also appears to be common in the US (Kilian et al., 2012).

Within food markets (aquatic organisms transported live within the Great Lakes basin for distribution and sale for human consumption), the species considered to pose the greatest known threat to the Great Lakes basin are Asian carps — especially bighead carp *Hypophthalmichthys* *nobilis* and grass carp *Ctenopharyngodon idella*. These species have extensive invasion histories and documented negative ecological impacts (Cudmore et al., 2012; Kolar et al., 2007; Mandrak and Cudmore, 2004; Wittmann et al., 2014). Individual grass carp have been collected sporadically throughout the Great Lakes basin for many years, and there is evidence that they are spawning in Lake Erie (Chapman et al., 2013) and are abundant in a major tributary of Lake Michigan (Wittmann et al., 2014). Grass carp is expected to impact water quality and macrophyte communities, including associated fish and invertebrates (Wittmann et al., 2014). Bighead carp have been collected at least three times in Lake Erie (GLFC, 2012). Unlike bighead carp and grass carp, both black carp *Mylopharyngodon piceus* and silver carp *Hypophthalmichthys molitrix* are not typically sold through food markets; however, black carp are occasionally distributed with grass carp, with which they are easily misidentified, and silver carp could be mixed accidentally with bighead carp shipments. The combination of a high concentration of live fish trade markets and high environmental suitability makes the lower Great Lakes particularly vulnerable to colonization by Asian carps (Cudmore et al., 2012; Herborg et al., 2007).

The importation of species as aquarium pets or for ornamental ponds contributes to a $25B USD-per-year worldwide industry (Padilla and Williams, 2004). Many species can be purchased through mail order and the Internet (Kay and Hoyle, 2001). Most fishes sold in the aquarium trade are native to tropical regions and cannot tolerate temperatures below 18 °C (Chapman et al., 1997). Based on temperature tolerances, only nine of 305 ornamental fish species surveyed by Rixon et al. (2005) could potentially survive current winter temperatures in the Great Lakes basin, and two species are considered as probable future invaders: the weather loach *Misgurnus fossilis* and the white cloud mountain minnow *Tanichthys albonubes*. Another species sold through the aquarium trade, the Oriental weatherfish *Misgurnus anguillicaudatus*, is already established in the basin and has the potential to spread further (Mills et al., 1993). Tropical species, such as pacu (*Colossoma* spp., and *Piaractus* spp.) and red-bellied piranha *Serrasalmus natterreri*, have been captured repeatedly but apparently cannot establish in the Great Lakes basin, owing to temperature constraints (Leach, 2003). As with other forms of commerce in live organisms, the aquarium trade is poorly regulated in Canada and the US. Some of the most damaging invasive species in the Great Lakes basin are available for purchase; for example, Eurasian watermilfoil is advertised for sale, despite being recognized as a costly invader across the US and Canada (Czarapata, 2005). These shipments are commonly contaminated; in a recent study of the ornamental plant trade in the Great Lakes basin, 90% of plants purchased were accompanied by non-native organisms (Keller and Lodge, 2007).

Canals and recreational boating

Historically, canals have proven to be a major vector for the introduction of non-native species to the Great Lakes basin (Mills et al., 2000), but their influence apparently diminished over the latter half of the previous century (Fig. 1). Canals are inextricably linked to both domestic shipping and recreational boating — one of the largest unregulated vectors of the spread of aquatic non-native species. Recreational boats can transport non-native species through bilge water, live wells, and hull fouling (e.g., Johnson et al., 2001; Kelly et al., 2013). Public awareness programs and voluntary compliance are the only strategies currently employed by local authorities to address this vector (CCFAM, 2004).

Among the native assemblages in these connecting watersheds, most potentially invasive species that are presently able to survive and establish in the Great Lakes basin may have already done so. Nevertheless there are current and emerging invasion threats. For example, *Hydrilla verticilla*, one of the most invasive aquatic weeds in the southern US, has expanded its range into New York state; it was discovered in the inlet of Cayuga Lake in 2011 and in the Erie Canal in 2012 (NYSDEC, 2012). Warm-water species that have access to the Great Lakes basin via canals are expected to colonize as climate change removes thermal barriers to their establishment (Mandrak, 1989). Indeed, it is believed that warmer-than-average summer and winter temperatures during the late 1940s facilitated the invasion of white perch *Morone americana* into the Great Lakes basin via canals in New York State (Johnson and Evans, 1990). Canals form an extensive network that links the Great Lakes basin to inland waters in Ontario via the Rideau Canal and the Trent-Severn Waterway, to the Hudson River and the Atlantic drainage via the Erie-Barge and Hudson-Mohawk canals, and to the Mississippi River basin via the Chicago Area Waterway System (CAWS). The CAWS – an artificial hydrological connection between Lake Michigan and the upper Mississippi drainage – is of particular concern because Asian carp species have proliferated in the Mississippi River after having escaped from aquaculture facilities decades ago. In 2010, a single bighead carp was captured in Lake Calumet, just 6 miles from Lake Michigan (Jerde et al., 2011). Although the risk of species transfer through the CAWS was long believed to have been reduced by an electric barrier system maintained by the US Army Corps of Engineers (USACE), bighead/silver carp DNA has been detected above the electric barrier (Jerde et al., 2011) and more recently in Lake Erie (Jerde et al., 2013).

In January 2014, the USACE released their report from their multi-year study, the Great Lakes and Mississippi River Interbasin Study (USACE, 2014), which aimed to evaluate a range of options and technologies to prevent the spread of non-native species between the Great Lakes basin and Mississippi. The report contains eight alternatives, and evaluates their potential to limit the transfer of non-native species. Most of the alternatives are centered on the CAWS, ranging from the continuation of current activities to the complete hydrological separation of the Great Lakes and Mississippi River basins. In the end, the USACE does not advocate the adoption of any one strategy, and instead suggests dialogue between federal, state, and local governments and associated regulatory agencies on how to manage the reciprocal threat of non-native species in these two basins (USACE, 2014).

Future scenarios

To identify future invasion threats, we followed the approach of Ricciardi and Rasmussen (1998) and selected two probable donor regions (i.e., Eurasia and the southern US) and for a subset of animal

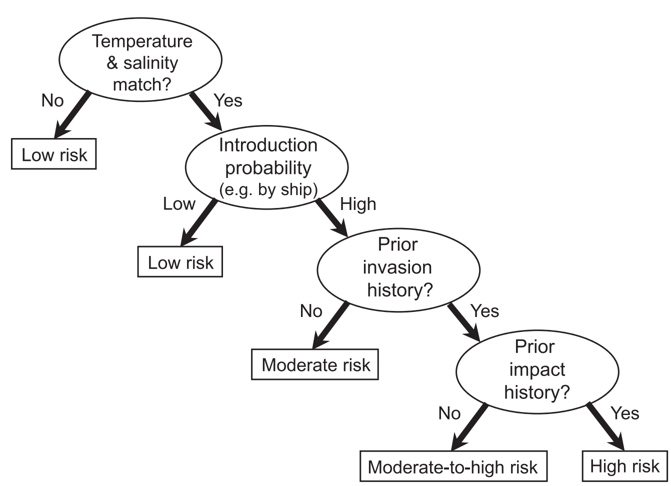

Fig. 4. Algorithm for predicting high-risk aquatic invaders (adapted from Ricciardi and Rasmussen, 1998), based on 1) whether there are areas of the Great Lakes that match temperature and salinity conditions in the native range of the species, 2) the probability of introduction through dominant vectors, 3) whether it has an invasion history elsewhere in the world and, if so, 4) whether it has exerted strong impacts somewhere in its invaded range.

species in these regions considered 1) whether physicochemical (temperature, salinity) conditions in the Great Lakes basin match known tolerances of each species; 2) whether the species is likely to reach the basin using an existing vector/pathway (e.g. in the case of Eurasian species, the probability of uptake and survival in a ship ballast tank); 3) whether the species has a history of invasion elsewhere in the world; and, if so, 4) whether it is has had significant negative impacts in its invaded range (Fig. 4). We apply this approach in the context of three different future management scenarios.

1. Status quo: while current ballast water regulations are effective, live trade continues to be poorly regulated for most species

In this scenario, current (2014) ballast water regulations remain in effect without further amendment. Although no new aquatic invaders have been found in the Great Lakes basin since the implementation of amended BWE regulations in 2006, the success of BWE is contingent on compliance. At least 4% of ballast tanks in transoceanic vessels arriving to the Great Lakes basin in 2007 were non-compliant with BWE regulations (Bradie et al., 2010). It is not clear what risk is posed by the propagule pressure associated with this proportion of untreated ballast tanks, and it is perhaps still too early to assess the overall effectiveness of current BWE procedures and the new USEPA and US Coast Guard regulations. The Great Lakes basin might remain vulnerable to the introduction of new non-native species via transoceanic shipping.

However, under current practices, the biggest threat for future invasions is live trade. If trade continues to be largely unregulated, and there persists a dearth of bi-national cooperation in addressing current and future invasion threats to the Great Lakes basin, then potentially damaging unintentional introductions will continue (Cudmore et al., 2012). Of immediate concern are bighead carp, silver carp, and northern snakehead *Channa argus* (Table 3). Environmental conditions in the Great Lakes basin are considered to be suitable for establishment of these fishes (Herborg et al., 2007; but see Cooke and Hill, 2010), which are expected to have strong impacts in at least parts of the basin. Bighead and silver carp feed primarily on phytoplankton and zooplankton, and thus may compete with juveniles of native fishes for food (Rixon et al., 2005). The possession or sale of Asian carps (particularly bighead carp) has been prohibited in Ontario since 2005 and, more recently, by all US states bordering the Great Lakes basin. However, it is doubtful whether current regulations targeting Asian carps are sufficient to prevent their establishment (Cudmore et al., 2012). Both bighead and silver carp environmental DNA (eDNA) have been detected in southern Lake Michigan and Lake Erie (Jerde et al., 2011, 2013), although whether or not the presence of eDNA infers the presence of live organisms is debatable.

Among the known invasion threats to the Great Lakes basin from the aquarium trade is the northern snakehead, which has been released by pet owners throughout North America (Chen et al., 2006) and perhaps cultivated in the wild for Asian food markets. One individual was collected from Lake Michigan near Chicago in 2004 (Nico and Fuller, 2014). Snakehead species have extensive invasion histories and documented impacts on native biodiversity (Courtenay and Williams, 2004; Saylor et al., 2012). There is a high probability that the northern snakehead will invade the Great Lakes basin, given the environmental suitability of the region and the absence of broadly applied regulation and enforcement.

2. The dystopian future: ballast water regulations prove ineffective, live trade continues to grow unabated and largely unregulated

In this scenario, concern over invasive species is subordinate to promoting trade through the basin. Increased propagule pressure resulting from the development of larger and faster ships combined with rapidly increasing ship traffic and live trade vectors will maximize invasion risk. Current ballast water exchange regulations – contrary to recent evidence – prove to be largely ineffective in preventing further invasions. Moreover, live trade continues to be largely unregulated, and current restrictions and enforcement prove to be insufficient to prevent even targeted species from establishing.

Ineffective ballast water management will leave the basin vulnerable to a host of new invaders, in addition to those that may invade the Great Lakes basin described under Scenario #1. Assuming that recent spatial patterns of shipping traffic persist (Ricciardi, 2006), most new invaders will arrive from Europe and will include at least five high-impact species: the killer shrimp *Dikerogammarus villosus*, Caspian mud shrimp *Chelicorophium curvispinum*, Baikalian amphipod *Gmelinoides fasciatus*, monkey goby *Neogobius fluviatilis*, and Amur sleeper *Perccottus glenii* (Table 3).

Dikerogammarus villosus is a Ponto-Caspian amphipod crustacean currently spreading through Europe and is considered a probable future invader of the Great Lakes basin (Ricciardi and Rasmussen, 1998). Field surveys and laboratory experiments link the predatory activities of *D. villosus* to rapid local declines in macroinvertebrate populations (Dick et al., 2002; van der Velde et al., 2000). The invasion of *C. curvispinum* in the Lower Rhine River during the 1980s is hypothesized to have caused enormous declines in populations of the zebra mussel and a hydropsychid caddisfly, through competition for hard substrata (van der Velde et al., 1994). *Gmelinoides fasciatus* has invaded the Baltic Sea basin, where it is presumed to have caused declines in a native amphipod (Kangur et al., 2010). The monkey goby has recently invaded several European inland waterbodies (Copp et al., 2005; Grabowska et al., 2009) and is a benthic generalist similar to the round goby. Its invasion of the Great Lakes would likely have significant impacts on fish and macroinvertebrate communities, but perhaps not qualitatively different from those currently produced by its congener. The Amur sleeper is one of the most invasive fishes in Europe in recent decades (Copp et al., 2005), and can reduce macroinvertebrate and amphibian species diversity (Reshetnikov, 2010). The establishment of any of these aforementioned species could have important ecological consequences for the Great Lakes basin.

Table 3
Examples of species predicted to invade the Great Lakes basin by 2063 under two different scenarios using a simple algorithm (Fig. 4). Scenario #1 represents the status quo: current regulations and management efficacy remain unchanged. In Scenario #2, live trade remains unregulated and ballast water regulations prove to be ineffective; species listed under this scenario are added to those predicted to invade under the previous scenario. Note that these examples are considered a small subset of potential invaders.

Scenario	Common Name	Species	Probability of Introduction	Probability of Establishment	Projected Impact
1	Bighead carp	*Hypophthalmichthys nobilis*	100%	High	High
	Silver carp	*Hypophthalmichthys molitrix*	High	High	High
	Black carp	*Mylopharyngodon piceus*	High	Medium	?
	Northern snakehead	*Channa argus*	100%	High	?
2	Killer shrimp	*Dikerogammarus villosus*	High	High	High
	Caspian mud amphipod	*Chelicorophium curvispinum*	High	High	High
	Baikalian amphipod	*Gmelinoides fasciatus*	High	High	High
	Monkey goby	*Neogobius fluviatilis*	High	High	?
	Amur sleeper	*Perccottus glenni*	Medium	High	High

3. The utopian future: effective, proactive bi-national governance minimizes invasion risk

In this final scenario, Canada and the US collaborate to enforce harmonized policies that minimize the risk of invasion. Adopted directives of the amended GLWQA (2012) lead to effective bi-nationally coordinated risk assessments on various pathways of introduction (including live trade, recreational boats, and connecting waterways) and coordinated timely response actions to prevent establishment of new species introductions. New technologies in ballast treatment are adopted. Current alternatives to mid-ocean ballast exchange include onboard ballast water treatment such as filtration, UV radiation, ozone, and biocides; but these systems cannot be applied universally, owing to limitations of space on board, feasibility of retrofitting, and steep installation costs (Pereira and Brinati, 2012).

Bi-national regulations are formed and effectively enforced to eliminate the live trade of any potentially invasive non-native species in the basin. Given that Asian carps can still enter the Great Lakes basin via the CAWS, additional barriers (electric and CO_2) are installed to reduce the spread of these and other species between the two basins. Alternatively, a bolder initiative that is considered is the hydrologic separation of the Great Lakes basin and Mississippi River basin (Rasmussen et al., 2011).

The influence of climate change

Although increased regulations of ballast water and live trade, and the (virtual or real) hydrological separation of the Mississippi River and Great Lakes basins can lead to the minimization of new invaders entering the Great Lakes basin, the influence of climate change will be superimposed on each of the above scenarios. Trends of increasing water temperatures have been detected in all five of the Great Lakes (e.g., Austin and Colman, 2007; McCormick and Fahnenstiel, 1999). Some non-native species that are already established may become more abundant and have greater impacts, whereas others may diminish, under warmer conditions. Those that currently reside in the lower Great Lakes and may spread to northern areas of the basin with shifting isotherms include the red swamp crayfish *Procambarus clarkii* and the Asian clam *Corbicula fluminea*, both of which are considered subtropical species. The red swamp crayfish is an opportunistic omnivore whose feeding activities can alter food webs (Gherardi and Acquistapace, 2007). It might withstand cold winter temperatures by burrowing in sediments (Gherardi et al., 2002). Consequently, even now it may be able to spread beyond the lower Great Lakes (Table 4). The Asian clam is one of the world's most invasive aquatic animals; its natural distribution includes Asia, Africa and Australia, but it has spread globally (Sousa et al., 2008) and invaded Lake Erie and southern Lake Michigan in the late 1970s and early 1980s (Mills et al., 1993). Its incursion into northern latitudes is apparently impeded by its intolerance of long-term exposure to water temperatures below 2 °C (Sousa et al., 2008) and, consequently, it has largely been confined to artificially heated waters downstream of power plants in the Great Lakes basin. However, increasingly moderate winters are expected to promote its northern spread (Weitere et al., 2009). Several fish species that previously invaded the lower Great Lakes may spread to the upper Great Lakes as thermal barriers are lifted (Mandrak, 1989). We used projected surface water temperatures for the year 2070 (Trumpickas et al., 2009) to predict the range expansion of these invertebrates and fishes throughout the Great Lakes basin (Table 4).

Finally, in addition to climate-driven range expansions of species already established within the Great Lakes basin, several non-native species might invade the basin as isotherms shift in the next few decades. These include two subtropical plants with extensive invasion histories and that are sold through the ornamental garden and aquarium trade in the Great Lakes region water hyacinth *Eichhornia crassipes* and water lettuce *Pistia stratiotes*, which have been found in multiple locations in Lake St. Clair and the Detroit River (Aldebayo et al., 2011). To date, there is no evidence that these species can overwinter in the Great Lakes basin, but the risk of their establishment will increase with a warming climate. In response to anticipated changes to surface water temperatures, Mandrak (1989) identified 19 fish species from the Mississippi and Atlantic Coastal basins as potential invaders of the lower Great Lakes. Most of these fish species lack invasion histories, and so it is difficult to predict their ecological impacts.

Conclusions and recommendations

The Great Lakes basin's invasion history spans two centuries and is characterized by distinct periods that reflect temporal changes in major vectors (Mills et al., 1993; Ricciardi, 2006). Shipping has been the dominant vector, accounting for 60% of invasions since the opening of the Seaway in 1959, and delivering many of the species that have profoundly transformed the basin. Recent ballast water regulations have likely reduced, but not eliminated, the risk of future ship-mediated invasions (Bailey et al., 2011). At the same time, the basin remains at risk of invasion by species associated with live trade and by southern species whose spread is promoted by climate change. The examples of probable future invaders identified in the aforementioned scenarios highlight a continuing vulnerability of the Great Lakes basin to further disruption. If the observed proportion of high-impact invaders remains relatively constant (c. 18%; Ricciardi and Kipp, 2008; Ricciardi, unpubl. data) and even if the current rate of invasion were to be reduced by half, then several new highly disruptive invaders will arrive in the coming decades.

Owing to myriad unforeseen opportunities for species introduction, it is virtually impossible to completely insulate the Great Lakes basin from further invasion. Nevertheless, there are theoretical and pragmatic reasons to invest resources toward substantively reducing the invasion rate. Firstly, efforts to prevent invasions are more cost-effective

Table 4
Species predicted to expand their ranges in the Great Lakes basin under climate change. Fish species listed are those currently established in the lower Great Lakes and are expected to spread northward by Mandrak (1989). Probability of establishment derived from the match between surface temperatures across the species present range and projected surface temperatures. Risk of establishment is considered to be high if the average of the maximum temperatures predicted by Trumpickas et al. (2009) under different warming scenarios for 2070 is equal to or greater than the baseline surface temperature of the lake(s) in which the invader is currently present. N = native; I = invaded range.

Common name	Species name	Present range	Probability of establishment elsewhere in the basin:			
			Erie	Ontario	Huron	Superior
Grass pickerel	*Esox americanus vermiculatus*	Erie (N), Ontario (N), Michigan (N), Huron (N)	–	–	–	Medium
Chain pickerel	*Esox niger*	Erie (I), Ontario (N)	–	–	High	Low
Spotted gar	*Lepisosteus oculatus*	Erie (N), Michigan (N)	–	High	High	Medium
River redhorse	*Moxostoma carinatum*	Erie (N), Michigan (N)	–	High	High	Medium
Tongue-tied minnow	*Exoglossum laurae*	Ontario (N)	High	–	High	Low
River shiner	*Notropis blennius*	Michigan (N)	High	High	High	Medium
Blue spotted sunfish	*Enneacanthus gloriosus*	Ontario (N)	High	–	High	Low
Red swamp crayfish	*Procambarus clarkii*	Erie (I), Michigan (I)	–	High	High	Low
Asian clam	*Corbicula fluminea*	Erie (I)	–	High	High	Low

(Leung et al., 2002). Reactive management of species that are already well established rarely leads to successful eradication, and usually can aim only to mitigate damage caused by these organisms. In general, the control of species that have established large populations is either impossible or requires massive amounts of money and labor to do so effectively. Secondly, an increasing accumulation of non-native species is predicted to cause a greater frequency of unpredictable and unmanageable impacts resulting from synergistic interactions among invaders (Ricciardi, 2001; Yule et al., 2006) and between invaders and other stressors (Allan et al., 2013; Mandrak and Cudmore, 2010). Therefore, major benefits might be gained from even a modest reduction in the invasion rate.

There are two urgent needs. The first is a harmonized policy framework for both Canada and the US that facilitates early detection and rapid response. Indeed, recent studies demonstrate that existing laws must be amended to allow for coordinated rapid response (e.g., Lodge et al., 2006; Thomas et al., 2009). The second need is harmonized legislation with respect to live trade, based on the assumption that protection against the establishment of species in trade is maximized by prohibiting live transfer through at-risk areas (Herborg et al., 2007). The complexity of these issues can be addressed only through cooperative action by multiple stakeholders. Coordinated efforts by legislators, educators, and scientists on a variety of fronts are necessary to manage invasion threats in the context of multiple drivers of change in the Great Lakes basin.

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