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Predicting Future Introductions of Nonindigenous Species to the Great Lakes

National Center for Environmental Assessment
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DISCLAIMER

ABSTRACT

The Great Lakes of the United States have been subjected to adverse ecological and economic impacts from nonindigenous species (NIS). Ballast water from commercial shipping is the major means by which NIS have entered the Great Lakes. To help resource managers assess the future arrival and spread of invasive species, 58 species were initially identified as having a moderate or high potential to spread and cause ecological impacts to the Great Lakes. Using a species distribution model (the Genetic Algorithm for Rule-Set Production or GARP), areas within the Great Lakes where 14 of these 58 potential invasive species could find suitable habitat, were identified. Based on the model and species depth tolerances, all of Lake Erie and the shallow water areas of the other four Great Lakes are most vulnerable to invasion by the 14 modeled species. Analysis of ballast water discharge data of vessels entering the Great Lakes via the St. Lawrence Seaway revealed that the original source of most ballast water discharges came from Canada and Western Europe. The Great Lakes ports at greatest risk for invasion by the 14 modeled species from ballast water discharges are Toledo, Ashtabula and Sandusky, OH; Gary, IN; Duluth, MN; Milwaukee and Superior, WI; and Chicago, IL. Since early detection is critical in managing for NIS, these results should help focus monitoring activities on particular species at the most vulnerable Great Lakes ports. This assessment demonstrates that successful invasions are best predicted by knowing the propagule pressure (i.e., the number of larvae/individuals entering a new area) and habitat matching (i.e., how similar is the invaded area to the native range of the species).

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LIST OF ABBREVIATIONS AND ACRONYMS

AVHRR	Advanced Very High Resolution Radiometer
BOB	ballast on board
BWD	ballast water discharge(s)
BWE	ballast water exchange
CFR	Code of Federal Regulations
EPA	Environmental Protection Agency
GARP	Genetic Algorithm for Rule-Set Production
GBIF	Global Biodiversity Information Facility
GIS	geographic information systems
K490	diffuse attenuation coefficient at 490 nm
MMT	mean monthly water surface temperature
MODIS	Moderate Resolution Imaging Spectroradiometer
NBIC	National Ballast Information Clearinghouse
NIS	nonindigenous species
NOAA	National Oceanic and Atmospheric Administration
NOBOB	no ballast on board
NOBOB-RM	no ballast on board but the vessel contains residual material
NVMC	National Vessel Movement Center
nLW	normalized water-leaving radiance
ppt	parts per thousand
sr	steradian (units of a solid angle and can also be called a squared radian)
USCG	United States Coast Guard
USGLP	U.S. Great Lakes ports (or ports of call)

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1. EXECUTIVE SUMMARY

Nonindigenous species (NIS) are organisms that enter an ecosystem beyond their native spatial range. The Sea Lamprey (*Petromyzon marinus*) was the first to enter the Great Lakes during the 1830s facilitated by the Erie and Welland canals. Since then, at least 185 other species have invaded the Great Lakes. Thirteen of these species have been labeled as invasive by causing ecological or economic harm. The zebra mussel (*Dreissena polymorpha*), for example, has impacted many Great Lakes native species and has imposed large expenses on the utility industry by clogging water intake pipes.

The objective of this report is to develop data and tools that U.S. Great Lakes resource managers can use to more effectively prevent the establishment of aquatic NIS. This study maps the habitats of the Great Lakes most vulnerable to the entry of aquatic NIS and identifies particular NIS with the potential to enter U.S. Great Lakes ports (USGLP).

Since the St. Lawrence Seaway opened in 1959, ballast water released from transoceanic vessels during commercial shipping operations has been identified as the predominant pathway for NIS to enter the Great Lakes. Transport of NIS occurs when a vessel takes-on ballast water containing NIS from outside the Seaway, the species survives in a ballast tank during transit, and is released when the ballast water is discharged into the Great Lakes. To become established in the new environment, the organisms must be able to survive, reproduce, and spread. To predict future invasions of NIS in the Great Lakes, the two most important determinants of successful invasions were evaluated: whether there is suitable habitat in the Great Lakes for nonnative species and whether there are a sufficient number of these organisms and their larvae arriving in the Great Lakes. First, a species distribution model was used to identify the areas of the Great Lakes which could provide suitable habitat for NIS of concern. Second, commercial shipping and ballast water discharge data were used to evaluate if there are a sufficient number of these organisms entering the Great Lakes to become established.

Based on a literature review of NIS life-history characteristics and invasion histories, 58 species that pose high or medium risk for becoming established in the Great Lakes and for causing ecological harm were identified. To predict the possible distributions of each of these species within the Great Lakes, spatial data sets that characterize aquatic conditions on a global scale were analyzed. These data sets were derived from remotely sensed space-based platforms, operated and made available by the National Aeronautics and Space Administration and the National Oceanic and Atmospheric Administration. Six of these data sets, each at a 4.6 km (21 km^2) spatial resolution, were found to be useful for NIS modeling. Three of the environmental variables are direct measures of water temperature and the other three indirectly relate to primary productivity and water clarity, indicators of habitat suitability.

The Genetic Algorithm for Rule-Set Production (GARP) model was used to determine habitat suitability. GARP predicts the potential distribution of species by comparing the environmental conditions of locations currently inhabited by the species (the reference area) with the environmental conditions in the region of concern. Adequate spatial distribution data were available to model only 9 of the 58 potential invasive species because the GARP model requires at least 30 spatially unique latitude and longitude points that describe the distribution of a particular species. In addition to these nine species, GARP was also used to predict regions within the Great Lakes that would provide suitable habitat for five species of concern that were selected by the U.S. Environmental Protection Agency's Great Lakes National Program Office. Since the existing location of these five species was already known, the model was validated by comparing the reported locations of three of these species with the predicted locations. Results from GARP modeling were used to produce 14 range maps, one for each of the modeled species, predicting their locations of suitable habitat within the Great Lakes. The overall results varied with each modeled species, but generally showed that all of Lake Erie and the shallower portions of the other Great Lakes appear to be most vulnerable for invasion by the 14 modeled species. Water depth appears to be the predominant factor limiting the potential spread of many of the modeled species. Yet, at least one species, the quagga mussel (*Dreissena bugensis*), is surviving at greater depths in the Great Lakes than in its native habitat.

Releases of ballast water into USGLP were analyzed using 2006–2007 data obtained from the National Ballast Information Clearinghouse. The ports that received the most ballast water discharges from vessels entering the Seaway with ballast on board (BOB), after ballast water exchange outside the Seaway, are Duluth, MN; Toledo, OH; Superior, Green Bay, and Milwaukee, WI; and Gary, IN. The most frequent original sources of ballast water came from Antwerpen, Belgium; Puerto Cabello, Venezuela; Haraholmen, Sweden; and Bremen, Germany. It is important to note that there were no clear relationships between foreign and USGLP relative to ballast water uptake and releases. For instance, 13 vessels that discharged ballast water in Toledo obtained ballast water from 12 different foreign ports.

Some vessels enter the St. Lawrence Seaway without ballast water, but may still contain residual water or sediment containing NIS in their ballast tanks, and are referred to as no ballast on board vessels containing residual material (NOBOB-RM). After entering the Seaway, these vessels can off-load cargo and pick up ballast water which would mix with the residual material and be subsequently released into Great Lakes ports. There were considerably more discharges into USGLP from NOBOB-RM vessels than from those vessels with ballast on-board. Those ports receiving the most ballast water from NOBOB-RM vessels are Toledo, Ashtabula, and Sandusky, OH; Superior, WI; and Duluth, MN. Assuming the observed results for 2006 and 2007 are representative of discharge and shipping patterns over the past several years, the port of greatest concern for receiving sufficient propagules and providing the most suitable habitat is Toledo, OH. Toledo is located on Lake Erie, a region that the GARP model predicted would have a high chance of providing suitable habitat for the modeled species. Other ports of concern for receiving sufficient propagules and offering suitable habitat are Gary, IN; Ashtabula and Sandusky, OH; Milwaukee, WI; and Chicago, IL. Duluth, MN and Superior, WI, with high transport potential but low habitat suitability, could be a source of interlake transport of NIS.

This study involved numerous assumptions resulting in uncertain findings. A major source of uncertainty for the GARP modeling is the lack of complete occurrence data for many of the modeled species, for many parts of the globe. Another source of uncertainty is due to the lack of an ideal suite of data for characterizing aquatic environments. Data on abiotic factors such as salinity, bathymetry, substrate, pH, and nutrient levels were not available globally at the 21 km^2 scale. The lack of species-specific data on significant biotic factors, such as competition and predation, also lead to uncertainty in the modeling results. Despite these limitations, a model validation exercise confirmed that GARP and the environmental variables used could produce useful predictions of potential NIS distributions. These predictions were validated using occurrence data from other regions to develop models that predicted known occurrences of three NIS already widespread in the Great Lakes.

There were also limitations with the vessel traffic and ballast water discharge analyses, used as a surrogate for measuring propagule pressure. First, the analysis was only based on 2 years of data, 2006–2007. A second source of uncertainty is due to the self-reporting nature of data entered into the National Ballast Information Clearinghouse. Self-reporting by vessels is not guaranteed to be accurate or complete records of actual vessel practices and should be used with caution. The analysis of discharges from NOBOB-RM vessels is also uncertain because the source of the residual material cannot be known for certain and could even be from ports within the Great Lakes. Further, this data set only includes information on the last five ports of call and species could remain in ballast tanks from visits to previous ports.

Both Canada and the United States implemented ballast water exchange procedures in 1989 and 1993, respectively. Although new NIS continue to be detected in the Great Lakes, it is possible the NIS were transported prior to 1993 and took several years to detect. Despite these procedures and subsequent regulations, it is likely that nonindigenous species will continue to arrive in the Great Lakes.

These findings support the need for detection and monitoring efforts at those ports believed to be at greatest risk. This study also demonstrates the importance of understanding invasion biology by evaluating the two most important predictors of invasion: propagule pressure and suitable habitat. Further, this may be the first time that remote sensing data were used in conjunction with GARP to predict the spread of aquatic invasive species.

2. INTRODUCTION—NONINDIGENOUS SPECIES POSE A THREAT TO LAKE ECOSYSTEMS

The U.S. Great Lakes have suffered ecological damage and economic costs from a number of aquatic nonindigenous species (NIS) that have successfully invaded this region (Mills et al., 1994; NOAA, 2007a). NIS that enter an ecosystem beyond their native spatial range are expected to continue to enter the Great Lakes (Ricciardi, 2006). Preventing the transport of NIS to the region is the best way to avoid their potential adverse impacts, but if this is not possible, the next best alternative is to monitor for their arrival and control their spread. Resource managers are most concerned with NIS that may become invasive. Invasive species are nonindigenous species that are likely to cause economic or environmental harm or harm to animal or human health losses, ecological impacts, or adversely affect human health (National Invasive Species Council, 2007). Our primary goal is to help scientists and managers to better focus aquatic NIS monitoring activities and resources by identifying new invasive species, their potential to spread, and the U.S. Great Lakes ports (USGLP) most susceptible to invasion. Another goal is to demonstrate the use of a habitat suitability model and ballast water discharge data to predict invasion potential. Clients for this report include the U.S. Environmental Protection Agency's (EPA's) Great Lakes National Program Office, Great Lakes port officials, the U.S. Coast Guard (USCG), environmental organizations, agencies in the United States and Canada concerned about invasive species, and invasion biologists.

Our findings are intended to improve detection and monitoring programs by providing managers with an approach for (1) identifying newly established populations of invasive species, (2) tracking or detecting spatial-range expansions, and (3) estimating potential impacts of introductions or spread by gathering baseline data on pre-existing populations and habitat.

Nonindigenous species are one of the greatest threats to the world's ecosystems (Elton, 1958), and represent the greatest threat to biodiversity in lakes worldwide (Sala et al., 2000). Nonindigenous invasive species are the second most important threat to threatened and endangered species in the United States, after habitat loss or alteration (Wilcove et al., 1998). To date, about 50,000 species have been introduced into the United States (Pimentel et al., 2000). While many beneficial food crops, such as corn, wheat, and rice are included in this number, about 4,500 introduced species are free-ranging and up to one-fifth of these are invasive (U.S. Congress, 1993) and cause economic losses, ecological impacts, or adversely affect human health. The economic cost of invasive species to the United States has been estimated at $97 billion (U.S. Congress, 1993) and $137 billion (Pimentel et al., 2000) annually. Crop weeds and crop plant pathogens are the most costly ($26 and $21 billion, respectively) followed by rats and cats ($19 and $17 billion, respectively). Pimentel (2005) estimated the total environmental and economic impact (damage and control costs) of biological invaders to the Great Lakes Basin at $5.7 billion per year.

Biological invasion occurs when an organisms arrives somewhere beyond its previous range. Currently, most invasions are a result of human actions, deliberate or accidental. Fortunately, most invaders do not become pests, or reach invasive levels, but predicting those that do is difficult, at best. Invasions and introductions have long fascinated biologists from a theoretical perspective. As the economic consequences of invaders has increased, however, this fascination must now be used to develop tools that will allow one to predict future invaders, especially those that may affect whole ecosystems, such as the Great Lakes.

2.1. NONINDIGENOUS SPECIES AND THE GREAT LAKES

The Great Lakes have been subjected to biological invasions since the 1830s, when the sea lamprey (*Petromyzon marinus)* became the first recorded species to enter the Great Lakes from the Atlantic Ocean (Mills et al. 1993). Ricciardi (2006) reports that 182 NIS are now established in the Great Lakes and the National Oceanic and Atmospheric Administration (NOAA) reports a similar number of 185 (NOAA, 2007a; Appendix A). While any NIS may cause alterations to ecosystem structure or function, 13 of the reported NIS have become invasive (Mills et al., 1994). The zebra mussel (*Dreissena polymorpha)*, illustrates the impact of an invasive NIS. The zebra mussel is out-competing *Diporeia*, a deep-water macroinvertebrate, for food (IAGLR, 2002). *Diporeia* is a key source of food for many Great Lakes fish and has been a dominant benthic organism since the Great Lakes were formed (IAGRLR, 2002). The loss of *Diporeia* from the Great Lakes system affects the structure and function of the food web and commercially important fish such as the lake whitefish (IAGLR, 2002). Zebra mussels also appear to be responsible for more frequent occurrences of toxic algal blooms (*Microcystis*) by selectively rejecting blue-green algae as food and removing competing algae (Vanderploeg et al., 2001). From an economic standpoint, dense populations of zebra mussels have clogged water intake pipes, imposing large costs on utilities.

The St. Lawrence Seaway, which opened in 1959, is a system of canals and locks that permit ocean-going vessels (as large as 225.6 m long, 23.8 m wide, and 7.9 m deep), to travel from the Atlantic Ocean to the Great Lakes. While shipping pathways to the Great Lakes existed prior to 1959, the opening of the Seaway and technological changes in commercial shipping drastically increased international trade. The opening of the Seaway resulted in an increase in the number of ships entering the Great Lakes (Sala et al., 2000; MacIsaac et al., 2001; Duggan et al., 2003), larger ships conveying larger volumes of ballast water, and ships that have plied the waters in many geographic locations distant from the Great Lakes (Grigorovich et al., 2003a; Holeck et al., 2004; Drake et al., 2005; Duggan et al., 2005). While the transportation of goods has been economically beneficial, the unintended side effect of increased international trade has resulted in the long-range transport of NIS to the Great Lakes.

2.1.1. Origin and Patterns of Species Invasions

Most NIS that have become established in the Great Lakes since 1985 are native to the Ponto-Caspian region or the Black, Azov, and Caspian Seas (Ricciardi and MacIsaac, 2000; Appendix A). The Baltic Sea has also served as the source of many invaders in part because it has a climate very similar to the Great Lakes (Leppakoski et al., 2002) The NIS from these seas include a diverse array of taxa including fish: the round goby (*Neogobius melanostomus*), the tubenose goby (*Proterorhinus marmoratus*), the rudd (*Scardinius erythrophthalmus*), the zebra mussel, the quagga mussel (*Dreissena bugensis*), and several cladocerans (e.g., the fishhook water flea, *Cercopagis pengoi*), amphipods (e.g., *Echinogammarus ischnus*), and harpacticoid copepods (e.g., *Nitocra incerta*; MacIssaac et al., 2001; NOAA, 2007a). The success of Ponto-Caspian species may be related to their ability to survive ballast water exchange due to a broader salinity tolerance developed through a geological history that includes fluctuating water levels and salinities (Dumont, 1998).

There is no direct (i.e., nonstop) shipping traffic between the Great Lakes and the Ponto-Caspian Sea (Colautti et al., 2003), implying that the dominance of the Ponto-Caspian region as a source of invaders might be due to indirect linkages. To account for invasions where no direct shipping connections exist between the occupied spatial range and the range that may be invaded, the potential natural and human transport patterns need to be considered. NIS can be transported from the Ponto-Caspian region to the Great Lakes via an intermediate step in Western Europe. In addition to direct invasion pathways from the Ponto-Caspian region to Western Europe, MacIsaac et al. (2001) proposed four indirect pathways along the major rivers: the Danube and Rhine River pathway; (2) the Dnieper, Pripiat, Nemuna, and Vistula River pathway; (3) the Volga River system pathway; and (4) the Don and Volga River pathway. Many of these connections are completed through man-made canals and waterways which have allowed considerable exchange of species between water bodies (Reid and Orlova, 2002). To fully understand past indirect linkages (which, in turn, might help predict future indirect linkages) it would be necessary to have complete shipping data both from the Great Lakes to the intermediate port and from the intermediate port to the Ponto-Caspian region.

The natural construction of the Great Lakes, whereby water flows and boat traffic moves from one lake into another, facilitates natural and human-induced dispersal within and between the lakes (Duggan et al., 2003). These dispersal patterns are likely to hasten the spread of a NIS once it has entered the Great Lakes but are unlikely to add new species.

2.1.2. Ballast Water and NIS

Cargo vessels frequently take on ballast water to maintain stability when traveling from port to port and especially when crossing an open sea. Some or all of the ballast water is later released when cargo is loaded at various ports and, with regards to this study, those Great Lakes ports shown in Figure 1.

Ballast water is the largest source of NIS to the Great Lakes as shown in Figure 2. Additional sources of NIS to the Great Lakes include fish stocking programs, private aquaculture, the bait industry, the aquarium and ornamental pond industry, live fish food markets, recreational boating, and canals and diversions (Kerr et al., 2005).

While ballast water discharge (BWD) is the most prevalent pathway, an increase in BWD does not directly translate to more species invasions. Most discharges of ballast water in the Great Lakes occur in Lake Superior (Colautti et al., 2003), yet Lake Superior has less invasive species than any of the other Great Lakes (Grigorovich et al., 2003b). The low NIS colonization rate in Lake Superior may be due to any of several factors including cooler temperatures, a high ratio of deeper waters, low food availability due to low productivity, and low calcium concentrations (Grigorovich et al., 2003b).

2.1.3. Measures to Control the Release of Ballast Water Containing NIS

In response to NIS invasions stemming from ballast water releases in the Great Lakes, voluntary ballast water exchange (BWE) guidelines were implemented by Canada in 1989 and made mandatory in 2006. Mandatory BWE regulations were instituted by the USCG in 1993. These regulations require vessels carrying ballast water and entering the U.S. Great Lakes from outside the U.S. Exclusive Economic Zone (usually 200 miles away from the United States) to comply with one of the following three options:

1) Vessels may exchange ballast water in open-ocean waters more than 200 nautical miles from any shore, and in waters more than 2,000 m deep, before entering the Snell Lock, at Massena, New York, provided that salinity of the ballast water is at least 30 parts per thousand (ppt).
2) Vessels may retain their ballast water on board (vessels in this status are referred to as Ballast-on-Board, or BOB vessels).

Figure 1. The five Great Lakes, some of the Great Lakes ports, and surrounding region.

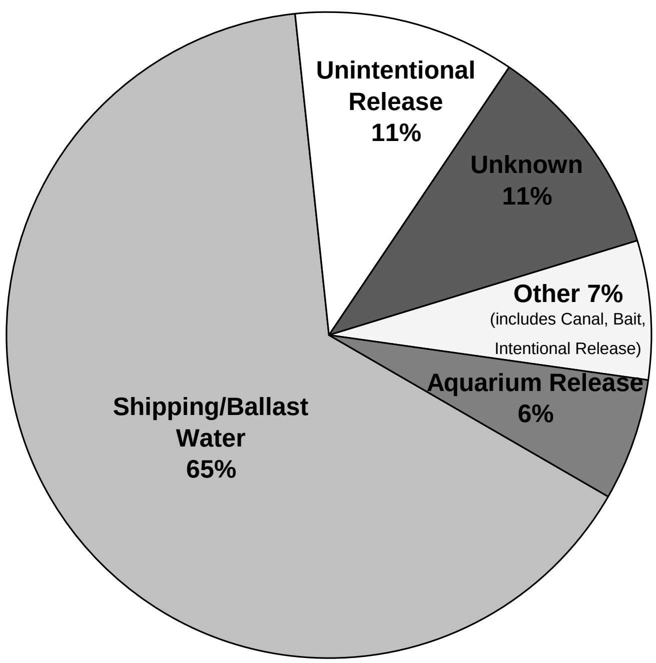

Figure 2. Sources of Great Lakes species invasions from 1960–2006 (based on data provided in Appendix A, which are derived from NOAA, 2007a).

3) Vessels may use an alternative environmentally sound method of ballast water management that has been submitted to, and approved by, the Commandant of the USCG or an authorized representative before the vessel's voyage (33 CFR 151.1510).

Compliance with these ballast regulations has been high. From July 1999 to June 2001, 93% of regulated ships reported performing the necessary level of active BWE before arriving in Massena. The remaining 7% of ships were forced by the USCG to perform some sort of alternative action, such as decontamination, prior to being allowed to enter the Great Lakes (USCG, 2001). USCG reported high rates of BWE compliance (89 +/- 10%) for the period 1992–2004 (Ruiz and Reid, 2007).

Ballast water exchange at sea works first by the dilution effect. Assuming a homogenous distribution of flora and fauna in the ballast tank, 95–99% of the fresh water (and organisms) would be replaced by seawater (NRC, 2008). Second, BWE can be effective since most remaining freshwater organisms in the ballast tank are killed by the resulting high salinity levels.

Despite these ballast water regulations, at least 13 new NIS are believed to have entered the Great Lakes from ballast water since 1993 (Appendix A; IAGLR, 2002; Holeck et al., 2004; NOAA, 2007a). It is possible that BWE has been effective and that all the species found after 1993 were introduced before 1993; it just took many years to detect and report them (Costello et al., 2007a). Others have noted that organisms can survive BWE, and that BWE practices have not been completely effective in terminating the flow of NIS into the Great Lakes (e.g., Grigorovich et al., 2003a, b; Holeck et al., 2004; Drake et al., 2005; Ricciardi, 2006). Recently, more stringent regulations have been implemented (e.g., 73 FR 37, p.9950), which should reduce the flow of NIS into the Great Lakes from commercial shipping.

2.1.4. NOBOB Vessels and Species Invasions

Vessels fully loaded with cargo generally carry no ballast water on board. Vessels with no ballast-on board, commonly called NOBOB vessels, entering USGLP were not required to flush their ballast tanks or use an alternative treatment method until 2006. It is possible that invasions may have occurred from NOBOB vessels arriving in the Great Lakes (MacIsaac et al., 2002; Johengen et al., 2005). The almost completely empty ballast water tanks in NOBOB vessels often still contain residual sediment and water from previous ballasting operations. These residuals cannot be pumped from the ballast water tanks since the pump-out ports cannot be closer than several inches from the bottom of the tank. Residual material in ballast water tanks of NOBOB vessels can contain thousands of live organisms, their resting eggs and cysts, and microorganisms, including human pathogens, all of which may be discharged into Great Lakes waters (Johengen et al., 2005). When a NOBOB vessel off-loads cargo at a Great Lakes port of call it often takes on Great Lakes water into its ballast tanks to reestablish ballast. This pumped in freshwater mixes with the residual material in the ballast tanks, thereby increasing the viability of organisms. When such a NOBOB vessel then moves to another port to take on cargo, it may then discharge some or all of the recently acquired ballast water, along with the NIS from the earlier residual material.

NOBOB vessels currently account for about 90% of all inbound traffic to the Great Lakes (MacIsaac et al., 2002). Due to the number of potential invasive species in the residual material in NOBOB vessels and due to the large relative proportion of NOBOB vessels entering the Great Lakes, NOBOB vessels could pose a significant invasion risk. MacIsaac et al. (2002) found that for bacteria, copepods, cladocerans, and rotifers, NOBOB vessels may be exerting 10 to 100 times as much propagule pressure as vessels with ballast on-board complying with the regulations.

2.1.5. Other Options for Controlling Species Invasions From Ballast Water

As a result of the threat from NOBOB vessels, Canada developed mandatory regulations in 2006, requiring that transoceanic NOBOB vessels arriving in Canada undergo ballast flushing to eliminate fresh or brackish water residuals in their ballast tanks. Coastal vessels entering Canadian ports must comply with fairly similar requirements, only the BWE or ballast flushing must occur in an area only 50 nautical miles from shore (GLBWWG, 2008). Since August 2005, NOBOB vessels entering U.S. waters have been strongly encouraged, but not required, to conduct saltwater flushing before entering the Great Lakes (71 FR 18, pages 4,605–4,606). The St. Lawrence Seaway Development Corporation published regulations, which became effective at the start of the 2008 navigation season, requiring all NOBOB vessels that have operated outside the exclusive economic zone (usually 200 miles from the United States) to conduct saltwater flushing of their ballast tanks before transiting the St. Lawrence Seaway, regardless of whether their destination is a U.S. or Canadian port (73 FR 37, p. 9,950).

It is not yet possible to measure the effectiveness of recent regulations or guidelines because there is a time lag between when a species is transported, colonizes, and reproduces to a large enough population, to be detected and reported. However, the National Research Council recommends that a binational science-based surveillance program be established to monitor for aquatic invasive NIS (NRC, 2008). The recommended program should involve dedicated lake teams, as well as academic researchers, resource managers, and local citizens groups, and it should leverage existing monitoring activities whenever possible.

NOAA is testing the effectiveness of BWE along with other various methods to treat ballast water using mechanical (e.g., filtration and separation), physical (e.g., sterilization by ultraviolet light, ozone, heat, electric current, or ultrasound), and chemical (e.g., chlorine dioxide) methods (NOAA, 2007b). The State of Michigan has established its own ballast water legislation, and other Great Lakes states are considering similar regulations (NRC, 2008). In 2007, the Michigan Department of Environmental Quality started prohibiting ballast water releases from oceangoing vessels into Michigan waters until a permit was issued by the state. Permits require one of four approved treatments, either sodium hypochlorite, chlorine dioxide, ultraviolet light radiation treatment preceded by suspended solids removal, or de-oxygenation (MDEQ, 2008). Because Michigan is currently an import state, there have been no permit applications to discharge ballast water into Michigan ports since Michigan's law was implemented in 2007 (telephone conversation on August 8, 2008 between Barry Burns, Michigan Department of Environmental Quality, and Vic Serveiss, U.S. EPA, NCEA). Therefore, oceangoing vessels visiting Michigan ports have not needed to install the Michigan approved ballast water treatment methods.

2.2. CONCEPTUAL FRAMEWORK

Owing to the fact that invasive species are a major threat to ecosystems, there is a need to develop predictive tools and to demonstrate their use to natural resource managers as they consider ways to manage the problem. The approach used in this assessment, as shown in Figure 3, is based on Williamson's (1996) conceptual framework regarding biological invasions. Specifically, Williamson's thesis states that successful invasions are best predicted by knowing the propagule pressure (i.e., the number of larvae/individuals entering a new area) and matching the invaded habitat with the habitat in the invader's historical range.

2.2.1. Propagule Pressure

Propagule pressure is a composite measure of the number of individuals of a species released into a region to which they are not native. It incorporates estimates of the absolute number of individuals involved in any one release event (propagule size) and the number of discrete release events (propagule number). The probability of establishment of an introduced species increases as propagule pressure increases (Menges, 1998, 2000; Simberlof and von Holle 1999; Kolar and Lodge, 2001). In considering the sources of propagules to the Great Lakes, ballast water becomes the primary concern as shown in Figure 3.

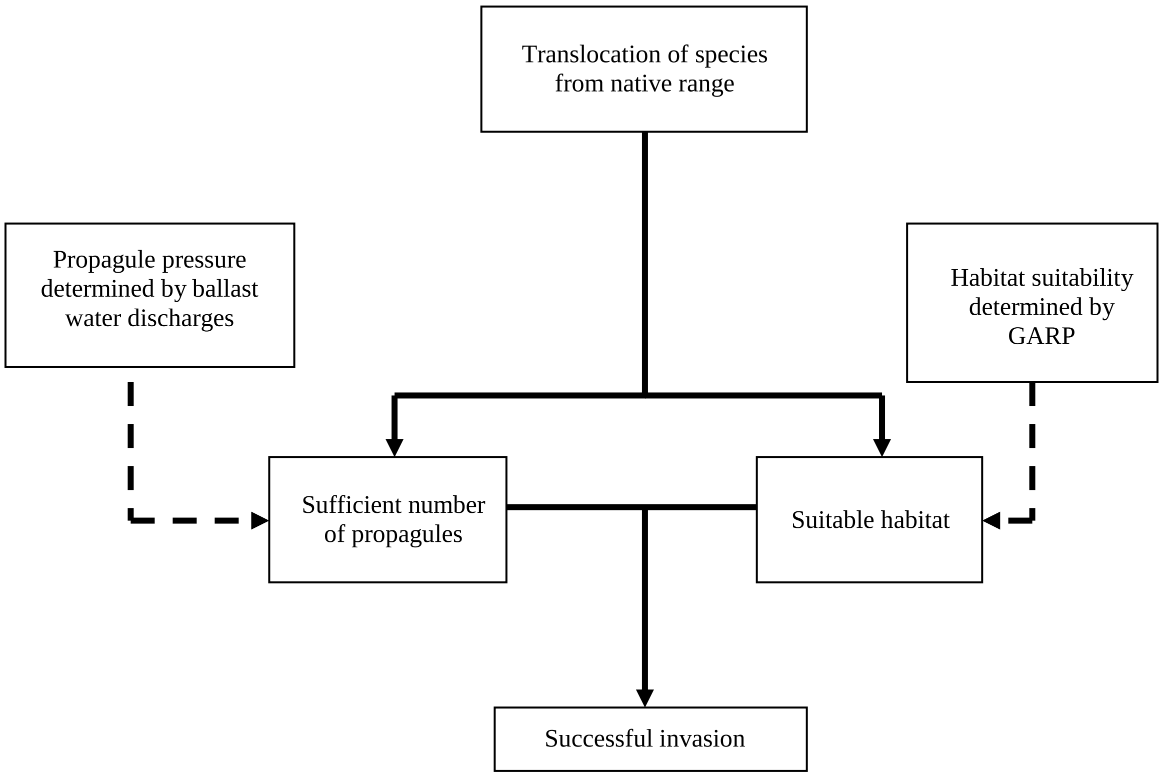

Figure 3. Conceptual framework for predicting future introductions of nonindigenous species into the Great Lakes of the United States.

The condition and life stage (resilient resting stages compared with sensitive juvenile stages) of propagules will also strongly affect the probability of establishment (Smith et al., 1999; Hayes and Hewitt, 2000; Wonham et al., 2001). Thus, management actions that reduce the number of released individuals, the number of introduction events, and the health of individuals released are likely to reduce the risk of invasion. Unfortunately, detailed quantification of these factors is limited and thus surrogate measures become necessary to estimate propagule pressure. As shown in Figure 3, the conceptual approach for this study uses ballast water discharge data as a surrogate measure for propagule pressure. Current scientific understanding of invasion biology suggests strongly that consideration of propagule pressure should be a major component of an assessment.

2.2.2. Habitat Suitability

2.2.2.1. *Species Distribution Modeling*

Assessing the degree to which a new environment is similar to the donor environment is a reasonable starting point to try to answer the question “Is a species likely to survive in this environment if it were introduced here?'' Good computer-based tools are available that provide a first-cut broad geographical answer to the question. Standard methods for modeling suitable habitat include traditional multivariate statistical methods (e.g., discriminate analysis, multiple regression, logistic regression), often coupled with geographic information systems (GIS) (e.g., Ramcharan et al., 1992; Buchan and Padilla, 2000). More recent methods that are tailor-made for identifying potential ranges include CLIMEX (Sutherst et al., 1999), Genetic Algorithm for Rule-Set Production (GARP) (Peterson and Vieglais, 2001; Drake and Bossenbroek, 2004) all of which are embodied in user-friendly and readily available software. Predicting suitable habitat is also possible for aquatic environments (Drake and Bossenbroek, 2004; Marchetti et al., 2004a), but currently less tractable than for terrestrial habitats because: (1) fewer aquatic physico-chemical data are available in appropriate electronic formats, and fewer distribution data have been collected for aquatic species; (2) terrestrial climatic data are often poor predictors of the aquatic environment; and (3) strongly predictive environmental variables for establishment are unknown for many aquatic species (Carlton et al., 1995). All of these predictive models have at least two intrinsic limitations. First, environment matching assumes that no evolution will occur in the nonindigenous species with respect to habitat requirements (Cox, 2004; Sakai et al., 2001). Second, biotic interactions in a new environment may limit or facilitate establishment independent of any climatic match (Torchin and Mitchell, 2004).

2.2.2.2. *Genetic Algorithms for Rule-Set Production (GARP)*

GARP develops predictions of the potential geographic extent of an invasion by first modeling relationships between known occurrences of a species and the corresponding abiotic environmental variables, and then projecting the modeled species-environment relationships to a region of interest. GARP modeling requires two types of inputs: (1) spatial data describing the location of species based on occurrence data and (2) digital data layers describing environmental conditions at locations coinciding with the species occurrence data. GARP develops outcomes consisting of a set of conditional rules in the form of 'if-then' statements that describe the ecological conditions of the species in its studied habitat (Stockwell and Peters, 1999). Habitats are matched by searching iteratively for nonrandom correlations between a species' known location and a variety of environmental parameters.

The GARP method is considered to be based on models of genetic evolution (Holland, 1975) because GARP models are built by an iterative process of rule selection, evaluation, testing, and incorporation or rejection of the rules produced (Peterson et al., 1999). With each iteration, rules are modified by selection, crossover, and mutation—resembling the genetic process. In the first phase, GARP selects a random population, based on a combination of initial prediction rules, which might represent suitable solutions for the problem. The fitness to the characteristics of the population is then evaluated for each pixel in the search space. If the performance of the rule is adequate as determined by the rule's significance measure, the rule is retained for further runs of the algorithm, until an end condition—consisting of a convergence limit and maximum number iterations—is satisfied (Stockwell and Peters, 1999). One of the main advantages of GARP is its ability to apply different types of rules at once to explain complex nonlinear relationships between the species occurrence and predictive variables. This implies that the algorithm can 'learn' through each iteration and apply the type of rule that describes best the relationship among the variables for any particular portion of the search space (i.e., all possible combinations of variables) (Stockwell and Peters, 1999).

2.2.2.3. *Modification of GARP for Aquatic Systems*

GARP has been used to predict a variety of species distributions including birds in Mexico (Feria and Peterson, 2002; Stockwell and Peterson, 2002; Anderson et al., 2003) and North America (Peterson and Cohoon, 1999); rodents in South America (Anderson et al., 2002 and Anderson et al., 2003); and invasive vector disease insects in South America (Peterson et al., 2002). This may be the first time that remote sensing data were used in conjunction with GARP to predict invasive freshwater aquatic species.

3. METHODS

For a nonindigenous species (NIS) to become established in the Great Lakes, the species must (1) move or be transported from its existing spatial range to the Great Lakes and (2) be able to colonize, become established, and spread in the new environment (Williamson, 1996; Theoharides and Dukes, 2007). Others have also combined these two analyses to predict NIS spread, though different names were used to characterize their respective efforts. Leung and Mandrak (2007) combined invasability and propagule pressure, to make predictions about zebra mussel spread. Herborg et al. (2007) combined introduction effort and environmental niche models to predict the potential spread of the Chinese mitten crab (*Eriocheir sinensis*) in North America. To address both requirements for successful invasion, we used information on ballast water discharges as a surrogate for propagule pressure and the Genetic Algorithm for Rule-Set Production (GARP) model to determine the suitability of habitat by matching the invaded habitat in the Great Lakes with the species native habitat.

3.1. HABITAT SUITABILITY USING THE GARP MODEL

Habitat suitability was modeled using a species distribution model to compare the environmental conditions associated with the distribution of invasive species in their home range with the conditions found in the Great Lakes. GARP was selected because it is a well established model, is one of the few models that accepts presence-only distribution data (e.g., locations where the species has been observed without corresponding information on where the species has *not* been observed), and incorporates multiple statistical approaches into a single framework.

3.1.1. Selection of Modeled Species

The first step to using GARP is to select the species to be evaluated. Species of interest (i.e., those thought to be potential invaders of the Great Lakes system) were identified based upon a review of the literature and best professional judgment. We searched for species' scientific names and the keywords "invasive" and "Great Lakes" in publications after 1990 using Web of Science and international databases, such as Fishbase (Froese and Pauly, 2007) and Global Invasive Species (IUCN, 2006). We augmented this general search strategy to include authors who have studied Great Lakes invasive species to find potentially relevant papers that did not specifically include the terms "invasive" or "Great Lakes" in the article's title, abstract, or keywords. Other sources include the U.S. Geological Survey, the States' Department of Natural Resources (for states adjacent to the Great Lakes), the Canadian Wildlife Federation, and the Great Lakes Panel on Aquatic Species. We initially identified 156 species of concern based on a review of the literature (see Appendix B).

Of the 156 species identified, using best professional judgment it was determined that 58 of these species pose the most risk for their potential to invade the Great Lakes and reach population levels that could cause ecological impact (see shaded entries in Appendix B). Twenty-eight of the 58 species identified are already in the Great Lakes. The remaining 30 species, not yet reported in the Great Lakes, were evaluated to see if sufficient data was available to run the GARP model. GARP requires at least 30 spatially unique occurrence points (i.e., latitude-longitude coordinates of locations where the species has been reported) to develop robust predictions (Stockwell and Peterson, 2002). For a variety of reasons, only 9 of the 30 species had sufficient data to be modeled. Of these nine, five species have not yet been detected in the Great Lakes, and the other four have been reported only infrequently. At the request of EPA's Great Lakes National Program Office, we modeled five additional species already found in the Great Lakes. Two of the five species, the zebra mussel and round goby, are currently widespread throughout the Great Lakes. The three other species, ruffe (*Gymnocephalus cernuus*), quagga mussel, and New Zealand mud snail (*Potamopyrgus antipodarum*), have been reported as established in the Great Lakes but are not yet widespread (USGS, 2007). Thus, a total of 14 NIS species were evaluated using the GARP model for the availability of suitable habitat in the Great Lakes (Table 1).

3.1.2. Model Inputs and Environmental Data Layers

3.1.2.1. *Environmental Data Layers*

Six specific parameters were used to define environmental variables suitable to develop data layers for GARP: mean, maximum, and minimum monthly surface water temperature; chlorophyll *a* concentration; the diffuse attenuation coefficient; and normalized water-leaving radiance (Table 2). These six parameters were chosen because they represent important environmental variables that tend to control the distribution of species. Three of the parameters are measures of temperature that affects species distribution worldwide. The other three are related to the productivity of aquatic systems. Chlorophyll *a* is an indicator of biological productivity. Water clarity, as measured by diffuse attenuation coefficient and the water-leaving radiance, is an indicator of the trophic state of the system. Water clarity also influences the depth of the photic zone and the ability of primary producers to acquire sunlight and flourish. Although some of these six data layers may be covariant, GARP is considered to be relatively robust to collinearity (Kluza et al., 2007). For the species modeled in this report, no literature

Table 1. Fourteen species modeled using GARP and the source of occurrence data

Species common name and year reported	Description	Useful occurrence data records	Data source
Species already widespread in the Great Lakes			
Gymnocephalus cernuus, ruffe—1986	fish	229	GBIF[a] USGS[b]
Dreissena polymorpha, zebra mussel—1988	mollusk	268	GBIF, USGS
Dreissena bugensis, quagga mussel—1989	mollusk	83	USGS
Neogobius melanostromus, round goby—1990	fish	145	GBIF, USGS
Potamopyrgus antipodarum, New Zealand mud snail—1991	mollusk	867	GBIF, USGS
Species reported in the Great Lakes but either not extensive or lacking spatial data			
Cercopagis pengoi, fishhook waterflea—1998	crustacean	152	GIS[c]
Scardinius erythrophthalmus, rudd—1989	fish	57	GBIF, CIMS[d]
Proterorhinus marmoratus, tubenose goby—1990	fish	171	CIMS, BSRDB[e]
Alosa aestivalis, blueback herring—1995	fish	408	GBIF
Species not yet reported in the Great Lakes			
Corophium curvispinum, N/A	amphipod	65	GBIF, CIMS
Neogobius fluviatilis, monkey goby	fish	50	CIMS
Pomatoschistus minutus, sand goby	fish	102	GBIF, BSRDB
Rutilus rutilus, roach	fish	117	GBIF, CIMS
Tinca tinca, tench	fish	50	CIMS

[a]Global Biodiversity Information Facility, 2007 (http://www.gbif.org/).
[b]USGS Nonindigenous Aquatic Species Database, 2007 (http://www.usgs.gov/pubprod/maps.html).
[c]Regional Biological Invasions Center. INVADER, 2007 (http://www.zin.ru/projects/invasions/gaas/invader/invader.htm).
[d]Caspian Interactive Map Service, 2007 (http://ipieca.unep-wcmc.org/imaps/ipieca/caspian/viewer.htm).
[e]Black Sea Environment Programme Red Data Book, 2007 (http://www.grid.unep.ch/bsein/redbook/index.htm).

Table 2. Environmental variables used to predict locations that would provide suitable habitat for the 14 modeled species in the Great Lakes. The spatial resolution of each of these six data layers is ~21 km^{2}.

Variable	Units	Source	Collection period
Mean monthly temperature	°C	AVHRR[a]	1985–2002
Maximum mean monthly temperature	°C	AVHRR	1985–2002
Minimum mean monthly temperature	°C	AVHRR	1985–2002
Chlorophyll *a* concentration	mg/m^3	MODIS[b]	2001–2005
Diffuse attenuation coefficient (K490)	m^{-1}	MODIS	2001–2005
Normalized water-leaving radiance (nLW551)	mW/(cm^2 µm sr)	MODIS	2001–2005

[a]Advanced Very High Resolution Radiometer.
[b]Moderate Resolution Imaging Spectroradiometer.

reliably supports the a priori weighting of any of the selected environmental variables as more important than any other variable.

3.1.2.2. *Environmental Data Sources*

Water temperature was derived from the satellite-based Advanced Very High Resolution Radiometer (AVHRR) Oceans Pathfinder Sea Surface Temperature Data set and is accurate to within 0.5ºC (http://podaac-www.jpl.nasa.gov/sst/). We used temperature data from 1985 through 2001. We used the MMT data to calculate three data layers for use by the GARP models: Maximum MMT, Mean MMT, and Minimum MMT. Maximum MMT represents the highest value of each of the 12 sets of monthly averages of data. To calculate the mean MMT, we assigned each pixel the average of the 12 monthly averages. The minimum MMT represents the lowest value of each of the 12 monthly averages. Chlorophyll *a* concentrations were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor. The Diffuse Attenuation Coefficient (K490) relates to the presence of light-scattering organic and inorganic particles in the water column and is inversely related to water clarity (http://oceancolor.gsfc.nasa.gov/PRODUCTS/k490.html). The normalized water-leaving radiance is the radiance of reflected light at 551 nm. Since water absorbs very little light at 551 nm, increases are due to light reflection out of the water, which are usually caused by nonabsorbing particles such as suspended sediments.

3.1.3. Use of GARP model

A stand-alone version of Desktop GARP (version 1.1.6) (Scachetti-Pereira, 2002) was used to model the distributions of the first nine NIS; Desktop GARP (version 1.1.6) within Open Modeler (version 1.0.5) was used for five of the species. There is no functional difference between the two desktop versions used. GARP relies on species occurrence or presence data and synthetic species absence data, termed pseudo-absence data. The use of pseudo-absence data is an intrinsic and accepted part of GARP modeling. To develop pseudo-absence data, investigators must identify a region surrounding the occupied range of the target species to which the species could easily spread. It is assumed that the reason the species is absent from the surrounding region is because environmental conditions are different and outside the species tolerance limits. The established range includes the species' occupied range and a surrounding unoccupied range. The pseudo-absence data are selected from a subset of locations within the investigator-defined study area that are not currently occupied by the species. The pseudo-absence points represent the locations presumed to be unsuitable for the target species and provide a contrast against which occurrence models can be developed. A new, random selection of pseudo-absence data was made for each model iteration.

GARP divides the occurrence data into training and test data sets. Test data sets are reserved to test predictive performance of models that are developed using the training data sets. GARP then uses the training data and one of the individual algorithms to develop a model, and the model is tested and improved until the best solution is found. For each of the 14 modeled species, GARP randomly assigned the data into 50/50 splits of training and test data sets. We produced 1,000 model runs from the training data sets (i.e., 14,000 total GARP runs) that are all slightly different and vary in predictive ability. Each individual GARP model run produces a map of '0s and 1s,' representing predicted absence and presence, respectively. The area of predicted presence for each run is simply the proportion of pixels that have a predicted value of 1. We used a procedure described by Anderson et al. (2003) to select the best subset of runs generated for each species to develop a final composite range map. The model is run for each species and compared to see which runs best predicted the known occurrence locations and omitted the fewest of the known occurrence locations of the modeled species. For each species, we retained the models with the lowest omission error rates when compared to the results of the test data sets.

Next, the median area of predicted presence for each species (simply the number of pixels that have a predicted value of 1) was determined from the models with the lowest error rates. The subset of models within 50% of this median value was then selected to form the final prediction of habitat suitability. Every pixel on the model output represents either a predicted presence or a predicted absence. The final composite prediction maps reflect the sum of the results from the models; that is, each pixel was assigned a value ranging from zero (i.e., no models predict presence) to 100 (i.e., all models predict presence). This value represents the relative environmental suitability of each location.

The final habitat suitability maps reveal the frequency with which a pixel is predicted to provide suitable habitable and depict the repeatability of that prediction with different models developed from different, randomly divided, training data sets. The higher the value of a pixel, the more likely the modeled species is expected to find suitable habitat at that location. Another interpretation is that pixels that have higher values represent higher quality habitat for the modeled species because these locations are predicted to be suitable by more models. Those pixels that are predicted to provide highly suitable habitat within the Great Lakes are characteristic of environments similar to those known to be occupied by the modeled species in their natural range.

3.1.4. Assumptions and Limitations

The use of species distribution models to predict the spread of NIS required three assumptions: (1) the available distribution data describe the full range of environmental conditions that the modeled species can tolerate; (2) the environmental variables selected to model potential spread govern the current and future geographic ranges of the NIS under study; and (3) biotic factors do not influence species distributions, unless such biotic factors can be included explicitly as environmental data layers. Failure to meet these three assumptions can limit the ability of GARP to predict invasive spread and can result in two types of errors, which arise from two broad sources: (1) limitations inherent in the data or the model themselves (these are often termed *data errors*), and (2) ecological processes relevant to the distribution of the species that are not included in the model (often called *biological errors*).

3.1.4.1. *Data Errors*

A major source of error in GARP modeling is the lack of complete occurrence data for the modeled species. GARP requires occurrence points that are both representative of the full range of environmental conditions associated with presence of the species and of the area inhabited by the species. In reality, the actual occurrence points reflect bias in both sampling and reporting efforts, which is influenced by resources, accessibility, transportation corridors, and visitation frequency. Further, the occurrence data extracted from online databases were collected *ad hoc*, and not for the purposes of constructing distribution models. If occurrence data do not describe the full environmental tolerances of the species, predictions will underestimate areas where a NIS could survive and establish itself in a particular region of the Great Lakes. For example, occurrence data for the monkey goby and the tench were available only for their distributions within the Iranian portion of the Caspian Sea. This may be part of the reason these two species have the smallest predicted distributions of any modeled species within the Great Lakes, perhaps suggesting under-prediction. Therefore, the predicted habitat suitability might not include all environments which the NIS could invade.

Some occurrence data were discarded because they did not fall in waters defined by the 21 km^2 spatial resolution available for the environmental data layers. These discarded occurrence points are more than likely in lakes and rivers smaller than 21 km^2 that could not be resolved by the satellite sensors used in this study. GARP requires that species absence data be developed by accurately selecting the region for which the species is absent because environmental conditions are different and outside the species tolerance limits. Determining the extent of the GARP prediction region assumes that these pseudo-absence points really are uninhabitable, and not, for example, simply suitable environments to which the target species has not yet dispersed.

Model errors can also result from modeling habitat suitability with a limited set of environmental variables. While we know that each of the six selected variables has a strong influence on species distributions, other abiotic factors known to influence species distribution are not captured by the variables that we used. For example, salinity impacts the survival of many aquatic organisms (Bailey et al., 2005), but salinity is not included in the GARP analysis. We were unable to locate a global database with spatial salinity data at the same scale of resolution as the six variables included in this study. Including salinity at a coarser resolution would have introduced coarse range boundaries where salinity was the limiting factor. Bathymetry data were available, but not used, because species occurrence data did not include the depth at which the species was found. As many aquatic species may only survive in waters to a certain depth, the model would show some deeper waters as suitable habitat and may contradict what is known about the depth limitations of a particular species. Nutrient levels may also be biologically important to some NIS. Calcium concentrations, for example, are likely a limiting factor for zebra and quagga mussel distributions (Cohen, 2007), but global spatial databases of calcium concentrations are not available. Failure to include such key factors can lead to over-predictions (predicting that the species can survive in an area where the habitat is actually unsuitable due to the environmental variable not included in the model). Detailed knowledge of the target species is required to reliably determine if one of more key factors have been excluded from the models. Because the consequences of under-prediction (failing to identify a place where NIS can establish) are much greater than those resulting from over-prediction, our approach is conservative and errs on the side of over-prediction.

3.1.4.2. *Biological Errors*

Even if the environmental variables could accurately reflect the abiotic factors controlling species distributions, the predictions are developed without considering biotic factors such as competition, predation, and parasitism. Biotic factors also are important determinants of the distributions of species, but it is not ordinarily possible to obtain data on biotic factors for incorporation into GARP, and failure to consider such factors can lead to poor predictions (e.g., Fitzpatrick et al., 2007). In a new environment, a species may be freed of restrictions (e.g., a predator may not exist), encounter new challenges in a new environment (e.g., competition from a species with a similar niche), or evolve and adapt. Thus, it is difficult to predict whether the impacts of excluding biotic factors would inhibit establishment or expand the colonization range of an introduced species. The fire ant in the southeastern United States is an example of an introduced NIS that established itself beyond the predicted range of a species distribution model, perhaps due to biotic factors that encouraged the species successfulness (Fitzpatrick et al., 2007).

3.1.5. Testing the GARP Model Performance

Despite the limitations described above, species distribution models are currently one of the few techniques readily available to predict the potential for an invasive NIS to become established in an area of interest (Peterson, 2003). Therefore, species distribution models should be considered a key component of a multi-faceted NIS prevention and management plans (Mack, 1996; Peterson and Vieglais, 2001).

The GARP model outputs were validated by testing the ability to correctly predict independent data that were not used to develop the model. Specifically, we evaluated how well GARP performed by assessing how well the model predicted the known distributions of three NIS that are already widespread throughout the Great Lakes using distribution data collected outside of the Great Lakes. Thus, occurrence data for the zebra mussel, ruffe, and New Zealand mud snail within the Great Lakes were withheld from the GARP model runs and the model tested for its ability to correctly predict suitable habitat. The performance of the GARP model was assessed using area under the curve of the Receiver Operating Characteristic curve (Sing et al., 2005). Area under the curve is a threshold-independent evaluation of model performance that measures the ability of the model to differentiate between sites where a species is present from sites where it is considered absent. Area under the curve represents the probability that, when a predicted-present site and a predicted-absent site are drawn at random, the predicted-present site will have a higher predicted value. The effectiveness of the GARP modeling is based on the scale for determining model performance devised by Swets (1988). More details on the model validation approach we used are provided in Appendix C.

3.1.6. Determining GARP's Power to Predict

GARP and other species distribution models make predictions about the suitability of habitat for a particular species within a region of concern. These models are developed by comparing the environmental conditions in the region containing the species to those found in the region of concern, in this case the Great Lakes. As noted previously, predictions from GARP and other species distribution models are valid only for the range of environmental conditions on which the model was developed. Reliable predictions cannot be made for any environment within the Great Lakes that are not similar to those found within the region containing the distribution of the study species. GARP does not have a method for determining when a reliable prediction cannot be made, and, instead, may report such environments as a predicted absence when they may indeed be habitable by the NIS. Reporting such areas as unsuitable habitat may be erroneous and could misdirect management attention away from these potentially susceptible areas.

We used a technique called "power-of-prediction analysis," devised expressly for this project, to distinguish between areas of predicted absence from areas for which a reliable prediction cannot be made (null prediction). Like GARP models for individual species, power of prediction analysis uses GARP to develop predictions. However, instead of developing a model of environments represented by the distribution of the study species, power of prediction analysis attempts to (1) model *all* environments within the region containing the distribution of the species and (2) compare these environments with those characterizing the Great Lakes.

To perform a power of prediction analysis, we identified a region encompassing the full range of environmental conditions to which the species is known to occur. For example, consider a hypothetical species in the Caspian Sea reported in regions with water temperatures between 15 and 20°C but not reported in regions with a water temperature from 10 to 15°C. GARP would then predict that places in the Great Lakes with water temperatures between 15 and 20°C provide suitable habitat and that all regions with temperatures less than 15°C are unsuitable. However, temperatures in the Great Lakes range from 6 to 20°C. This presents a problem regarding areas within the Great Lakes that range from 6 to 10°C, which is below any temperature found in the Caspian Sea. When considering temperature, in an isolated, univariate way, it is likely the species would not tolerate temperatures from 6 to 10°C if it could not tolerate 10 to 15°C. Yet, it is not correct to assume that all locations beyond a particular extreme, in this case less than 10°C, are unsuitable. The species experiences the environment in a multivariate manner and that could produce surprising and counterintuitive results. For example, a terrestrial species might be able to survive and reproduce in locations that were hotter, if they were also wetter.

Even though GARP cannot make a reliable prediction for such areas, GARP and many other species distribution models will report areas with temperatures outside of the range from 10 to 20°C as unsuitable for the species, when in reality the GARP model has no information to draw such a conclusion (Heikkinen et al., 2006). We used power of prediction analysis to denote the geographic extent of predictive power. We performed power of prediction analyses for 11 of the 14 modeled species. Power of prediction analysis was not performed for two of the invasive species already established in the Great Lakes—quagga mussel and round goby—due to the lack of occurrence data outside the Great Lakes. Also, no power of prediction analysis was needed for the blueback herring because GARP model runs predicted that the blueback herring can encompass essentially the entire area of the Great Lakes. Appendix D provides more details on how we applied the power of prediction analysis to this study.

3.2. DETERMINING PROPAGULE PRESSURE USING BALLAST WATER DISCHARGE DATA AND VESSEL TRAFFIC PATTERNS

The probability that a NIS can become established increases with increased propagule pressure (Simberloff and Von Holle, 1999; Kolar and Lodge, 2001; Lockwood et al., 2005). Propagule pressure, as explained in the introduction, is the number of individuals (including larvae, seeds, and spores) released in a nonnative region over a specified period of time (Simberloff and Von Holle, 1999). We used two sources of data as a surrogate for propagule pressure: Data from the U.S. Coast Guard's (USCG's) National Vessel Movement Center (NVMC) and the National Ballast Information Clearinghouse (NBIC). Ultimately, the NBIC data proved to be the most useful in predicting propagule pressure. The NBIC collects, analyzes, and interprets data on ballast water management practices of commercial ships that operate in the United States. NBIC was created by the USCG and the Smithsonian Environmental Research Center (NBIC, 2008) pursuant to the National Invasive Species Act of 1996 (16 USC 67 § 4712). NBIC's data are electronic and are accessible on the Internet (http://invasions.si.edu/nbic/).

3.2.1. Analysis of Ballast Water Discharge Data

The principal aim of the NBIC database is to quantify the amounts and origins of ballast water discharges in U.S. coastal systems and to determine the degree to which such water has undergone open-ocean exchange or alternative treatments designed to reduce the likelihood of ballast-mediated invasions by exotic species (NBIC, 2008). NBIC data come from national ballast water management reporting forms submitted to the USCG by vessels arriving to ports and places in the United States. The data includes port of arrival, date of arrival, and last port of call, along with the source of ballast water (either a specific port or a latitude/longitude coordinate at sea), date of ballast water intake, type of ballast water management, date discharged, and the volume discharged.

This database allowed us to locate the source of ballast water and to determine those Great Lakes ports receiving the most ballast water discharges with the most potential to transport NIS. NBIC data from for 2004–2007 for Illinois, Indiana, Michigan, Minnesota, New York, Ohio, Pennsylvania, and Wisconsin were downloaded and analyzed using a relational database (Microsoft® Office Access). The original data set contained records of 44,461 vessel arrivals and 121,031 ballast water discharges. By excluding records of vessels arriving in ports outside the Great Lakes system, the NBIC data set was reduced to 63,574 ballast water discharges.

Since NIS that were in the ballast tank before ballast water exchange at sea may survive the exchange and can later be released in the Great Lakes, we needed to determine the original source of ballast water. Discharges of ballast water that originated within the Great Lakes (which we defined as west of Quebec City, see Figure 1) was excluded along with discharges of ballast water that was derived from outside 200 nautical miles of any shore and deeper than 2,000 m. We analyzed the remaining 618 ballast water discharges because these waters have the most risk of transporting NIS. We identified the most common original source of ballast water and the U.S. Great Lakes ports (USGLP) receiving the most discharges.

As discussed previously, some vessels enter the St. Lawrence Seaway declaring to have no ballast on board (NOBOB) but as they traverse the Great Lakes, they take on ballast water which can mix with residual water or sediment in the ballast tanks. We combined NBIC with NVMC data since the later includes information on the last five ports of call. Starting with NBIC records, we matched the NBIC arrival port and arrival date to the corresponding data in the NVMC data set. For each of the vessel records with matching sets of data, we obtained the last five ports of call records from the NVMC database. If one of more of the last five ports of call were not in the Great Lakes, we considered the vessel to have entered the Great Lakes with no ballast on board but containing residual material (NOBOB-RM). We then calculated the number of ballast water discharges and the volume of ballast water discharged from each of these vessels.

3.2.2. Assumptions and Uncertainty

Although NBIC employs a rigorous quality assurance and quality control protocol, the accuracy and completeness of the self-reported data cannot be guaranteed (NBIC, 2008). The NVMC data set also has limitations. Although a vessel may have stopped at a foreign port during one of its last five ports of call it does not necessarily mean that ballast water was taken on at that port. It is possible that any residual material in the ballast tank may be from within the Great Lakes and not the foreign port of call included in the last five ports of call records. This would lead to over-predicting the potential for NIS release. Similarly, it is also possible that we missed a source of residual material because it may have been picked-up sometime earlier than the last five ports of call. This would lead to an under-estimation of NIS releases. Finally, we assumed that the data from 2006–2007 used in this study are representative of discharge and shipping patterns over the past several years.

4. RESULTS

We first present results comparing the Great Lakes with the rest of the world, especially the Ponto-Caspian region with respect to six environmental parameters used to model species distribution. We next identify those locations within the Great Lakes that would provide suitable habitat for each of the 14 modeled nonindigenous species (NIS). And third, we identify the ports within the U.S. Great Lakes that received the most ballast water discharges from the vessel traffic we analyzed, including the identification of ports around the globe that provided the original source of ballast water discharged at a U.S. Great Lakes port.

4.1. COMPARISON OF THE GREAT LAKES TO THE PONTO-CASPIAN SEA

The Ponto-Caspian region has been identified as a significant source of nonindigenous species entering the Great Lakes. The comparison of the Great Lakes to the Ponto-Caspian region, based on the six environmental parameters used in the Genetic Algorithm for Rule-Set Production (GARP) modeling, reveals that the regions are indeed quite similar. Figures 4–7 illustrate the environmental conditions for those parameters used in the habitat suitability modeling as shown in Table 2. Latitudinal differences and discernable patterns in deeper open ocean waters are clearly evident.

4.1.1. Temperature

Overall, the maximum monthly temperature (MMT) shows a strong latitudinal gradient (Figure 4). The Great Lakes, shown mostly in yellow, have a spatial mean of 9.9ºC and range from 5.9º–13.7ºC. Lake Superior is colder than the other four lakes and has a spatial mean of 7.9°C with a range of 5.9°–11.1°C. The Caspian and Black Seas are somewhat warmer and less variable (in terms of maximum MMT) than the Great Lakes, with a spatial mean of 13.7°C and a range of 12.1°–16.1°C. The impact of climate change will likely cause the Great Lakes to reach MMT levels even more similar to the Ponto-Caspian Sea region (IPCC, 2007).

4.1.2. Chlorophyll *a* Concentrations

Due to upwelling, the western edges of continents display high concentrations of chlorophyll *a* (dark blue color in Figure 5), a surrogate measure of productivity. Colder arctic waters are also more productive. The global spatial mean concentration of chlorophyll *a* is 0.24 mg/m^3. The Great Lakes, shown mostly in blue in Figure 5, show a mean spatial productivity level of 1.7 mg/m^3, ranging from 0.19–62.3 mg/m^3. The Caspian and Black Seas are similar to the Great Lakes with a spatial mean of 2.2 mg/m^3 and range from 0.2–56.2 mg/m^3.

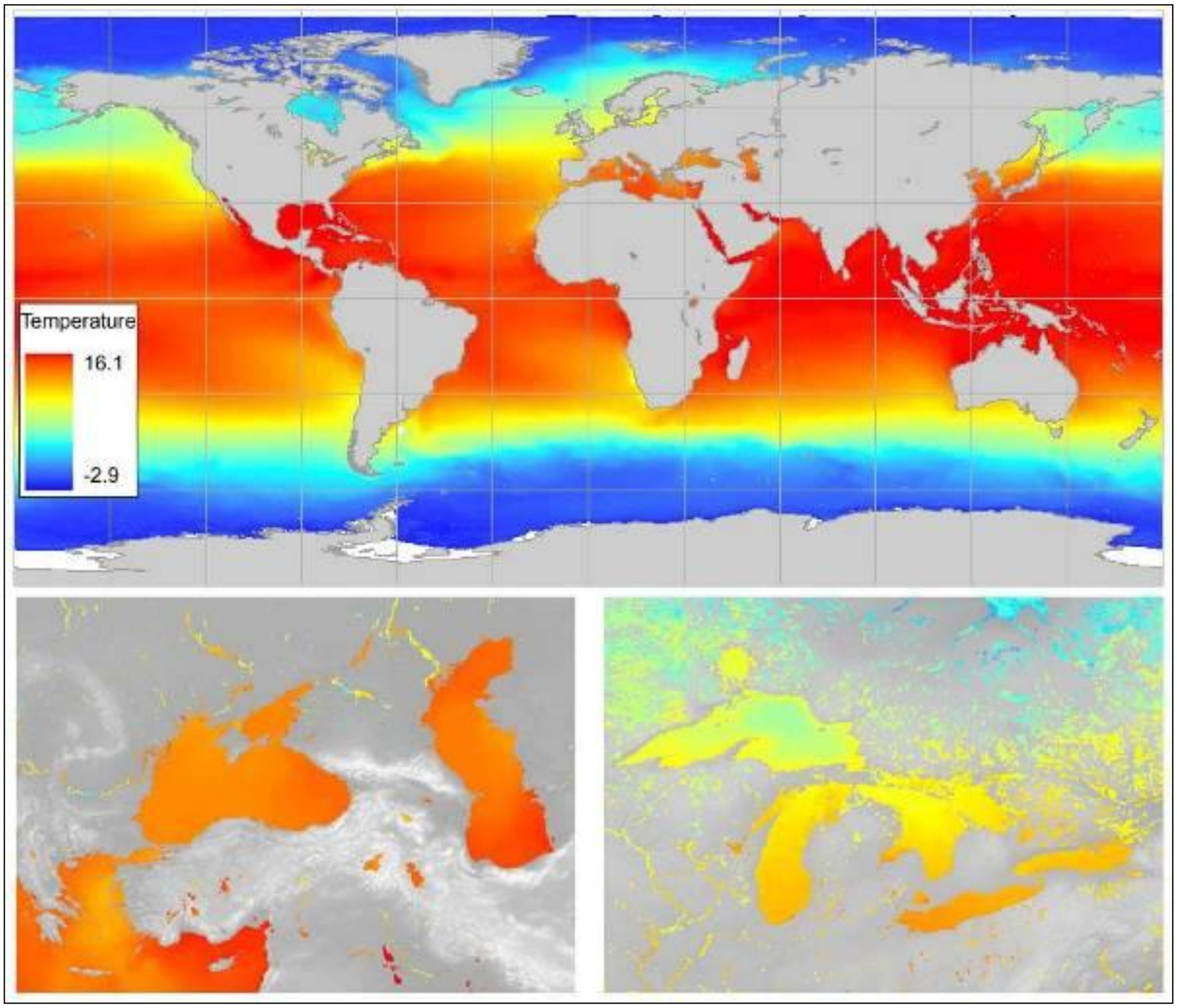

Figure 4. Maximum monthly mean temperature (MMT) (°C) as determined by AVHRR sensor (1985–2001). Warmest temperatures are indicated by red; cooler temperatures are indicated by shades of blue. Global view (top), Ponto-Caspian region (left), and Great Lakes (right).

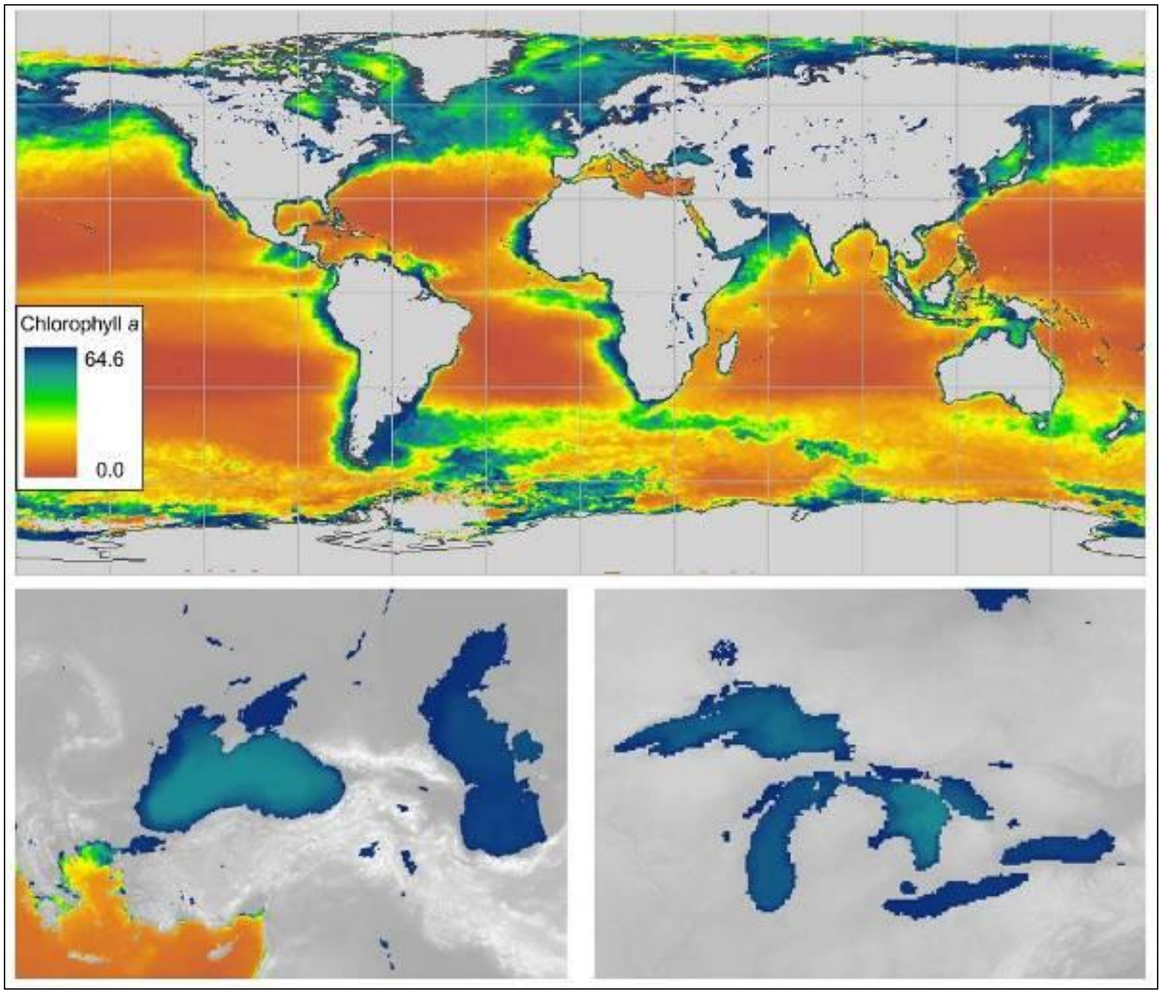

Figure 5. Average chlorophyll *a* concentration (mg/m^3) as determined by MODIS (2001–2005). High chlorophyll *a* concentrations are represented with blue and dark green. Brown and yellow indicate low concentrations of chlorophyll *a*. Global view (top), Ponto-Caspian region (left), and Great Lakes (right).

4.1.3. Diffuse Attenuation Coefficient (K490)

Overall, open ocean waters are generally clearer than waters with higher biological productivity. The more light that is scattered from the surface, the Diffuse Attenuation Coefficient (K490), the greater the amount of suspended solids, a measure of productivity. Greater K490 values imply more light attenuation and lower water clarity. The global mean K490 is 0.032/m, which translates to a photic zone depth of ~144 m. The K490 of the Great Lakes, shown mostly in blue in Figure 6, is much higher than the global average and has a spatial mean of 0.099/m (equivalent to a photic zone depth of ~47 m) and ranges from 0.037–0.741/m. The Caspian and Black Seas also are fairly turbid and similar to the Great Lakes with a spatial mean of 0.11/m (photic zone depths of ~42 m) and range from 0.05–0.72/m.

4.1.4. Normalized Water-Leaving Radiance

As with the Diffuse Attenuation Coefficient, this is a measure of the productivity of waters. As shown in Figure 7, and consistent with the previous figures, waters near the continents are generally more productive. The Great Lakes have a spatial mean of 1.5 mW/(cm^2 µm sr) and a range of water clarity from 0.0–5.1 mW/(cm^2 µm sr). Lake Superior, being much deeper (averaging 147 m and with a maximum depth of 406 m) than the other Great Lakes, has a spatial mean of 0.5 mW/(cm^2µm sr) indicating that Lake Superior is less productive. The Caspian and Black Seas have a spatial mean of 2.4 mW/(cm^2 µm sr), similar to the lower Great Lakes.

4.2. HABITAT SUITABILITY FOR MODELED SPECIES

The results of using the GARP species distribution model reveals that the Great Lakes offers suitable habitat for all of the 14 modeled species in this study, with Lakes Erie and Ontario the most likely to be invaded. Five of the species modeled are already established in the Great Lakes and the remaining nine, selected from an original list of 156 species, are most likely to invade and become established in the Great Lakes. Figures 8 through 10 illustrate the suitability of habitat within the Great Lakes for the blueback herring (*Alosa aestivalis*), quagga mussel (*Dreissena bugensis*) and round goby (*Neogobius melanostromus*). Unfortunately, due to limits with occurrence data, a power of prediction analysis could not be performed for the quagga mussel and round goby. There was no reason to perform a power of prediction analysis for the blueback herring because it is predicted to find suitable habitat throughout the Great lakes. Figures 11 through 21 show the suitable habitat for the fishhook waterflea (*Cercopagis pengoi*), zebra mussel (*Dreissena polymorpha*), ruffe (G*ymnocephalus cernus*), monkey goby (*Neogobius fluviatilis*), New Zealand mud snail (*Potamopyrgus antipodarum*), tubenose goby (*Proterorhinus*

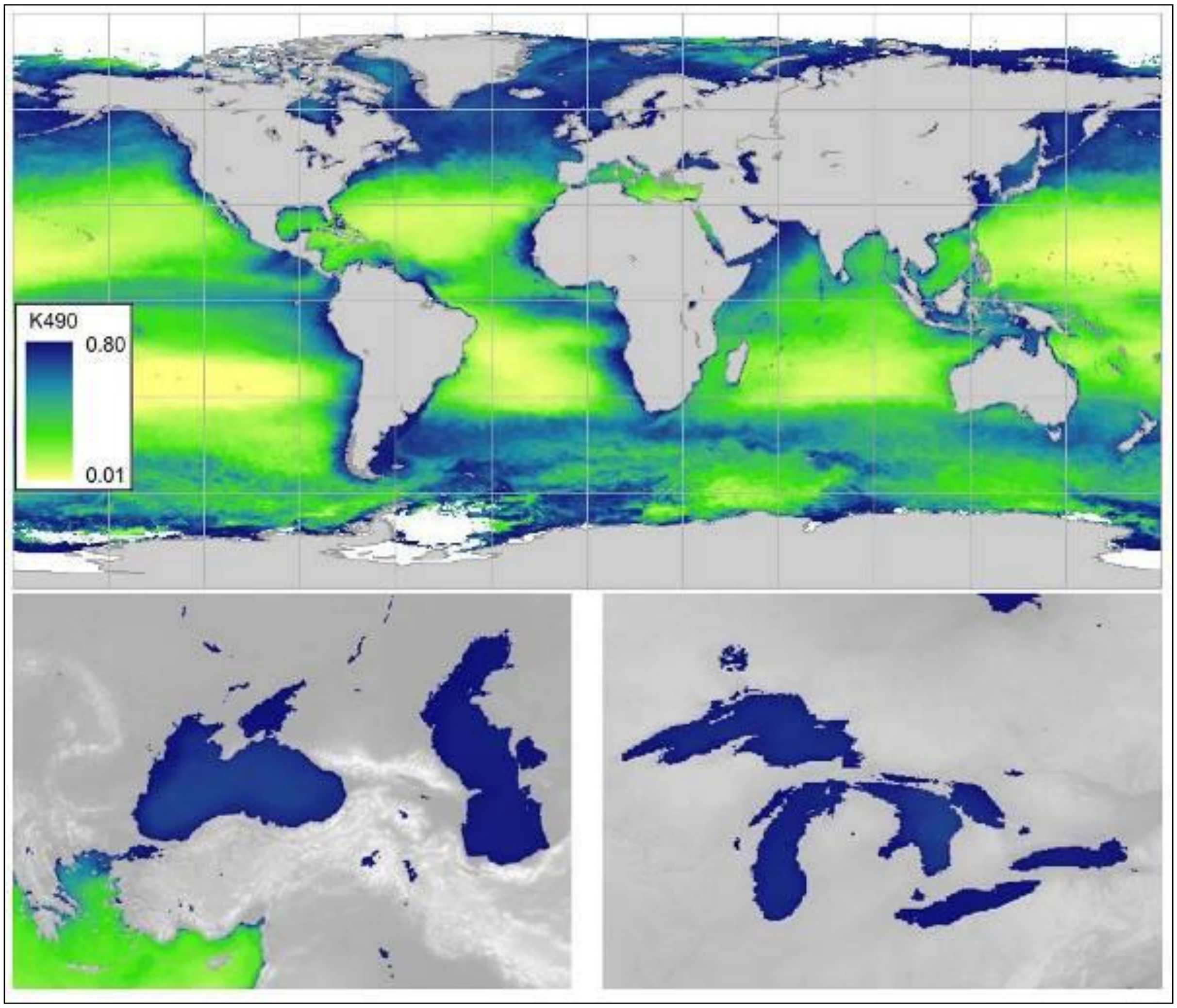

Figure 6. Average diffuse attenuation coefficient (m^{-1}) at 490 nm as determined by MODIS (2001–2005). Yellow and green colors indicate less light absorption, blues indicate greater attenuation of light. Global view (top), Ponto-Caspian region (left), and Great Lakes (right).

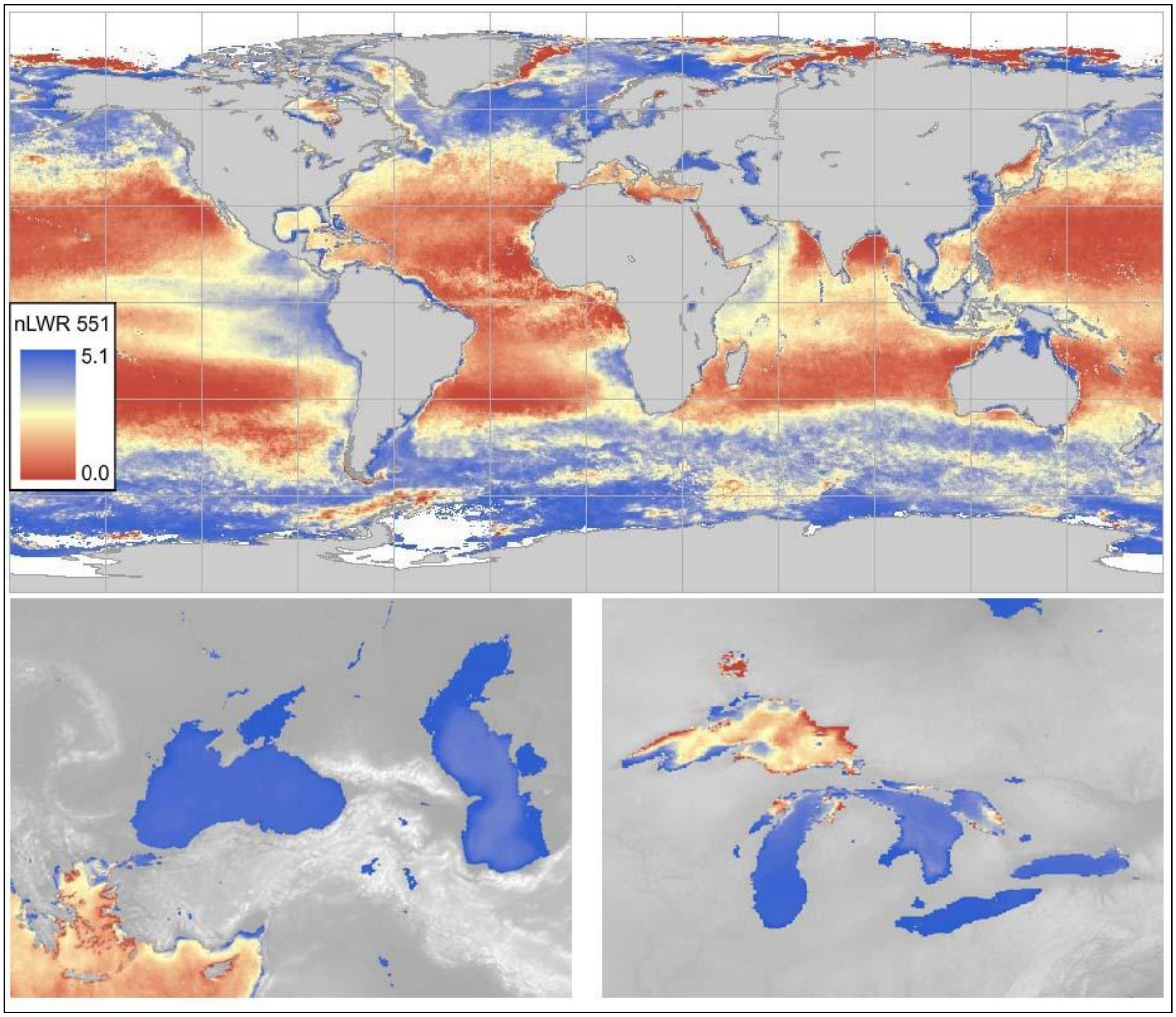

Figure 7. Average normalized water leaving radiance (mW/cm^2 µm sr) as determined by MODIS (2001–2005). Blues are higher values (i.e., higher concentrations of particles in the water which reflect more light), and reds and yellows indicate lower values (i.e., less light is emitted). Global view (top), Ponto-Caspian region (left), and Great Lakes (right).

marmoratus), rudd (*Scardinius erythrophthalmus*), an amphipod (*Corophorum curvispinum*), sand goby (*Potamoschistus minutus)*, roach (*Rutilus rutilus*), and tench (*Tinca tinca*). These figures also show areas where no reliable prediction could be made based on a power of prediction analysis.

The habitat suitability maps are based on the best 100 of 1,000 model runs for each species. The color scale (from blue to red) in the figures reflects the number of GARP model runs, from 0 to 100, that predict the modeled species would find suitable environmental conditions in the location being considered. Specifically, the red colored regions indicate where nearly all GARP model runs predicted that NIS would find suitable habitat. The blue-colored areas indicate where few or no GARP models runs predicted that NIS would find suitable habitat. The power of prediction analysis helps to distinguish between areas with a low likelihood of providing suitable habitat from areas where a prediction could not reliably be made. The gray regions denote areas where no reliable prediction can be made about the potential distribution of an invader. The color scale does not imply any measure of credibility or precision, but rather expresses commonality among predictions developed via a stochastic process of model generation.

To further validate the GARP model, results for the three species already reported in the Great Lakes (zebra mussel, ruffe, and the New Zealand mud snail) were compared with their current spatial distribution. This analysis indicates that GARP modeling is a good predictor of habitat suitability according to the scale for evaluating the performance of species distribution models devised by Swets (1988). The model performance scores are 0.79 for the zebra mussel and ruffe and 0.74 for the New Zealand mud snail. These scores, representing the area under the curve of predicted accuracy (Sing et al., 2005), suggest that the six environmental data layers that were selected as inputs for the GARP modeling are appropriate for predicting the locations that would provide suitable habitat. Appendix C provides more information on model validation.

4.2.1. Blueback Herring

If the blueback herring, a medium-sized fish, enters the Great Lakes it is very likely to find suitable habitat throughout the Great Lakes system, according to GARP (Figure 8). Only the deeper portions of Lake Superior and other isolated spots in other Lakes may not provide suitable habitat for this species. Without a power of prediction analysis, it is not possible to know if the blue colored areas reflect unsuitable habitat or areas where no prediction is possible. The blueback herring and alewife are of similar shape and general appearance, and distinguishing between them is difficult. Bluebacks tend to have a smaller eye than alewives, with the eye diameter usually smaller than the snout length. As their name implies, these fish often have dark blue backs. An anadromous fish, the blueback herring spends the greater part of its life in salt water and returns to fresh water to spawn. It usually spawns later in the spring than the alewife, when water temperatures are a bit warmer. During spawning, many eggs are deposited over the stream bottom where they stick to gravel, stones, logs, or other objects. A few surviving, spent fish move back to the sea after spawning. Young fish usually move to sea when about l month old and 1 1/2 to 2 inches long. Bluebacks feed on plankton, various small floating animals, small fish fry, and fish eggs. Although the Great Lakes are distant from marine waters, the blueback herring can spend its whole life and develop reproducing populations entirely in freshwater (VA Inland Fisheries, 2008). If blueback herring became established in the Great Lakes, they could impede recovery of depressed populations of indigenous fishes such as cisco and lake trout (Owens et al., 1998).

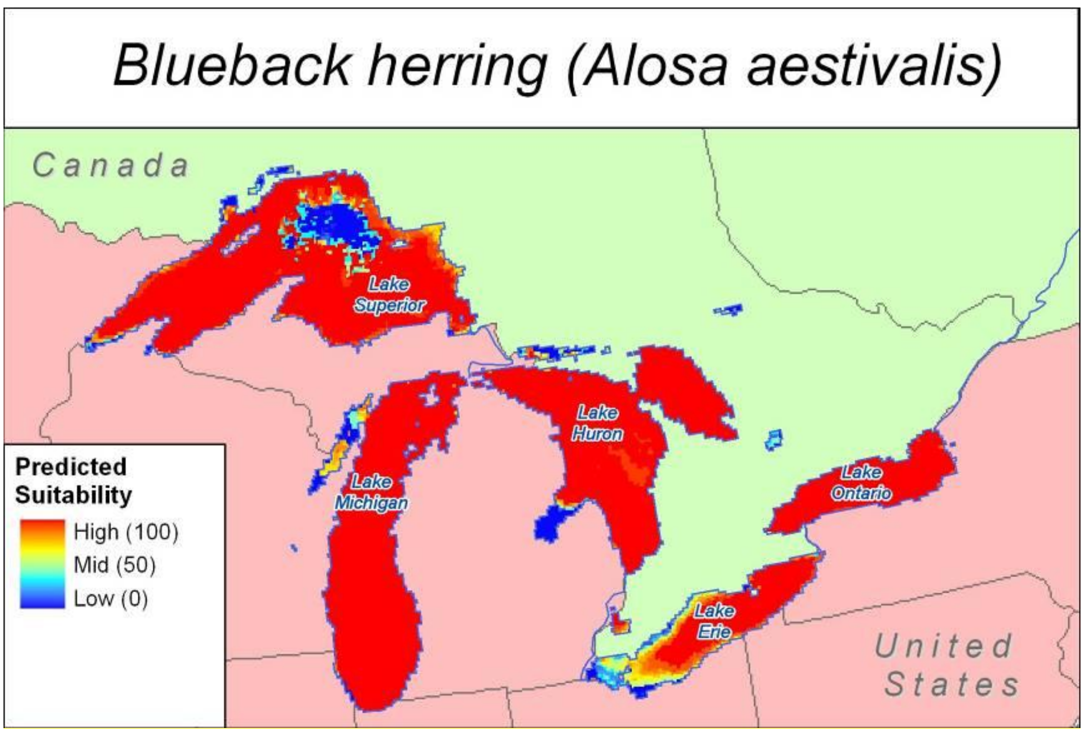

Figure 8. GARP-predicted habitat suitability of blueback herring (*Alosa aestivalis*) in the Great Lakes.

4.2.2. Quagga Mussel

The quagga mussel, a mollusk, already occupies most shoreline areas in Lakes Erie and Ontario and southern Michigan (Figure 9). According to GARP modeling, the rest of Lake Erie and the southern shoreline zones of Lakes Michigan and Huron also are likely to provide suitable habitat for this species. Without a power of prediction analysis, predictions cannot reliably be made for the other regions. However, the species has already been reported in several of these locations, including the shorelines of Lake Michigan, Lake Superior, and Lake Huron. Quaggas are prodigious water filterers, removing substantial amounts of phytoplankton and suspended particulate from the water. As such, their impacts are similar to those of the zebra mussel. By removing the phytoplankton, quaggas in turn decrease the food source for zooplankton, therefore altering the food web. Impacts associated with the filtration of water include increases in water transparency, decreases in mean chlorophyll *a* concentrations, and accumulation of pseudofeces (Claxton et al., 1998). Quagga mussels prefer silty or sandy lake bottoms and can live in warm or cold water. MacIsaac (1994) correctly speculated that the quagga mussel was still expanding its nonindigenous range in the Great Lakes. It has spread to depths greater than it occupies in its native range (Mills et al., 1996) and is abundant to a depth of 150 m (Wisconsin DNR, 2008) and 174 m in Lake Ontario (Watkins et al., 2007). By 1999, the quagga mussel dominated southern Lake Ontario, where the zebra mussel was once dominant (Mills et al., 1999), and it continues to spread into regions previously occupied by the zebra mussel (Watkins et al., 2007). The ability to spread to areas that can be potentially occupied by the zebra mussel further supports the notion that spread and colonization may occur until the species reaches its depth limitation.

4.2.3. Round Goby

The GARP model predicts the round goby, a medium-sized, bottom-dwelling fish, would find suitable habitat throughout Lakes Erie and Ontario and along the shorelines of the other Lakes (Figure 10). In fact, this species became established in all five Great Lakes by 1998 (Rasmussen, 2002). Round gobies perch on rocks and other substrates in shallow areas, yet they have also been reported to flourish in a variety of habitat types (USGS, 2008a). Gobies also have a well developed sensory system that enhances their ability to detect water movement. This allows them to feed in complete darkness, giving them an advantage over other fish in the same habitat (Wisconsin Sea Grant, 2008). Zebra mussels may have facilitated the invasion of the round goby and other Eurasian species by providing an abundant food source (Ricciardi and MacIsaac, 2000). The distribution of the round goby around the inshore areas of the Black and Caspian seas indicates their potential for widespread occupation of inshore habitats with cover, especially plants, in the lower Great Lake, yet they can migrate to deeper water (50–60 m) in

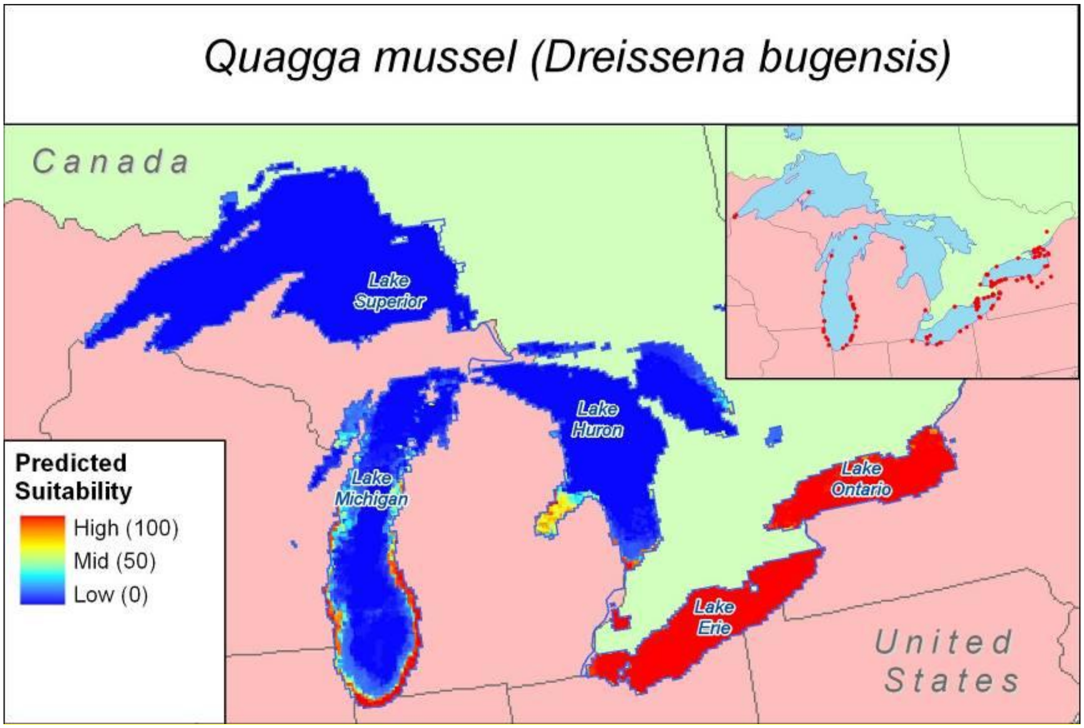

Figure 9. GARP-predicted habitat suitability of quagga mussel (*Dreissena bugensis*) in the Great Lakes. Inset map shows the locations where the species has been reported.

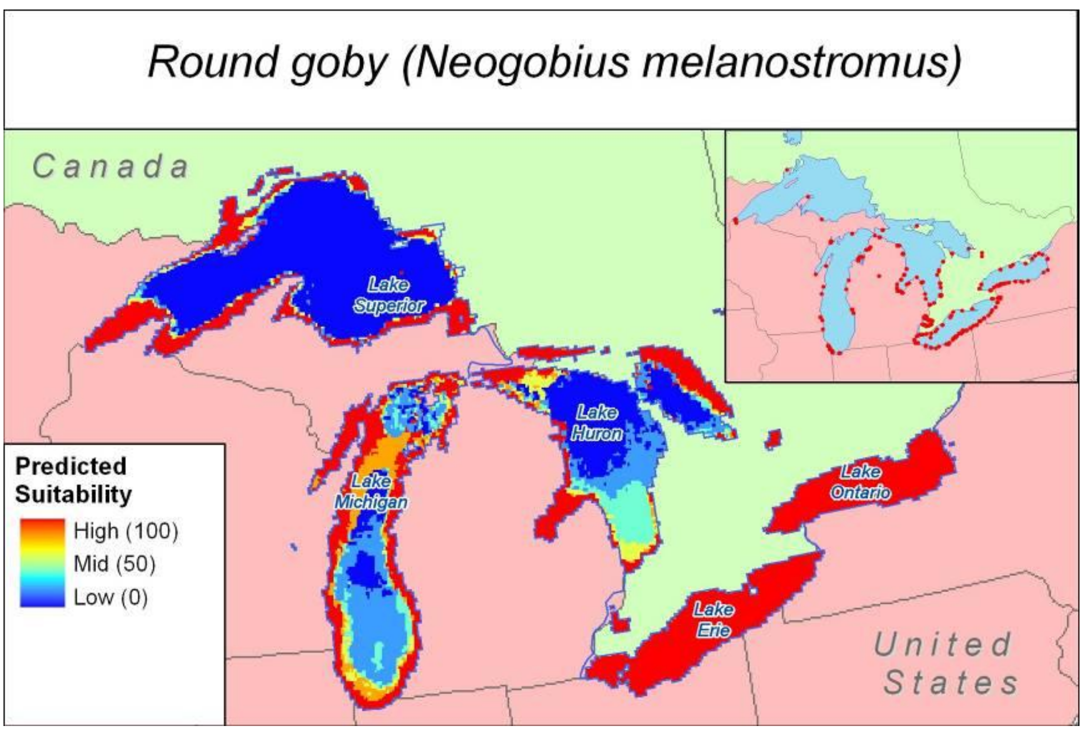

Figure 10. GARP-predicted habitat suitability of round goby (*Neogobius melanstromus*) in the Great Lakes. Inset map shows the locations where the species has been reported.

winter (Jude et al., 1992). The numbers of native fish species have declined in areas where the round goby has become abundant (Crossman et al., 1992). This species has been found to prey on darters, other small fish, and lake trout eggs and fry in laboratory experiments. They also may feed on eggs and fry of sculpins, darters, and logperch (Marsden and Jude, 1995) and have also been found to have a significant overlap in diet preference with many native fish species. They compete with rainbow darters (*Etheostoma caeruleum*), logperch (*Percina caprodes*), and northern madtoms (*Noturus stigmosus*) for small macroinvertebrates (French and Jude, 2001).

4.2.4. Fishhook Waterflea

According to the GARP model, if transported to the Great Lakes, the fishhook waterflea, a free-swimming macroinvertebrate, would likely find suitable habitat throughout the region, except for the deeper waters of Lake Superior (Figure 11). The fishhook waterflea has been reported in Lakes Ontario, Michigan (USGS, 2008b), and Erie (University of Minnesota, 2006). The species is predicted to spread to the other Great Lakes, and, once established, it becomes difficult to eradicate (University of Minnesota, 2006). Unlike several of the other modeled species, population densities of the fishhook waterflea increase with distance from shore (IUCN, 2006), suggesting that this species may be able to occupy, given sufficient time, the entire region including the deeper waters of Lake Superior.

4.2.5. Zebra Mussel

The zebra mussel, a mollusk, has already invaded the shoreline areas of all five Great Lakes (Figure 12). The GARP model predicts the zebra model could potentially find suitable habitats throughout most of the Great Lakes region. Zebra mussels were first discovered in North America in 1988 in the Great Lakes. The first account of an established population came from Canadian waters of Lake St. Clair, a water body connecting Lake Huron and Lake Erie. By 1990, zebra mussels had been found in all the Great Lakes. The following year, zebra mussels escaped the Great Lakes basin and found their way into the Illinois and Hudson rivers. Zebra mussels are notorious for their biofouling capabilities by colonizing water supply pipes of hydroelectric and nuclear power plants, public water supply plants, and industrial facilities. Zebra mussels can have profound effects on the ecosystems they invade. They primarily consume phytoplankton, but other suspended material is filtered from the water column including bacteria, protozoans, zebra mussel veligers, other microzooplankton, and silt. Large populations of zebra mussels in the Great Lakes and Hudson River reduced the biomass of phytoplankton significantly following invasion. Diatom abundance declined over 80% and

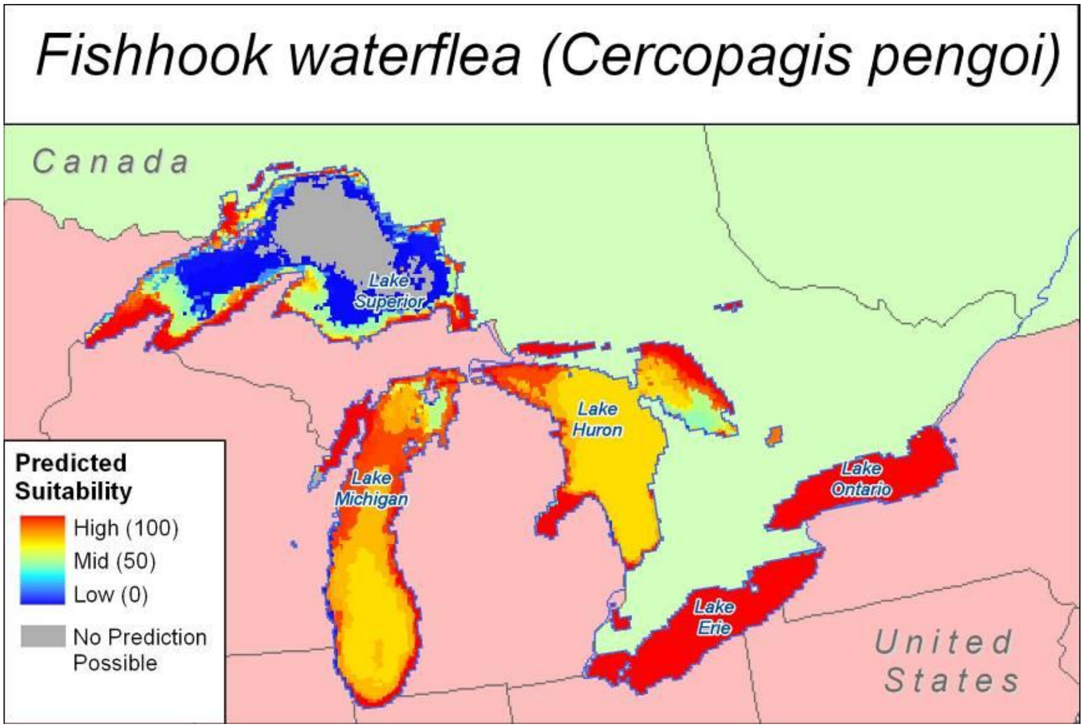

Figure 11. GARP-predicted habitat suitability of fishhook waterflea (*Cercopagis pengoi*) in the Great Lakes.

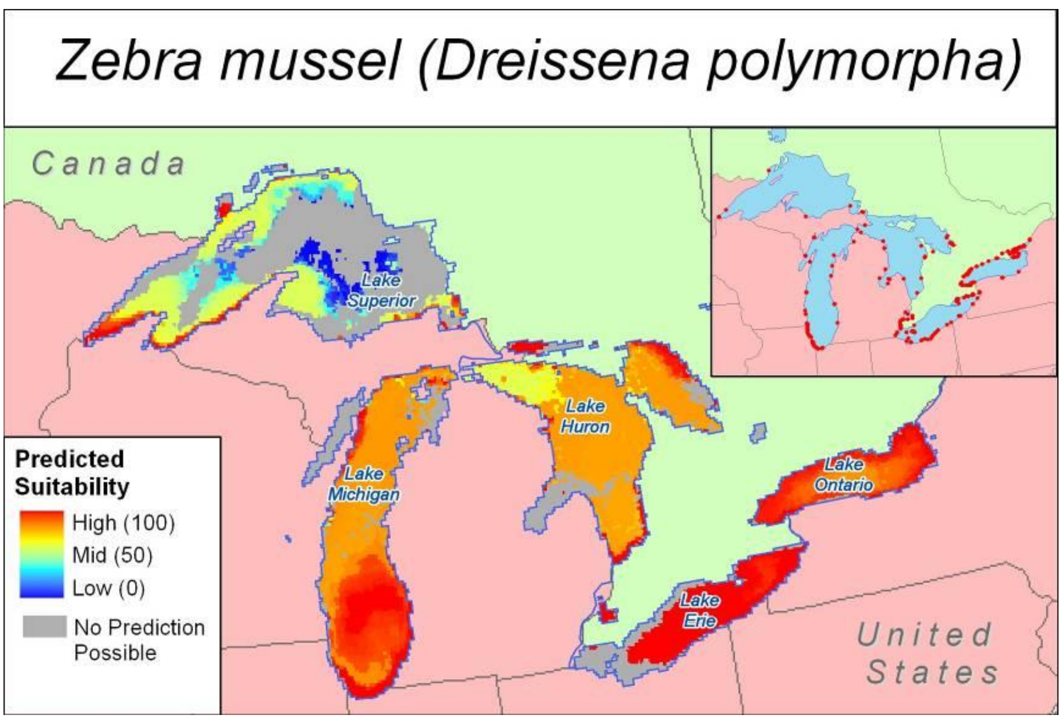

Figure 12. GARP-predicted habitat suitability of zebra mussel (*Dreissena polymorpha*) in the Great Lakes. Inset map shows the locations where the species has been reported.

transparency, as measured by Secchi depth, increased by 100% during the first years of the invasion in Lake Erie (Holland, 1992). Zebra mussels represent one of the most important biological invasions into North America, having profoundly affected the science of Invasion Biology, public perception, and policy. Zebra mussels are described as poor O_2 regulators, which may explain their low success rate in colonizing eutrophic lakes and the hypolimnion. Mellina and Rasmussen (1994) noted that calcium (Ca^{2+}) levels and water temperatures in the open waters of Lake Superior are too low for the zebra mussel. Zebra mussels require 10 mg/L of Ca^{2+} to initiate shell growth and 25 mg/L to maintain shell growth (USGS, 2008c). Zebra mussels are generally within 2 to 7 m of the water surface (O'Neill, 2004) but, on rare occasions, have been found at depths exceeding 90 m (Watkins et al., 2007). The depth limitation of the species should further restrict the maximum potential spread of the species to Lake Erie and to the shallower waters of the other four Great Lakes (NOAA, 2008). Competition with the quagga mussel also appears to limit zebra mussel spread. Zebra mussels were outcompeted and almost completely replaced by quagga mussels in Lake Ontario between 1995 and 2003 and this trend could occur in other Lakes (Watkins et al., 2007).

4.2.6. Ruffe

The ruffe, a small to medium-sized fish, has already invaded Lake Superior and GARP modeling predicts it will find suitable habitat almost everywhere in all five Great Lakes (Figure 13). GARP models are not able to make a prediction about some of the deeper waters of Lake Superior. Established in the western portion of Lake Superior since about 1988 it has expanded in an easterly direction. It has now become the dominant species in the St. Louis River estuary (Leigh, 1998). Based on bottom trawl samples, ruffe make up an estimated 80% of fish abundances in the southwestern regions of Lake Superior (Leigh, 1998). Ruffe exhibit rapid growth and high reproductive output, and adapt to a wide range of habitat types; therefore, the species may pose a threat to native North American fish. There is much concern that ruffe may have a detrimental effect on the more desirable species in Lake Superior, such as yellow perch and walleye, by feeding on the young of these species or by competing for food (Fuller and Jacobs, 2008). Ruffe are often associated with bottom waters and can tolerate lacustrine and lotic systems and depths to 85 m (Sandlund et al., 1985). The species intolerance to deeper waters may limit its range of potential suitable habitat to Lake Erie, southern Lake Michigan, and the shallower waters of the other Great Lakes.

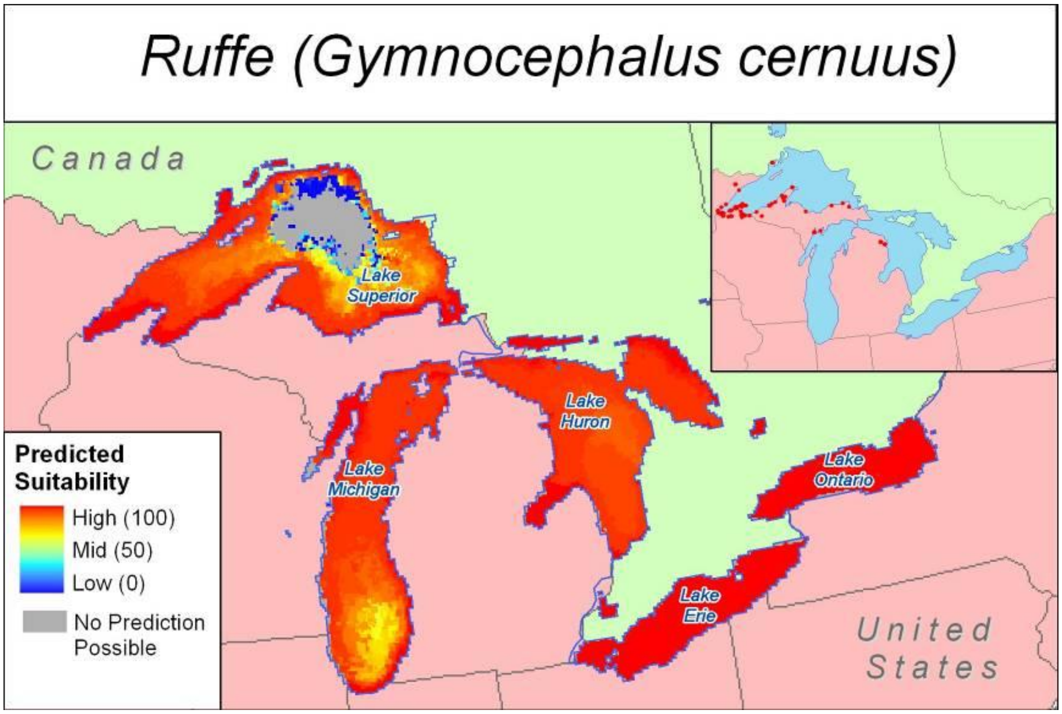

Figure 13. GARP-predicted habitat suitability of ruffe (*Gymnocephalus cernuus*) in the Great Lakes. Inset map shows the locations where the species has been reported.

4.2.7. Monkey Goby

The GARP model predicts that the monkey goby, a member of the goby fish family, could find suitable habitat in most of Lake Erie and in some portions of Lake Ontario and Lake Huron (Figure 14). Predictions cannot be made for most of the Great Lakes because of data limitations. The monkey goby is closely related to the round goby. Currently, the monkey goby is confined to Eurasia but it has traveled up the Danube, Dnieper, and Volga Rivers from its native waterways and is becoming an invasive nuisance in these areas. Similar to other *Gobiidaes*, the monkey goby prefers shallow water and would likely not survive in deeper waters.

4.2.8. New Zealand Mud Snail

The New Zealand mud snail, another mollusk, is predicted by GARP modeling to find suitable habitat in most if not all of Lakes, Erie, Ontario, and Michigan (Figure 15) and shorelines of Lakes Huron and Superior. It was first established in Lake Ontario in 1991 (Zaranko et al., 1997) and in Lake Erie in 2005 (Levri et al., 2007). It may also be established in Lake Superior, where some individuals were found in 2001 (Grigorovich et al., 2003b). Mud

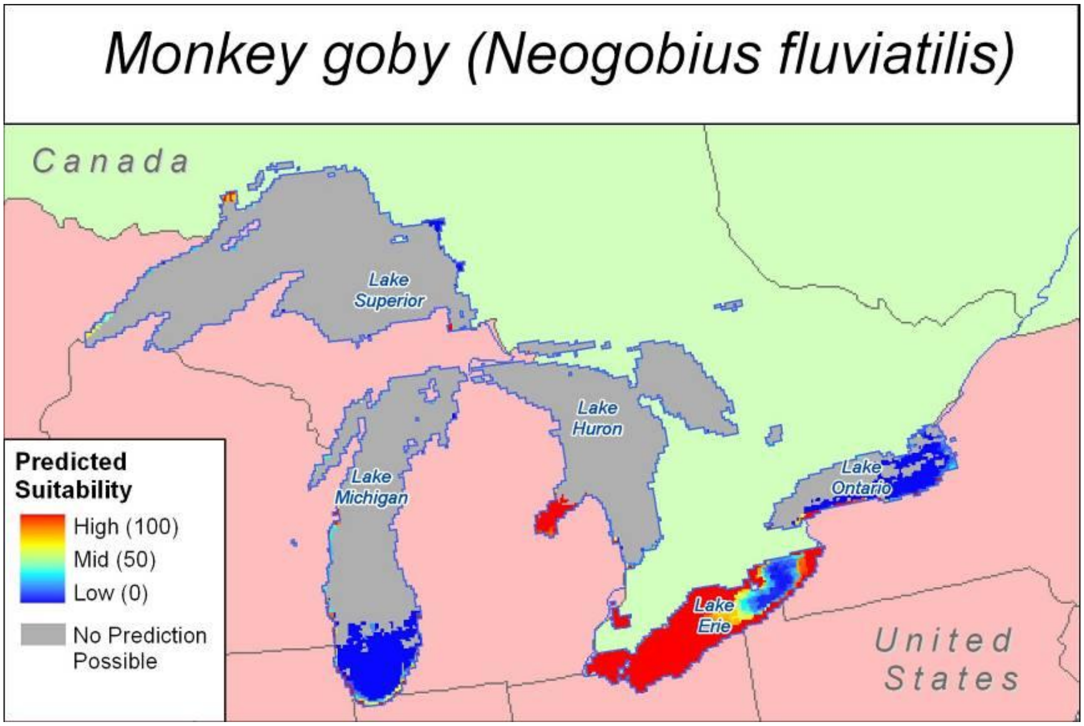

Figure 14. GARP-predicted habitat suitability of monkey goby (*Neogobius fluviatilis*) in the Great Lakes.

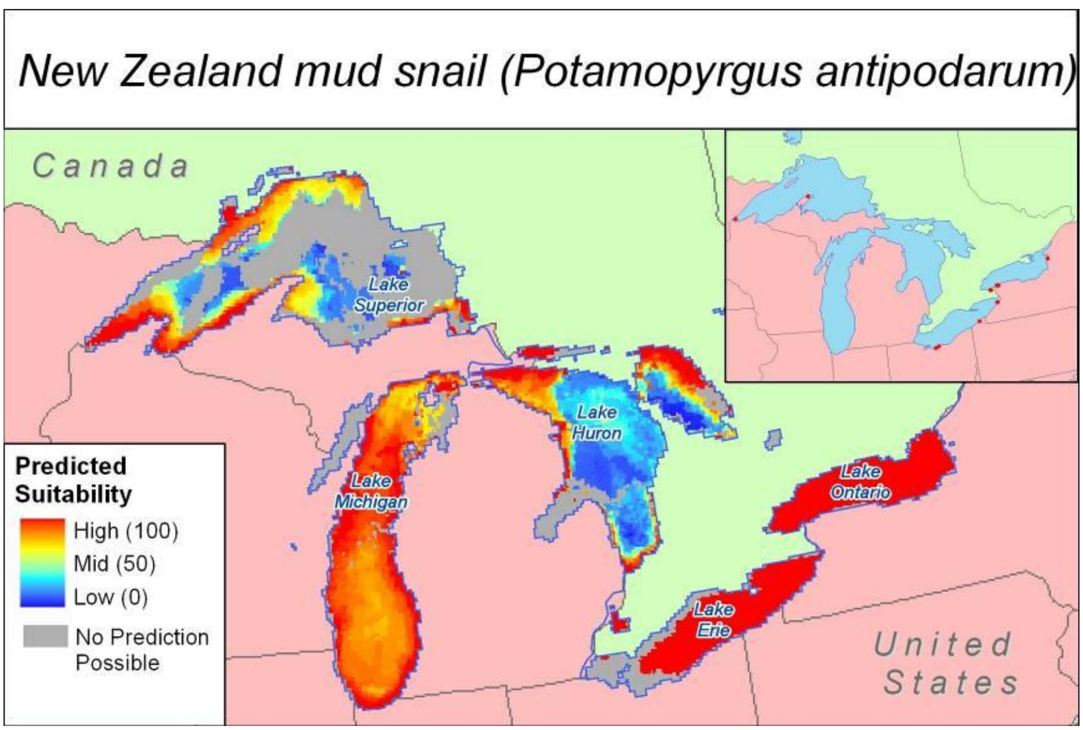

Figure 15. GARP predicted habitat suitability of New Zealand mud snail (*Potamopyrgus antipodarum*) in the Great Lakes. Inset map shows the locations where the species has been reported.

snail populations consist mostly of asexually reproducing females that are born with developing embryos in their reproductive system. This species can be found in all types of aquatic habitats from eutrophic mud bottom ponds to clear rocky streams. It can tolerate a wide range of water temperatures (except freezing), salinity, and turbidity in clean as well as degraded waters. They feed on dead and dying plant and animal material, algae, and bacteria. It can tolerate a broad range of ecological factors thus facilitating its further spread. In moist conditions, this snail can withstand short periods of desiccation. Since this snail is found at depths from 5 to 45 m (Levri et al., 2007) it is unlikely the species will survive in deeper waters.

4.2.9. Tubenose Goby

The tubenose goby, another member of the goby fish family, is predicted by the GARP model to become established in Lake Erie and the shoreline areas of the other Great Lakes (Figure 16). Predictions could not be made for most of the rest of the region. Their distribution around the inshore areas of the Black and Caspian Seas indicates their potential for widespread occupation of inshore habitats where cover, especially plants, occurs in the lower Great Lakes (Jude et al., 1992). Tubenose gobies have been shown to have a significant overlap in diet preference with rainbow darters, *Etheostoma caeruleum*, and may compete with these native fish for food (French and Jude, 2001). The usual habitat for this species is shallow bays, offshore banks, or flowing water of streams. However, the tubenose goby also can be found in ponds and canals overgrown with vegetation. Where current is strong, it hides under boulders. It is often found under stones or among weeds, to which it retreats rapidly if disturbed. Some individuals can be found at depths greater than 3 m in the sea. The preferred conditions probably restrict its probable range of suitable habitat to shallower waters.

4.2.10. Rudd

Already occurring in the Great Lakes with an unknown frequency at this time, significant portions of Lakes Erie and Ontario as well as portions of Superior and Michigan are prone to invasion by the rudd, a medium-sized, thick-bodied fish (Figure 17). The rudd's tolerance of a variety of habitats has likely contributed to its widespread distribution. In streams and rivers, this fish usually prefers long, slow pools and backwaters. The rudd can be expected to compete for invertebrate food sources with native fishes. In addition, being omnivorous, the rudd can shift its diet to plants, unlike most native fishes. Because rudd are fairly hardy, Nico et al. (2008) indicate that the fish will fare better than many native fishes in waters that are eutrophic or

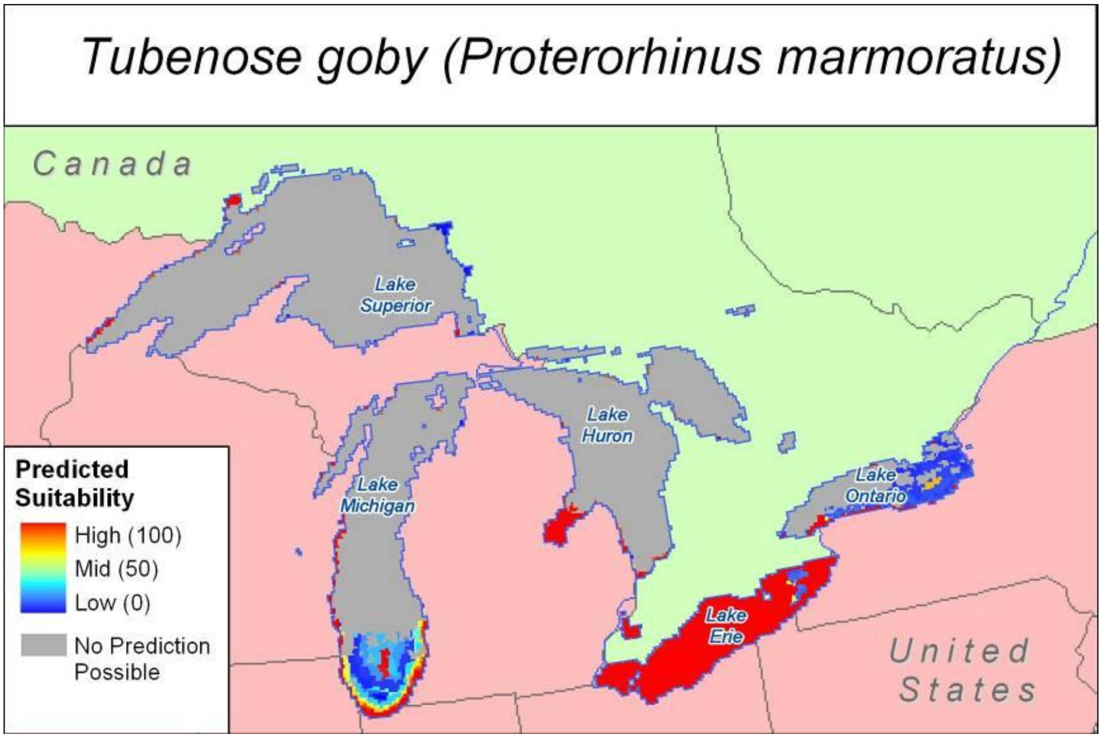

Figure 16. GARP-predicted habitat suitability of tubenose goby (*Proterorhinus marmoratus*) in the Great Lakes.

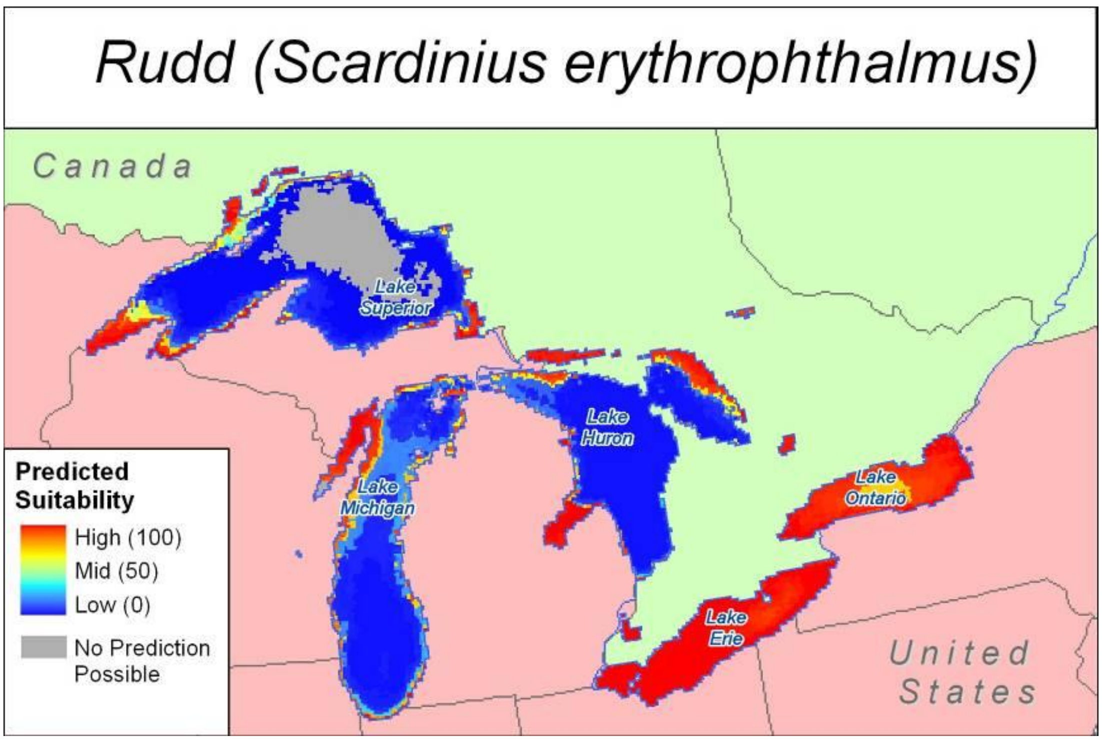

Figure 17. GARP-predicted habitat suitability of rudd (*Scardinius erythrophthalmus*) in the Great Lakes.

polluted. Predictions cannot be made about the habitat suitability for rudd in parts of Lake Superior, but, given the species preference for littoral waters, it is unlikely the rudd would find suitable habitat in the deeper regions of all the lakes.

4.2.11. Corophium Curvispinum (an Amphipod)

According to the GARP model, almost all of Lake Erie and the southern shores of Lakes Ontario, Huron, and Michigan are prone to invasion by the amphipod *Corophium curvispinum.* Predictions for the other locations in the Great Lakes were not possible due to limited data (Figure 18). This amphipod builds tubes on firm surfaces such as rocks, wood, submerged vegetation, or bivalve shells on otherwise sandy or muddy substrata in shallow waters (Frammandearter, 2008). *C. curvispinum* prefers rivers, estuaries, and other areas with brackish water, but it can also tolerate freshwater environments.

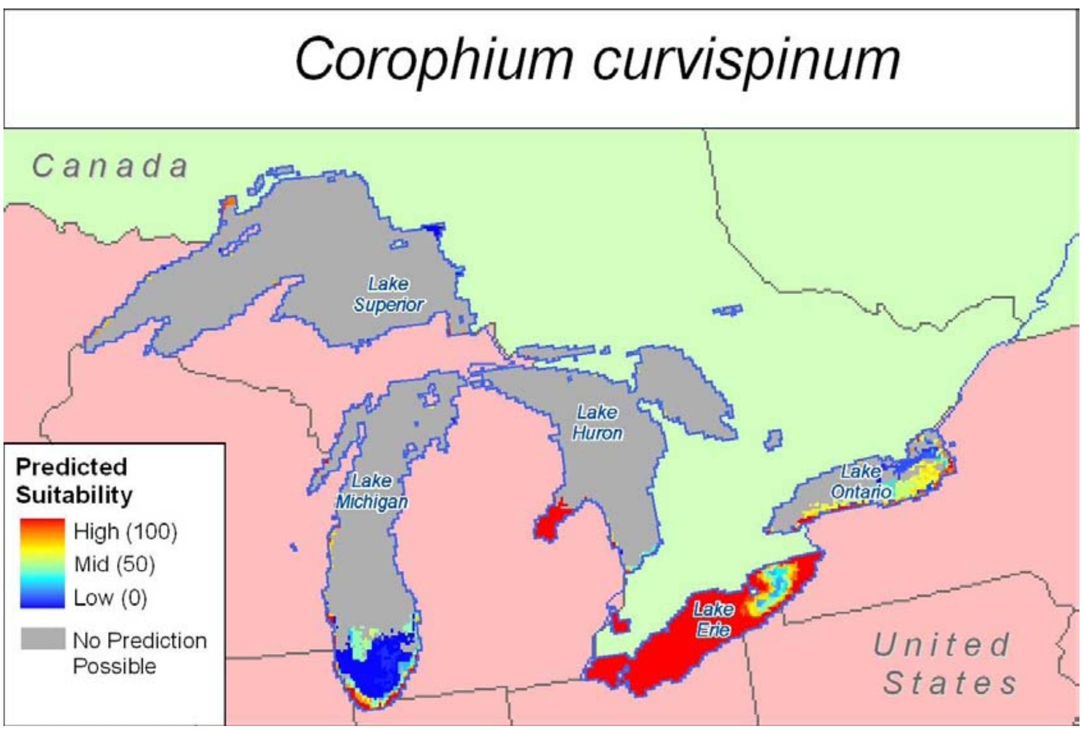

Figure 18. GARP-predicted habitat suitability of *Corophium curvispinum* (no common name reported) in the Great Lakes.

4.2.12. Sand Goby

The sand goby is predicted by GARP modeling to find suitable habitat almost everywhere in all five Great Lakes (Figure 19). This occasionally schooling species occurs primarily in inshore sandy and muddy areas (Froese and Pauly, 2008). The sand goby is a coastal goby of European waters from the Baltic to the Mediterranean Sea and can grow up to 10 cm in length. Some variation from the GARP modeling prediction is expected because similar to other gobys, the sand goby is unlikely to find suitable habitat in deeper waters.

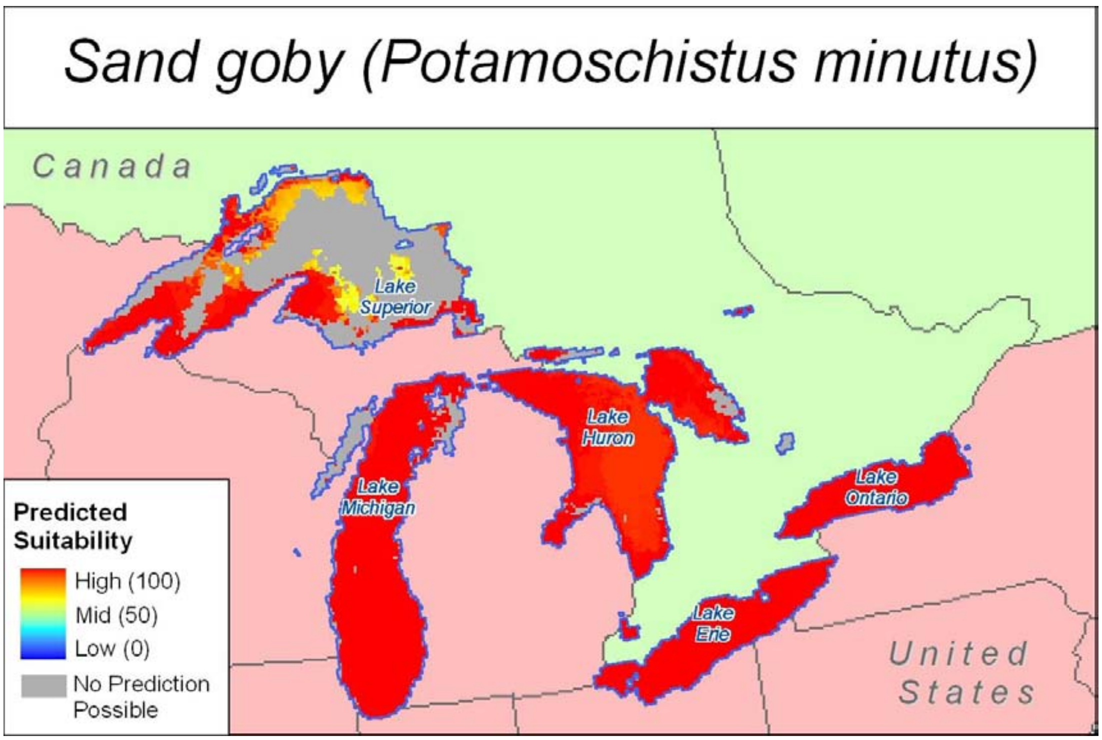

Figure 19. GARP-predicted habitat suitability of sand goby (*Potamoschistus minutus*) in the Great Lakes.

4.2.13. Roach

GARP predicts that Lakes Erie and Ontario would provide suitable habitat for the roach, a medium-sized fish in the carp family. Most of the other regions would be unsuitable (Figure 20) although predictions cannot be made about the suitability of habitat of parts of Lake Superior. Adults inhabit slow-flowing or still muddy waters and are abundant in their native rivers, lakes, canals, and reservoirs. Brackish water populations in the Baltic and the Black Sea are anadromous and they are known to thrive in poor quality, even polluted water (Nico and Fuller, 2008). As omnivores, they feed on insects, crustaceans, mollusks, and plants.

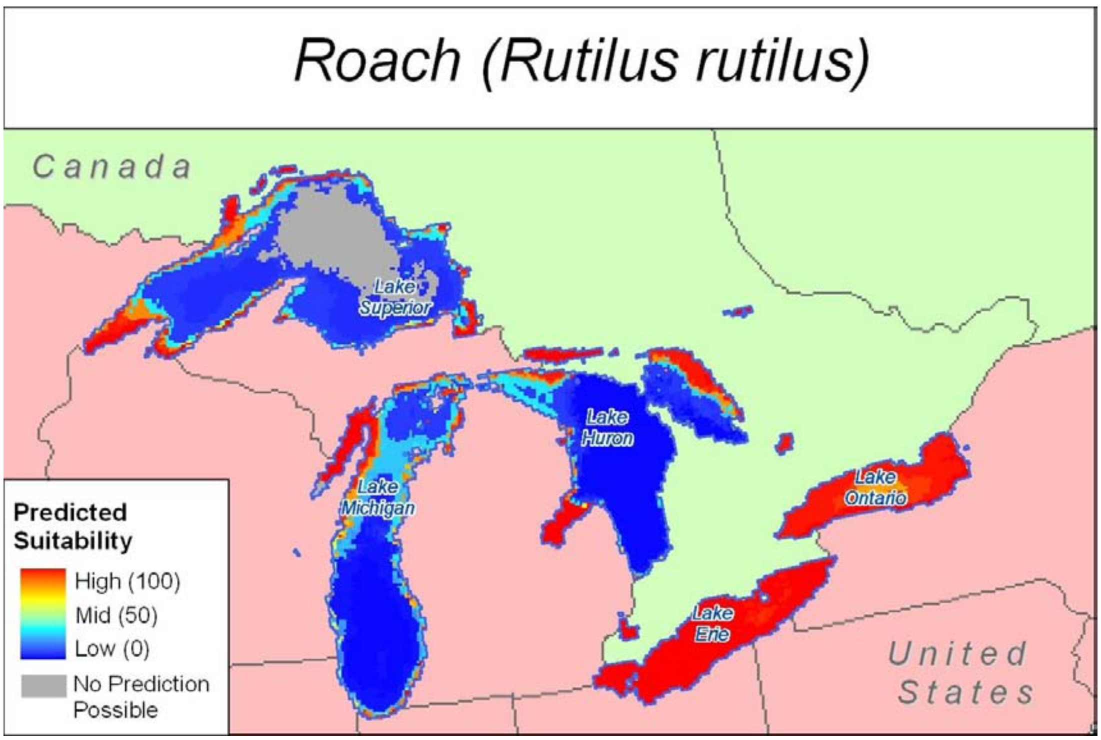

Figure 20. GARP-predicted habitat suitability of roach (*Rutilus rutilus*) in the Great Lakes.

4.2.14. Tench

The tench, a medium-sized fish already established in many rivers within the United States, is likely to find suitable habitat in most of Lake Erie and small portions of Lake Ontario and Lake Huron (Figure 21) according to GARP models. The diet consists mainly of aquatic insect larvae and mollusks. Nico and Fuller (2008) considered it a potential competitor for food with sport fishes and native cyprinids and noted that the species is known to stir up bottom sediments, possibly affecting water quality, similar to the common carp.

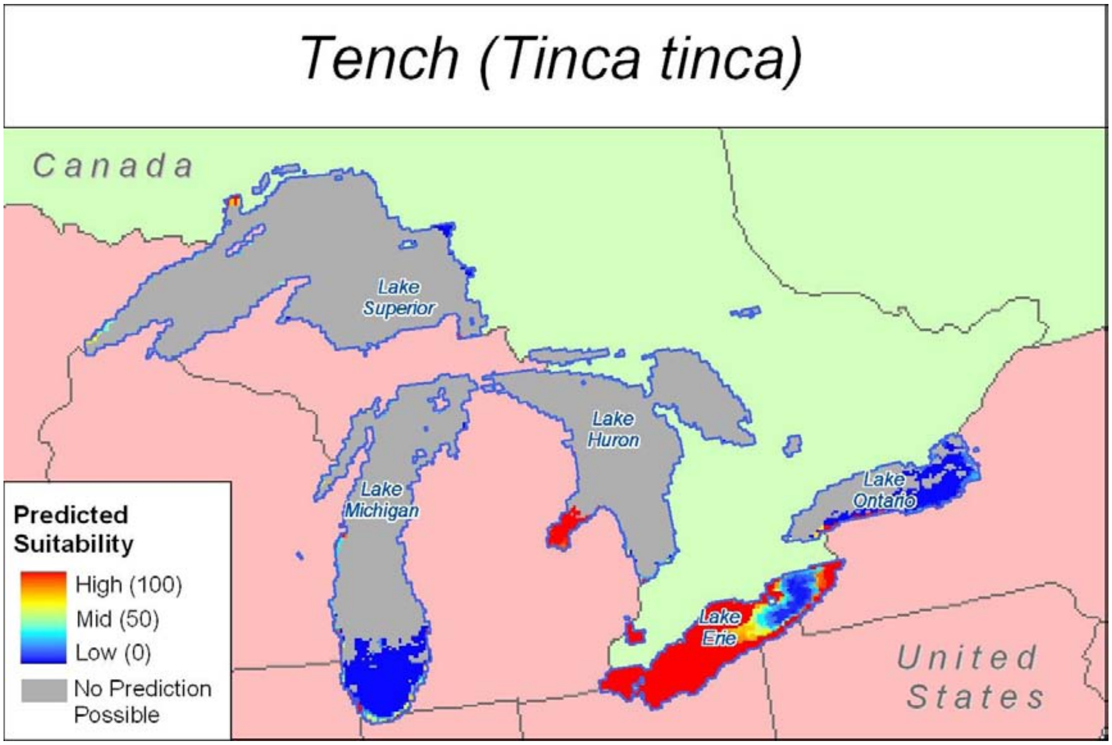

Figure 21. GARP-predicted habitat suitability of tench (*Tinca tinca*) in the Great Lakes.

4.3. VESSEL TRAFFIC AND GREAT LAKES PORTS

The U.S. Great Lakes receive substantial vessel traffic from around the world because of the commodities shipped in and out of the area. The second phase of this study was to better understand whether there is sufficient numbers of propagules (e.g., larvae, seeds, spores, adults) entering the Great Lakes for species to become established. As described in the methods section, we used vessel traffic and ballast water discharges as a surrogate for propagule pressure since no data exists that actually measures the number of propagules released from discharges. By analyzing ballast water discharges, we were able to identify those ports that are at greatest risk.

4.3.1. Analysis of Vessels With Ballast on Board (BOB)

In accordance with U.S. Coast Guard (USCG) regulations, ballast water from transoceanic vessels with ballast on board is exchanged at sea prior to entering the St. Lawrence Seaway. Despite the ballast water exchange (BWE), some ballast water and residue may remain and NIS may survive in the ballast tank and then potentially be released when the ballast water is discharged. We evaluated ballast water discharges (BWD) into U.S. Great Lakes ports from vessels entering the Seaway whose original source of ballast water (i.e., the ballast in the tank prior to open ocean exchange) was taken-on from areas outside of the Great Lakes. To interpret these results one must consider that transoceanic vessels carry multiple ballast tanks and each tank may have a different history of ballast water source, exchange, and discharge. Therefore, each ballast tank discharge was counted as a BWD. A transoceanic vessel may carry over 20,000 metric tons of ballast water and have as many as 20 ballast tanks, implying one vessel-trip could have up to 20 ballast discharges at any one Great Lakes port.

Our study found that in the period of 2006–2007, 618 ballast tanks and 382 thousand metric tons of ballast water were discharged at Great Lakes ports from 107 different vessels. From a global perspective, the BWDs that were evaluated and could be linked to a particular port usually came from the eastern and western areas of the northern Atlantic Ocean (Figure 22). The Gulf of St. Lawrence region, near the St. Lawrence Seaway was the original source of ballast water for over 1/3 of the 618 discharges (Figure 23). Western Europe was the second-most common source, with most of the ballast originating from the southeastern portion of the North Sea (Figure 24).

Fifty-eight different foreign ports provided the original source of ballast water ultimately discharged at Great Lakes ports. Figure 25 identifies the most important ports based on the number of vessels leaving these ports and entering the Great Lakes. However, the most common source of ballast water was obtained while in transit and not at any particular port of call. The ports of Antwerpen, Belgium; Puerto Cabello, Venezuela; Haraholmen, Sweden; and Bremen, Germany are responsible for the greatest number of discharges, not including those ports near the entrance to the St. Lawrence Seaway (Figure 25). These ports, however, are not necessarily the source of the greatest volume of BWD. For instance, Haraholmen was ranked fourth among nonNorth American ports in terms of number of tanks discharged, but was ranked eighth in terms of metric tons of BWD (Figure 25 and Appendix E, Table E-1). In this study it was rare to find more than one vessel originating from the 58 foreign ports (Appendix E, Table E-1). Only six ports from outside North America were the source of two or more vessels included in this analysis.

Duluth received more than twice the BWDs and twice the volume of ballast water as any other Great Lake port in 2006–2007 (Figure 26). The ports of Toledo, Superior, Green Bay, Gary, and Milwaukee, also received over 10,000 metric tons of ballast water (Figure 26 and Appendix E, Table E-2). Appendix E, Table E-3 provides detailed information for those vessels with ballast on board discharging to Great Lakes ports in 2006–2007.

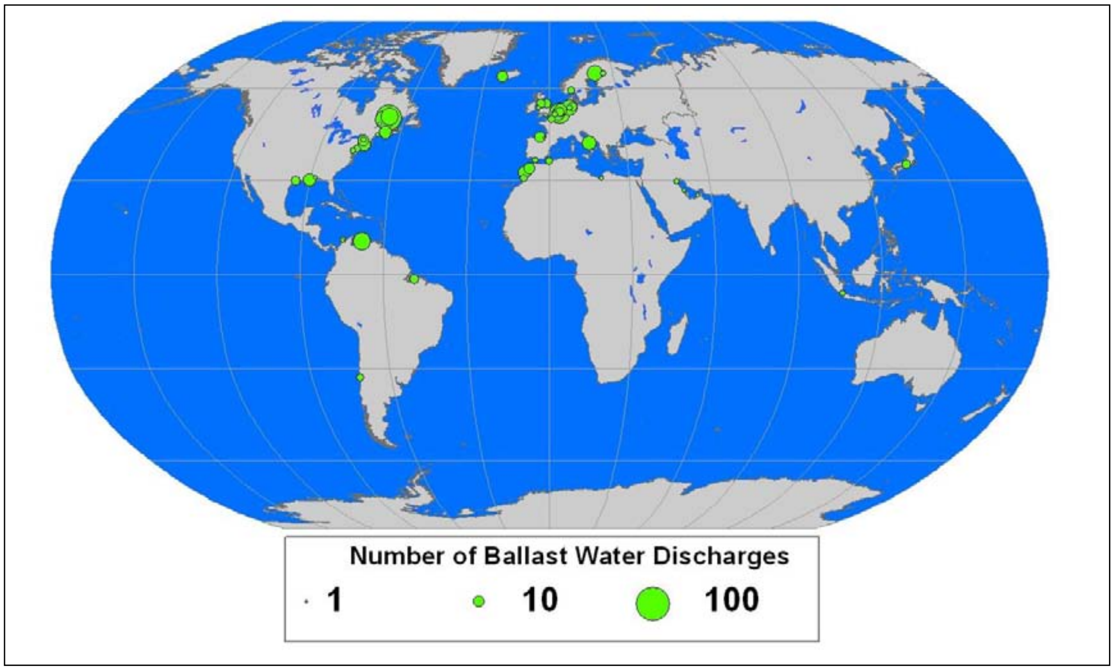

Figure 22. Location of the original source of ballast water taken-on prior to ballast water exchange and discharge in the U.S. Great Lakes. The area of each green circle is proportional to the number of ballast tank discharges.

Figure 23. Location of the source of ballast water taken-on from Canadian ports in or near the Gulf of St. Lawrence prior to ballast water exchange and discharges in the U.S. Great Lakes. The area of each green circle is proportional to the number of ballast tank discharges.

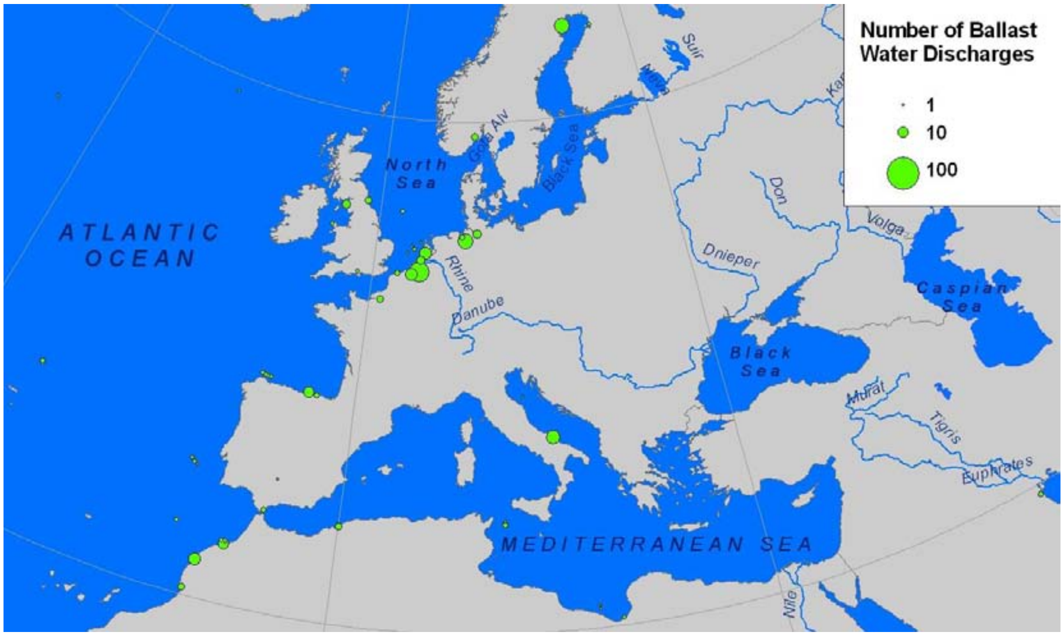

Figure 24. Location of the source of ballast water taken-on from European ports prior to ballast water exchange and discharges in the U.S. Great Lakes. The area of each green circle is proportional to the number of ballast tank discharges.

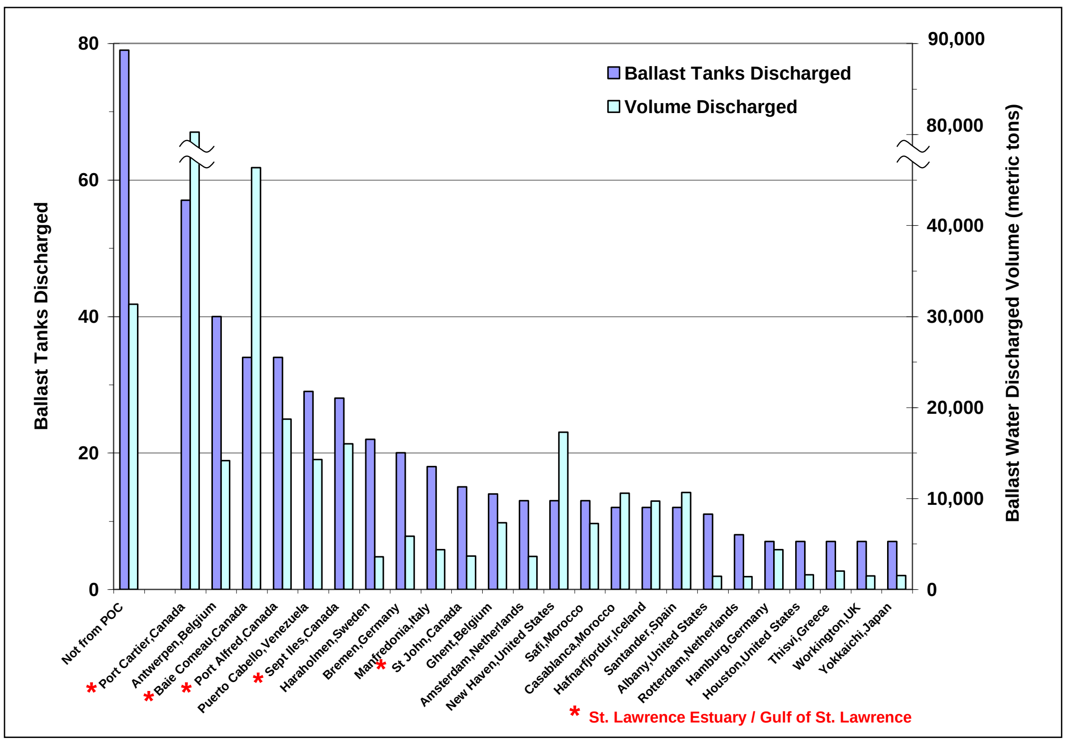

Figure 25. Frequency, volume, and original source of ballast water (prior to ballast water exchange) discharged into U.S. Great Lakes ports, from sources outside the Great Lakes.

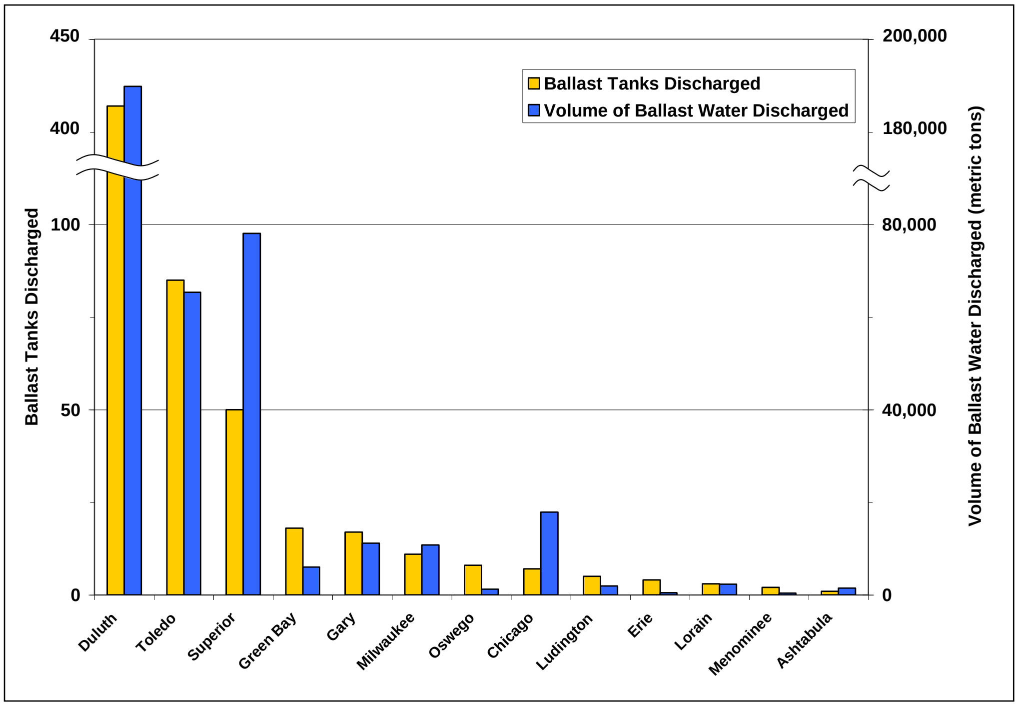

Figure 26. Frequency and volume of ballast water discharges (after ballast water exchange at sea) from ballast on board vessels, when the original source of ballast water came from outside the Great Lakes.

4.3.2. Analysis of Vessels with No Ballast on Board (NOBOB)

Some vessels enter the St. Lawrence Seaway with no ballast on board but may have organisms that remain and survive in the residual material left in the ballast tanks, and are referred to as NOBOB-RM vessels. These NOBOB-RM vessels can then take-on ballast water in the Seaway (most likely when cargo is off-loaded) and later discharge the ballast water along with residual materials at a Great Lakes port. We combined the 2006 NVMC data with the 2006 NBIC data to identify these types of vessels. There were 1,730 discharges of ballast water at Great Lakes ports from NOBOB-RM vessels in 2006. This is substantially more than the discharges from vessels with ballast on board, supporting the notion that NOBOB vessels may pose a much greater risk. The distribution of the potential sources of ballast water from NOBOB-RM vessels is somewhat similar to the vessels with ballast on board. Over half of the last five ports of call by these vessels were in southeastern Canada with Western Europe the second most common source of ballast water (Figure 27 and Appendix E, Table E-4).

Some of the foreign ports of origin are different between BOB and NOBOB vessels. For example, ten NOBOB-RM vessels included a stop at Europa Point, Gibraltar as one of the last five ports of call before discharging ballast water into the Great Lakes. Other vessels stopped at

Riga, Latvia; and Santos, Brazil (Figure 27 and Appendix E, Table E-4). Yet, we did not find any vessels with ballast on board stopping at these ports. Some ports are visited by both types of vessels, especially Sept Iles, Canada; and Ijmuiden, Netherlands (Figure 27 and Appendix E, Table E-4).

Several of the Great Lakes ports, including Duluth, Toledo, and Superior, receive ballast discharges from both NOBOB-RM vessels and vessels with ballast on board. Most Great Lakes ports received far more ballast discharges from NOBOB-RM vessels than BOB vessels in 2006. Several ports receive most of their ballast water from NOBOB-RM vessels, including Sandusky, Conneaut, Buffalo, and Calumet as shown in Figure 28 and Appendix E, Table E-5. Ashtabula was the extreme case, receiving 297 discharges from NOBOB-RM vessels (Figure 28) and only one discharge from a BOB vessel (Figure 26). When both vessel types are considered, the Great Lakes ports at greatest risk of receiving sufficient propagule pressure to facilitate invasion are Duluth, MN; Superior and Milwaukee, WI; Toledo, Ashtabula, and Sandusky, OH; Gary, IN; and Chicago, IL.

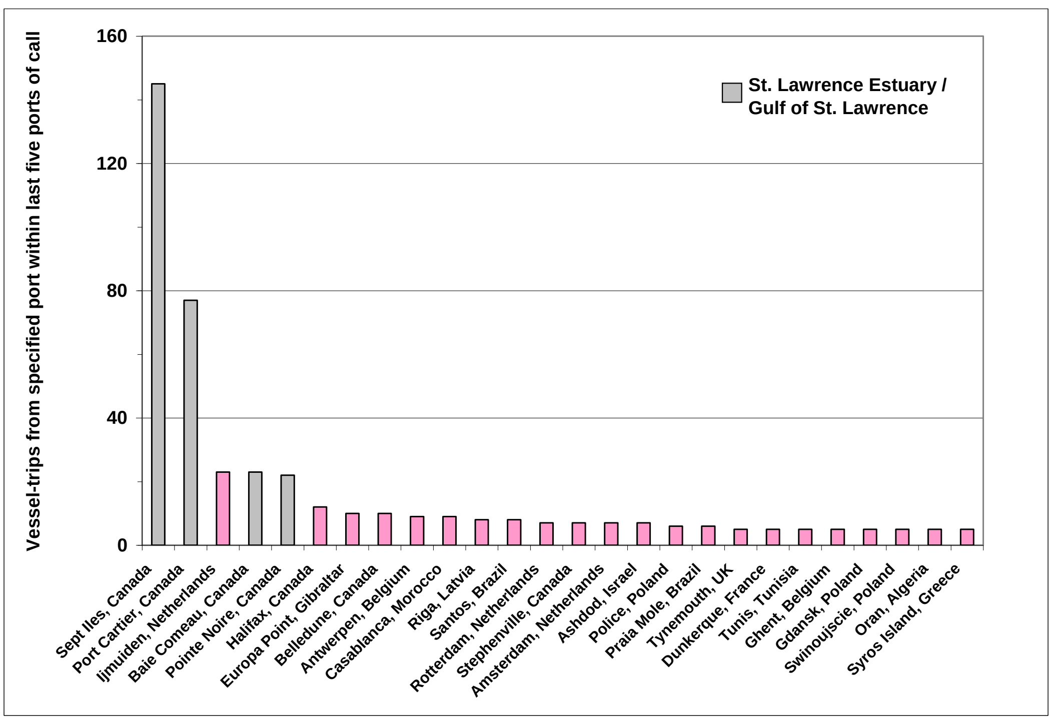

Figure 27. Possible source locations of residual materials discharged from vessels that entered the St. Lawrence Seaway with no ballast on board, based on last five ports of call in 2006. After entering the Seaway these vessels picked up ballast water and discharged the ballast water (along with residual materials) at a U.S. Great Lakes port.

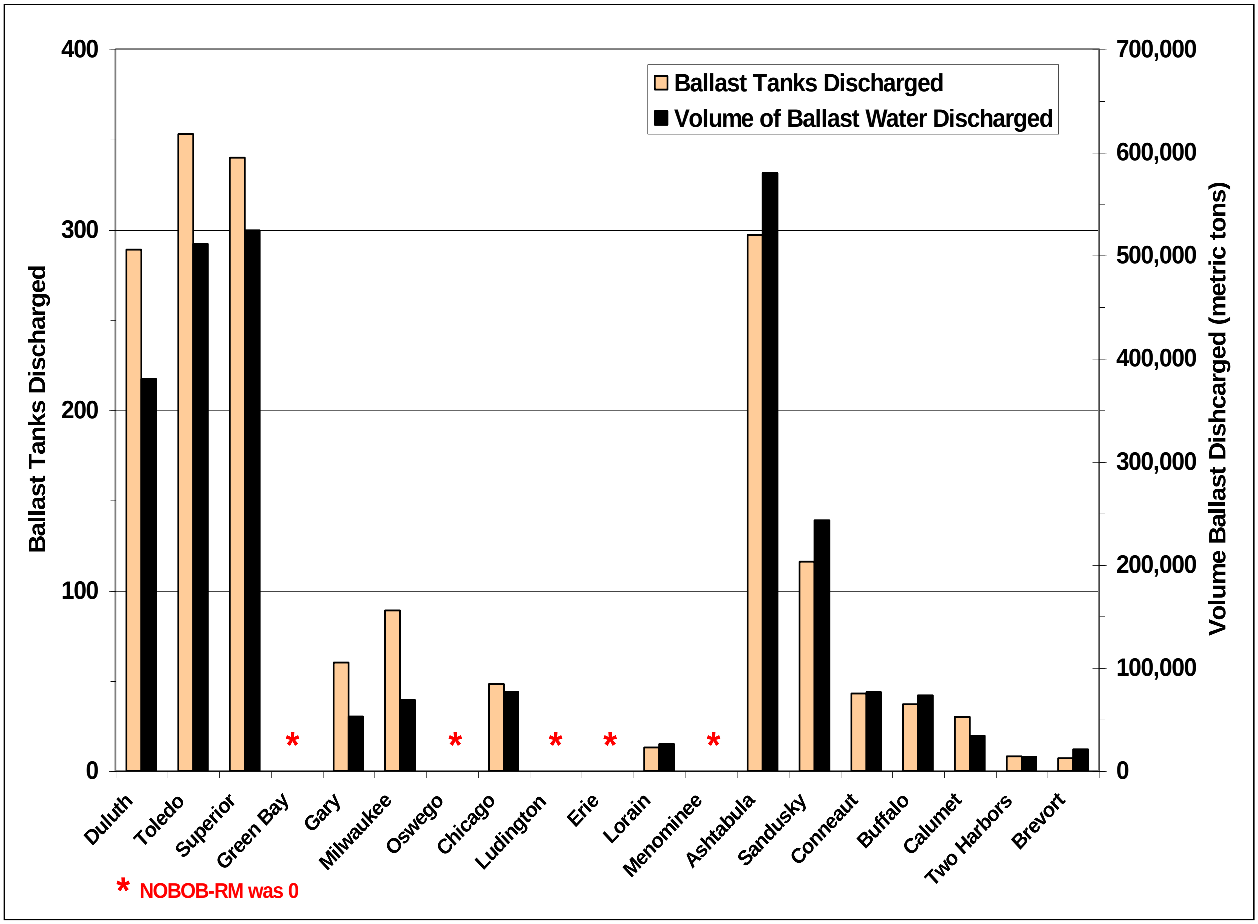

Figure 28. Frequency and volume of discharges in 2006 from NOBOB-RM vessels. NOBOB-RM vessels are vessels that entered the Seaway without ballast on board, picked up ballast water in the Great Lakes, and then discharged the ballast water along with residual material at a Great Lake port. NOBOB-RM vessels must also have visited a port outside the Great Lakes during one of the last five ports of call. Ports listed from left to right according to the results shown in 26 to facilitate comparison.

5. DISCUSSION

The Great Lakes system has been adversely affected by invasive species. Preventing the transport of these species to the Great Lakes from outside the system is the best way to avert potential ecological and economic impacts. Our analysis of ballast water discharges using vessel traffic data, evaluating similar habitats using the Genetic Algorithm for Rule-Set Production (GARP) niche model, and a literature review indicate that invasions are likely to occur over the next decade or so. If it is not possible to eliminate the transport of nonindigenous species (NIS) to the Great Lakes, the next best alternative is to monitor for the arrival of potentially invasive species and to control their spread as soon as they arrive.

Since we began our investigation, additional ballast-water control measures have been implemented. Beginning with the 2008 navigation season, all vessels must either undergo ballast water exchange (BWE) or flushing before entering the St. Lawrence Seaway (73 FR 37, p. 9,950), even those vessels that heretofore were declared as having no ballast on board. However, even with the more extensive requirements, additional NIS may still reach the Great Lakes. Some saltwater tolerant species may survive the BWE or flushing, and other vectors (e.g., hull fouling organisms) continue to pose a threat. This report provides information that may help resource managers prioritize monitoring efforts by identifying potential invaders and ports at risk.

The National Research Council recommends that a binational (United States and Canada) science-based surveillance program be established to monitor for aquatic NIS and that the program involve dedicated lake teams, as well as academic researchers, resource managers, and local citizens groups (NRC, 2008). Since early detection and rapid response is a priority of the National Invasive Species Council (NISC, 2007), the ports and species we identified could be used to structure an early warning and detection system to help evaluate the effectiveness of ballast exchange regulations and practices.

5.1. PREDICTING THE SPREAD OF SPECIES

This study identified 30 potentially invasive species with medium or high risk for spreading to the Great Lakes and causing ecological impacts and another 28 potentially invasive species that have already become established in one or more of the Great Lakes (see Appendix B). Habitat suitability maps are provided along with a summary of invasion potential for 14 modeled species. All of the modeled species are predicted to have the capability to colonize Lake Erie and the shallower waters of the other lakes. Several species may be able to colonize the entire Great Lakes region. Literature regarding the species environmental tolerances reveals that the predominant limitation to the spread of several modeled species is their tolerance to water depth. However, managers need to recognize that when NIS are transported to a new environment, species-tolerance "surprises" can occur. For instance, the quagga mussel has been found at deeper depths in the Great Lakes than in its native range (Watkins et al., 2007).

Table 3 summarizes the habitat suitability and current status for the 14 modeled species. The modeled species are categorized into two groups: (1) NIS already established in the Great Lakes and having the potential to spread to at least parts of all five lakes; and (2) NIS, not yet established but with the potential to invade the Great Lakes.

5.2. POTENTIAL MONITORING SITES BASED ON VESSEL TRAFFIC

The source of most of the ballast water discharged into the Great Lakes came from 58 different ports located predominantly in Canada and Western Europe, thereby complicating surveillance programs. If just a few foreign ports were the original source of ballast water (prior to exchange) then programs could focus on species found at those foreign ports. The six ports which received the most ballast water from vessels with ballast on board in 2006–2007, in rank order, were Duluth, MN; Toledo, OH; Superior, WI; Green Bay, WI; Gary, IN; and Milwaukee, WI (see Figure 26 and Appendix E, Table E-2). The first three ports, Duluth, Toledo, and Superior, account for 86% of the total volume of ballast water discharged into the Great Lakes. There was no evidence of a frequent, repeated connection from any specific foreign port to a specific port within the Great Lakes. For instance, 11 different vessels discharged ballast water in Toledo in 2006–2007 (see Appendix E, Table E-3). If all 11 vessels obtained ballast water from a single foreign port than monitoring could be targeted for those species occurring at that particular port. Unfortunately, the 11 vessels discharging ballast water in Toledo took-on ballast from 10 different foreign ports.

Invasive species can also be transported to the Great Lakes via vessels with no ballast on board but with residue left in the tanks (NOBOB-RM vessels). A different set of foreign ports were found to be the source of ballast water from these vessels (see Figure 27), although ports in Canada and Western Europe predominated. Consistent with the vessels with ballast on board, it was rare to find a frequent connection between particular Great Lakes ports and foreign ports. The ports receiving the greatest volume of ballast water from NOBOB-RM vessels are Duluth, MN, Toledo, OH, and Superior, WI accounting for 54% of the total volume discharged from these vessels in 2006–2007. Ashtabula and Sandusky, OH receive 32% of the ballast water released from NOBOB-RM vessels.

Table 3. Composite results for 14 species modeled using GARP

Species/common name	Summary of invasion potential
Species already established in the Great Lakes and potential for spread to all five Great Lakes	
Neogobius melanostromus—round goby	Already spread to all five Great Lakes, with large populations in Lakes Erie and Ontario. Likely to find suitable habitat throughout Lake Erie and in all Great Lakes waters at depths less than 60 m.
Potamopyrgus antipodarum—New Zealand mud snail	Already occurs in isolated areas of Lakes Erie, Ontario, and Superior. Likely to find all shallower waters (<50 m depth) as suitable habitat. High spread potential.
Dreissena bugensis—quagga mussel	Already found in all five Great Lakes, with large populations established in Lakes Erie and Ontario. The only possible identified limitation for spread is a species depth limitation which is questionable and currently appears to be as deep as 200 m.
Dreissena polymorpha—zebra mussel	Already occurs in all five Great Lakes. Likely to find suitable habitat in most of Lake Erie and portions of other lakes where water depth is less than 60 m. May be outcompeted by the quagga mussel.
Gymnocephalus cernuus—ruffe	Already found in Lakes Superior, Michigan, and Huron. The species is probably capable of colonizing most areas within the Great Lakes where water depth is less than 85 m.
Species that may invade at least parts of all five Great Lakes	
Alosa aestivalis—blueback herring	Models predict it could find the entire region as suitable habitat, except possibly the deeper waters of Lake Superior.
Pomatoschistus minutus—sand goby	It is likely this species would find all shallower waters as suitable habitat.
Rutilus rutilus—roach	Already reported in Lakes Erie and Ontario. Predicted to find suitable habitat throughout these lakes, and probably into other shoreline areas.
Scardinius erythrophthalmus—rudd	Predicted to find suitable habitat throughout Lake Erie and into the shallower waters of the other four Great Lakes.
Cercopagis pengoi—fishhook waterflea	Established in Lake Ontario and reported in Lakes Erie and Michigan. Predicted to find suitable habitat throughout the region. Densities increase in deeper waters.
Tinca tinca—tench	Found currently in St. Lawrence River. Potential to spread to shallower waters of most of Lake Erie, and to isolated portions of the other Lakes. Tench can spread rapidly once established.
Proterorhinus marmoratus—tubenose goby	Already reported as present in Lake St. Clair and western Lake Erie. May be able to occupy all shallow waters of all five Great Lakes.
Corophium curvispinum—(an amphipod)	Capable of invading Lake Erie and shallower waters. Not enough data is available to predict if it can find suitable habitat elsewhere.
Neogobius fluviatilis—monkey goby	May be capable of inhabiting shallower waters of all five Great Lakes.

Since it is unknown which type of vessel (ballast on board [BOB] or NOBOB-RM) is more likely to transport NIS, ports receiving ballast water from either type of vessel are presumed to be at risk. In order to recommend ports for monitoring we cannot just consider the transport potential, we also need to consider the potential to find suitable habitat. The results of GARP modeling and the literature review reveal that Lake Erie and shallower portions of the other Lakes provide the most favorable habitat for the modeled species, and that the deeper portions of Lake Superior are less hospitable to species invasions (Grigorovich et al., 2003b). However, the shallower portions of Lake Superior, especially the Duluth-Superior harbor, are at greater risk for invasion.

Assuming the observed vessel traffic and ballast-water discharge information for 2006 and 2007 is representative, the port of greatest concern for receiving sufficient propagules and providing the most suitable habitat is Toledo, OH. Toledo is located on Lake Erie, a region that the GARP model predicted would have a high chance of providing suitable habitat for the modeled species. Other ports of elevated concern for receiving sufficient propagules and offering suitable habitat are Gary, IN; Milwaukee, WI; Chicago, IL; and Ashtabula and Sandusky, OH. Ports with high transport potential but generally low habitat suitability are Duluth, MN and Superior, WI. The spread of invasive species from beyond the Duluth-Superior harbor may be limited by the colder and deeper waters in the main portion of Lake Superior. Yet, since inter-lake transport can occur to other ports, Duluth and Superior also warrant a monitoring program. Managers may wish to emphasize detection programs at the ports of concern that were identified and may wish to focus on the list of 58 potentially invasive species with a moderate or strong chance to invade and cause ecological or economic impacts. For the 14 modeled species, the focus can be narrowed based on the summary shown in Table 3.

Given the new regulations which require all vessels entering the Seaway to undergo either ballast water exchange or flushing at sea, additional research on the tolerance of invasive species to saltwater would enable managers and scientists to better focus monitoring activities on those species that are likely to survive salt water flushing. Subsequent analyses of the NBIC database is recommended to determine if the 2006–2007 data are indeed representative.

In summary, we have provided a list of NIS of concern, predicted locations that would provide suitable habitat for 14 modeled species, identified those U.S. Great Lakes ports receiving the most ballast water from sources originating from outside the Great Lakes, and predicted the ports most at risk of invasion. Our findings support the need for detection and monitoring efforts at those ports believed to be at greatest risk. This study also demonstrates the importance of understanding invasion biology by evaluating the two most important predictors of invasion, as suggested by Williamson (1996): propagule pressure and suitable habitat. Further, this may be the first time that remote sensing data were used in conjunction with GARP to predict the spread of aquatic invasive species.

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