Aquatic Invasions (2013) Volume 8, Issue 4: 361–374
doi: http://dx.doi.org/10.3391/ai.2013.8.4.01

Research Article

The Laurentian Great Lakes as a beachhead and a gathering place for biological invasions

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Received: 2 May 2013 / Accepted: 26 August 2013 / Published online: 14 October 2013

Handling editor: Vadim Panov

Abstract

Invasive species alter ecosystems and harm economies. Improved understanding of past invasions can inform and improve current and future management efforts. We investigated the global and North American distribution of nonindigenous species (NIS) prior to their establishment in the Laurentian Great Lakes (GL). For the subset of NIS first recorded in North America in the GL, we also investigated the likelihood of these species to spread beyond the basin. With respect to biological invasions, we assessed if the GL basin is a beachhead (i.e., most NIS in the basin originating from outside North America) or a gathering place (i.e., most NIS arriving in GL already in North America). We found that the GL are both a beachhead and a gathering place, depending on the vector of introduction to the basin. Ballast water release introduces most beachhead NIS (43 of 65, 66%), whereas canals, authorized release, and unauthorized release primarily introduce gathering place NIS (67 of 101, 66%). Overall, gathering place NIS currently outnumber beachhead NIS in the GL (101 vs. 65). Regarding spread of beachhead NIS beyond the GL, we found that time elapsed since discovery in the GL predicts secondary spread with 87% accuracy. Our classification model suggests that beachhead NIS established populations outside the GL basin within 77 years of discovery there, suggesting that numerous NIS may be poised to spread beyond the GL basin in the near future. Given the established policy goal of both Canada and the United States to reduce harm from invasions, several recommendations arise from our analysis: (1) maintain, strengthen, and monitor the efficacy of ballast water regulations to prevent the introduction of additional beachhead NIS, (2) conduct risk assessments of NIS that are already in North America but not yet in the GL to prioritize management actions, and (3) seek regional coordination of regulations of vectors of gathering place NIS to shore up weak policy links.

Key words: biological invasions; nonindigenous species; Great Lakes; human-mediated dispersal; vectors; invasion history; prevention

Introduction

Human-mediated spread of species beyond their native range is an important issue in natural resource conservation and management (Vitousek et al. 1997; Mack et al. 2000). Some nonindigenous species (NIS) establish populations and become invasive. Invasive species threaten native species biodiversity and impair ecosystem services (Wilcove et al. 1998; Sala et al. 2000). The ecological impacts of invasive species may also cause large economic losses (Pimentel et al. 2005; Rothlisberger et al. 2012). The rate and volume of global commerce and transportation networks have increased in recent decades. In many regions, these increases are linked to the growing number of NIS that are introduced and become established (Levine and D'Antonio 2003; Ruiz and Carlton 2003). With scarce resources to manage invasions, prevention is the most cost-effective way to avoid future damage (Leung et al. 2002). Effective prevention requires a good understanding of the source and introduction vectors of potential invasive species (Vander Zanden and Olden 2008).

Biological invasions in the Laurentian Great Lakes (GL) are numerous and relatively well studied. A variety of vectors, ranging from horticulture to ballast water release, have introduced aquatic NIS to the GL. The type and severity of impacts to the GL ecosystem vary widely among species. Some species appear to have neglible effects on the ecosystem (e.g., aquatic moth *Acentria nivea*), whereas the effects of a few have been dramatic (e.g., dreissenid mussels) (Mills et al. 1993a; Scholtens and Balogh 1996; Kelly et al. 2009). Other studies provide excellent summaries and analyses of the invasion history of the GL basin (Mills et al. 1993b; Grigorovich et al. 2003; Holeck et al. 2004; Ricciardi 2006). This paper builds upon previous work to consider species occurrences prior to their discovery in the GL, and range expansion in North America for those species first discovered in North America in the GL. Our purpose is to learn whether the GL basin is a beachhead or a gathering place for NIS in North America.

To assess whether the GL are a gathering place or a beachhead for NIS in North America, we summarize historical data on NIS in the GL. As shorthand, we refer to species discovered in the GL basin that are new arrivals to the inland waters of North America as **beachhead NIS**. Beachhead NIS include species that are native to the coastal waters of North America, but whose first non-marine North American record was in the GL. We call species that are now present in the GL basin, but which were first recorded in North America outside of the GL basin, **gathering place NIS**. Gathering place NIS also include species that are endemic to regions of North America outside the GL basin. We also consider whether a species' beachhead versus gathering place status is related to other variables such as introduction vector, taxonomic group, or time period of discovery. Our analysis considers the full historical range of human-mediated GL invasions because such an examination reveals how the collection of GL NIS reached its current state and, based on history as well as on recent trends, how additional NIS are likely to enter the GL in the future.

We hypothesized that the GL are a beachhead (i.e., critical initial entry point) for freshwater NIS in North America. A well-known example consistent with this hypothesis is the spread of zebra and quagga mussels from the GL to inland waters outside of the GL, including possibly Lake Mead (Arizona-Nevada, USA) and other waterways in Utah and California (Stokstad 2007). If NIS do not spread beyond the GL, they cannot directly disrupt ecosystems outside of the basin. With knowledge of which beachhead NIS will spread, resource managers could prioritize these species and their probable vectors for efforts to prevent spread (Vander Zanden and Olden 2008). Therefore, we also investigate if readily available data can accurately predict which beachhead NIS are most likely to spread beyond the GL basin. Thus, understanding if the GL are an invasion beachhead, a gathering place, or both has implications for predicting which NIS are likely to establish future populations, and for developing management strategies to prevent future harm to the GL and other aquatic ecosystems in North America.

Methods

Species distribution prior to discovery in Great Lakes

We gathered data on 182 aquatic NIS (including wetland plants) established in the GL basin. This data originated from previously published studies and from the Great Lakes Aquatic Nonindigenous Species Information System (GLANSIS 2013). The species we considered included 178 of the species that Ricciardi (2006) identified as NIS established in the GL. Ricciardi (2006) included 182 species on his list of established NIS, but we removed four species from this list based on the conclusions of taxonomic experts that these species are not established NIS in the GL (Reid and Hudson 2008). To the 178 species from Ricciardi (2006), we added four recently discovered species – Viral hemorrhagic septicemia virus (VHSV) (Kelly 2007), bloody red shrimp *Hemimysis anomala* (Kelly 2007), water lettuce *Pistia stratiotes* (Adebayo et al. 2011), and water hyacinth *Eichhornia crassipes* (Adebayo et al. 2011). For each species, we recorded common name, scientific name, taxonomic category, endemic region, year of discovery in the GL, and individual GL basin where originally discovered (e.g., Lake Ontario).

We recorded the current and historical distribution of each NIS in North America. Regarding historical distribution, we focused on whether the species was novel to North America when it was discovered in the GL basin (i.e., a beachhead NIS) or not (i.e., a gathering place NIS). While it is possible that a species first established outside the GL was first collected in the GL or vice versa because of chance or elevated detection effort, it is impossible to know how often this has actually occurred. Therefore, this study relies on published records of first occurrences in North America. For beachhead NIS, we recorded whether the species was confined to the GL basin at present or if it had spread beyond the basin (Appendix S1 in Supporting Information). For the authorized release vector the first North American record refers to where the species was first discovered in North America outside of cultivation.

To determine if species were beachhead or gathering place NIS, we referred to distribution data from the species-specific sources cited in Mills et al. (1993b), Ricciardi (2006), Kelly (2007), and from sources cited in the species accounts in GLANSIS (2013) and the United States Geological Survey's Nonindigenous Aquatic Species database (NAS 2013). For several plant species, we also queried the United States Department of Agriculture (USDA) PLANTS database (USDA 2013), the USDA Forest Service Fire Effects Information System (FEIS 2013), and the Invasive Species Compendium (CABI 2013) to verify current and historical distribution data. We used the same sources to locate records of beachhead NIS with populations established outside of the GL basin. To evaluate our hypothesis of the GL as a beachhead for biological invasions of North America, we calculated the proportion of beachhead NIS in the GL (i.e., beachhead NIS/total NIS) and compared it directly to the proportion of gathering place NIS. For beachhead NIS, we also tallied how many have spread beyond the GL basin versus how many remain confined to it.

We identified one of six vectors of introduction to the GL for each species. We used the same vectors as Ricciardi (2006) and Kelly (2007). In cases where there are multiples possible vectors, we selected the one identified in GLANSIS or by Ricciardi (2006) as the primary vector (i.e., the vector most likely to have introduced propagules which resulted in establishment). The vectors were canals, authorized release (including cultivation), unauthorized release (including aquarium dumping and live bait release), solid ballast dumping, ballast water release, and unknown. We included aquarium dumping and live bait release with unauthorized release because these releases are accidents or oversights that are not intended to result in population establishment, as opposed to authorized release associated with stocking or cultivation where establishment is intended.

We investigated whether a species' beachhead versus gathering place status depended on other variables. To inspect for such relationships among variables, we cross-tabulated data with respect to two to three variables at a time. Cross-tabulated variables included introduction vector, lake where first discovered, time period of discovery, taxonomic group, and whether a species is a beachhead NIS or gathering place NIS.

Predicting secondary spread of beachhead NIS

To investigate if readily available data can accurately predict which beachhead NIS will spread beyond the GL basin, we used recursive partitioning to generate a decision tree (De'ath and Fabricius 2000). The response variable was the current distribution of each species (i.e., whether it remains confined to the GL basin or not). The explanatory variables were introduction vector, year of discovery in the GL, lake basin where discovered originally, endemic region, and taxonomic category.

Recursive partitioning analysis generates decision trees that are a result of balancing accurate classification of the training dataset (i.e., a sufficiently complex tree could correctly classify 100% of the training observations) against robustness in accurately classifying new observations (i.e., model is not overfit to the training data). Comparing decision tree predictions to known values of the response variable in an independent dataset is the ideal way to assess how well the model achieves this balance (Venables and Ripley 2002). Lacking an independent dataset, we used leave-one-out cross-validation (LOOCV) to calculate each candidate model's misclassification rate (Venables and Ripley 2002). Misclassification rate is the number of species wrongly predicted to be in a category (i.e., confined to GL vs. spread beyond) divided by the total number of species the model predicts to be in that category. For example, if a candidate model predicted 50 species to be confined to the basin and five of those 50 had already spread beyond it, the misclassification rate (i.e., all false negatives in this example) would be 10% (i.e., 5/50). In evaluating the misclassification rates for each model, we considered both specificity (i.e., false positives: species predicted to spread outside the basin, but which had not) and sensitivity (i.e., false negatives: species predicted not to spread, but which had). We generated 31 candidate models from all possible combinations of our five explanatory variables (i.e., year discovered in GL, introduction vector to GL, taxonomic group, individual GL basin where first discovered, endemic region), and selected the best model based on lowest LOOCV misclassification rate. The number of explanatory variables in each model ranged from one to five.

Results

Species distribution prior to discovery in Great Lakes

Of 182 NIS established in the GL basin, 101 were classified as gathering place NIS, 65 as beachhead NIS, and 16 had an indeterminate first record in North America (and thus no assignment was possible) (Table 1). Vectors differed in the number of beachhead versus gathering place NIS each vector introduced to the GL (Table 1). Ballast water release (BW) introduced 66% of beachhead NIS. Conversely, BW introduced only 16% of gathering place NIS (Table 1). Unintentional and authorized release introduced 55% of gathering place NIS. Unintentional and authorized release introduced only 12% of beachhead NIS. Canals introduced 11% of gathering place NIS and less than two percent of beachhead NIS (Table 1).

Individual lake basins differed with respect to their ratio of beachhead to gathering place NIS. For the basins of Lake Huron, Lake Michigan, Lake St. Clair, and Lake Superior, NIS were approximately evenly divided between beachhead NIS and gathering place NIS (Table 1). However, the basins of Lake Erie and Lake Ontario had over two (25 v. 11) and one-and-a-half (31 v. 22) times as many, respectively, more gathering place NIS than beachhead NIS (Table 1). Moreover, out of 13 species that were widely distributed throughout the GL by the time they were discovered in the basin, only one was a beachhead NIS.

The relative abundance of beachhead versus gathering place NIS differed according to taxonomic group (Tables 2 and 3). In several groups, the number of beachhead NIS was approximately the same as the number of gathering place NIS: algae (12 beachhead NIS v. 13 gathering place NIS); and mollusks (9 v. 9). In contrast, some taxa were overrepresented among beachhead NIS. More than twice as many crustaceans were beachhead NIS as gathering place NIS (11 v. 5). In the Other taxonomic category, there were 4 times as many beachhead NIS as gathering place NIS (20 v. 5). Taxa in the Other category include oligochaetes, flukes, amoebae, and several others (Appendix S1). Finally, vascular plants and fishes exhibited the opposite pattern. There were six times as many gathering place as beachhead NIS among vascular plants (42 v. 7) and four times as many fishes (21 v. 5) (Table 2).

The taxonomic composition of beachhead NIS differed from that of gathering place NIS. Of the 101 gathering place NIS, 42% were vascular plants (Table 2). The majority of these were introduced to the GL through deliberate or unauthorized release associated with cultivation or through the solid ballast vector (Table 2). No vascular plants were introduced through ballast water release. After plants, the next most abundant taxonomic group of gathering place NIS was fishes (21 species). These were mostly introduced to the GL via canals and authorized and unauthorized release (Table 2).

Taxonomic groups and vectors

The characteristics of a vector appear to influence the taxonomic categories of species that vector is likely to introduce (Tables 2 and 3). This may be because the traits of particular taxonomic groups make them more likely to be associated with one vector as opposed to another. For example, species with planktonic life stages are particularly vulnerable to ballast water entrainment. Of 26 species of nonindigenous algae in the GL, ballast water release introduced 23. Furthermore, nearly all the species introduced by ballast water from other taxonomic categories have planktonic life stages. On the other hand, vascular plants are not likely to be associated with ballast water release as zero of the 63 species that ballast water introduced were vascular plants. Introductions of vascular plants were most often attributed to authorized release (27 species) and unauthorized release (14 species). Unauthorized release is the only vector that has introduced species from all nine taxonomic categories. Unauthorized release includes a wide variety of possible introduction events, ranging from the escape from cultivation of ornamental plants to aquarium dumping of unwanted pets and their associated parasites and pathogens.

Secondary spread of beachhead NIS

Out of 65 beachhead NIS, 68% have not yet been recorded outside of the GL basin (Figure 1, Table 3). However, all beachhead NIS introduced to the GL by canals and authorized release have spread beyond the basin, as have 75% of those introduced by solid ballast dumping. At the other end of the spectrum, only 16% of the 43 beachhead NIS introduced by ballast water have spread beyond the basin (Figure 1, Table 3).

The location of initial North American establishment was indeterminate for 16 NIS in the GL basin. Most of the indeterminate species were vascular plants that were discovered in the GL basin in the 19th and early 20th centuries, and which are now widely distributed in North America (Table 2). We treat these 16 as neither beachhead nor gathering place NIS. Better knowledge of the introduction and establishment history of these species might increase the denominator, but not the numerator, of the fraction of beachhead NIS still confined to the basin. At the extreme, if all 16 indeterminate species were actually beachhead NIS, the percent remaining confined to the basin would decline from 68% to 54% [44 out of (65+16)] (Table 1).

Table 1. Location of first record in North America of 182 NIS in the Great Lakes (GL) basin, cross-tabulated by individual GL where the species was first discovered in the GL region and the vector of introduction to the basin. Vector abbreviations: canals (C), authorized release (RA), unauthorized release (RU), ballast water release (BW), solid ballast dumping (SB), and unknown (U).

First Record:	GL Basin (n = 65)						Elsewhere (n = 101)						Unknown (n = 16)						
	Introduction Vector to the GL basin																		
Lake basin of first GL record	C	RA	RU	BW	SB	U	C	RA	RU	BW	SB	U	C	RA	RU	BW	SB	U	Row Total
Erie	1	1		9			3	3	12	4	1	2		1		1			38
Huron			1	2				2	2	1		1		1					10
Michigan		1	1	7	1	1	1	3	6	7	1	1						1	31
Ontario		2		11	6	3	7	8	9	3	3	1	1	1	1		2	1	59
St. Clair				7					1			3							11
Superior		1		7	1	1		2	3	1		2							18
Unknown												1			1				2
Widespread		1						5				2		5					13
Column Total	1	6	2	43	8	5	11	23	33	16	5	13	1	8	2	1	2	2	182

Table 2. Nonindigenous species in the Great Lakes (GL) basin of which the first North American record is outside the GL basin or is indeterminate, crosstabulated by taxonomic group and introduction vector to the GL. Vector abbreviations: canals (C), authorized release (RA), unauthorized release (RU), ballast water release (BW), solid ballast dumping (SB), and unknown (U).

	First in North America outside of GL Basin (n=101)							First in North America indeterminate (n=16)						
	Introduction Vector to the GL basin													
Taxon	C	RA	RU	BW	SB	U	Taxon Total	C	RA	RU	BW	SB	U	Taxon Total
Alga			1	11		1	13				1			1
Bacteria										1				1
Crustacean			2	2		1	5							
Fish	7	8	5	1			21							
Insect			1			1	1							
Mollusk	3	1	4	1			9							
Other			5				5							
Pathogen			2	1		1	4							
Plant	1	14	13		5	9	42	1	8	1		2	2	14
Column Total	11	23	33	16	5	13		1	8	2	1	2	2	

Table 3. Current North American distribution of nonindigenous species (NIS) first recorded in North America in the Great Lakes (GL) basin (i.e., beachhead NIS) (n = 65), crosstabulated by taxonomic group and introduction vector. Vector abbreviations: canals (C), authorized release (RA), unauthorized release (RU), ballast water release (BW), solid ballast dumping (SB), and unknown (U).

	Confined to the GL basin (n = 44)						In and Out of the GL basin (n = 21)					
	Introduction Vector to the GL basin											
Taxon	C	RA	RU	BW	SB	U	C	RA	RU	BW	SB	U
Alga			1	10						1		
Bacteria												
Crustacean				8		1				2		
Fish			1	2				1		1		
Insect												
Mollusk				1	1					2	5	
Other				15		2	1			1		1
Pathogen						1						
Plant					1			5			1	
Column Total	0	0	2	36	2	4	1	6	0	7	6	1

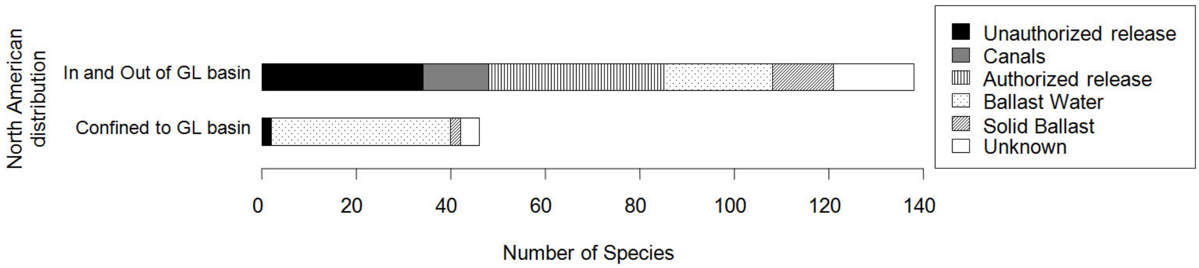

Figure 1. Current North American distribution with respect to the Great Lakes (GL) basin of 182 nonindigenous species (NIS) in the GL. Shading within each bar shows vector of introduction to the GL basin. The upper bar labeled "In and Out of GL basin" represents both beachhead NIS that have spread beyond the GL basin and gathering place NIS. By definition, gathering place NIS are in and out of the GL basin. The lower bar labeled "Confined to GL basin" represents beachhead NIS whose North American range is currently restricted to the GL basin.

Predicting secondary spread of beachhead NIS

The decision tree with the lowest combined misclassification rate (i.e., % false positives + % false negatives) had one explanatory variable: years since discovery in the GL basin. This model identified 77 years since discovery in the GL as the threshold for predicting if a species was still confined to the GL basin. That is, if a species was discovered in the GL less than 77 years before present, it is predicted to be confined to the GL basin at present. If discovered in the GL more than 77 years before present, a species is predicted to have spread beyond the basin. The misclassification rate for species confined to the GL basin was 18% (9 false negative predictions out of 51 species predicted to be confined to the basin). The misclassification rate for species that had spread beyond the basin was 13% (i.e., 2 false positive predictions out of 15 species predicted to have spread beyond the basin).

Discussion

The Great Lakes as a beachhead

Historically, ballast water release has been the most important vector for introducing species novel to North America (i.e., beachhead NIS) to the GL. Out of 65 beachhead NIS, ballast water release introduced 43 species (66%, Table 3). However, introductions by this vector may have been reduced in recent years as a result of federal regulations and binational coordination between the United States and Canada (USCG 1993; Government of Canada 2006; SLSDC 2008; Bailey et al. 2011). Since 2006, no new NIS associated with transoceanic shipping have appeared in the GL (Bailey et al. 2011), suggesting that preventative regulations are working. Current policies in development or in the early stages of implementation include more stringent ballast water release regulations and improved on-board ballast water treatment technologies (e.g., ultraviolet irradiation) (NRC 2008). While promising, these initiatives will require close monitoring to quantify their efficacy (Costello et al. 2007). Such monitoring is essential because globally there are numerous potentially invasive freshwater species that have not yet become established in the GL (Keller et al. 2010). Maintaining and strengthening policies to reduce the likelihood of the introduction and establishment of additional NIS via ballast water release in the GL are important for the conservation of freshwater resources across the entire continent (Drake and Bossenbroek 2004; Drake and Lodge 2006).

Even as the risks of ballast water introductions of novel species are reduced, the risk of species already established in the GL spreading beyond the basin remains a threat. Of 65 beachhead NIS, approximately one-third (i.e., 21 species) have already spread beyond the GL basin to other parts of North America (Figure 2, Table 3). Our classification model indicated beachhead NIS are likely to spread away from the basin within 77 years of being discovered in the GL region. Because numerous beachhead NIS arrived in the GL after the 1959 opening of the St. Lawrence Seaway, most of the beachhead NIS that are confined to the GL basin have been there for less than 50 years. This suggests that beachhead NIS currently in the GL will continue to spread and

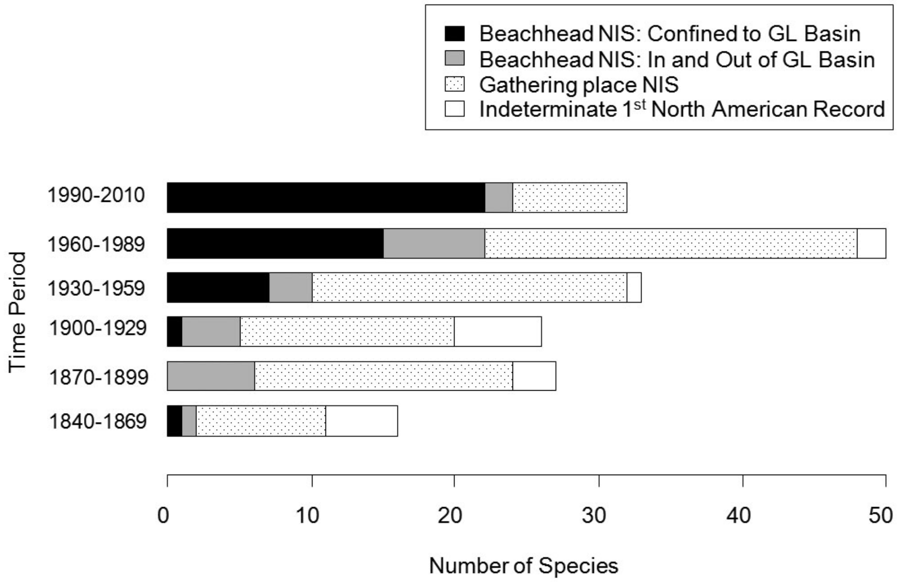

Figure 2. Date of first detection of 182 nonindigenous species (NIS) in the Great Lakes (GL) basin. Shading within each bar shows current North American distribution and if the species are beachhead or gathering place NIS, or if the location of the first North American record is indeterminate.

establish populations throughout North America. Thus, because of ballast water release in previous decades, the GL are poised to remain an important source for freshwater invasions throughout the rest of North America. This assumes that current populations of beachhead NIS that are now established outside the GL originated from the GL. Even if this assumption is invalid in some cases, our findings suggest that once discovered in the GL, beachhead NIS are likely to establish populations outside the basin within several decades. Whether beachhead NIS in the GL are the source of introductions beyond the basin or an indicator that an independent introduction event (i.e., from a non-GL source) will lead to the establishment of the species elsewhere in North America, the discovery of novel species in the GL provides early warning for the rest of the continent. A future analysis could investigate how many species had their first global nonindigenous occurrence record in the GL. This could clarify the relative importance of the GL as an early warning site of global significance for freshwater invasions.

The fact that time since discovery in the GL emerged as the strongest predictor of spread beyond the GL is consistent with the known importance of lag times during incipient invasions (Crooks 2005), and removes any support for complacency about species that have been present in the GL for multiple decades. As time elapses after the discovery of beachhead NIS in the GL, it becomes more and more likely that the species will expand its North American range beyond the basin (Figure 2). The 77 years predicted to elapse, on average, before spread beyond the basin gives an indication of when managers should expect beachhead NIS to appear outside of the GL basin. Interestingly, the many beachhead NIS (45 species) introduced by ballast water release since the 1959 opening of the St. Lawrence Seaway have been in the GL for a maximum of 55 years, as of 2013. Thus, our model predicts that many of these NIS may expand their ranges beyond the basin in the next couple of decades. This finding may be useful to help prioritize prevention and monitoring efforts on species that are poised to escape the GL after decades of establishment and spread within the GL.

There is, however, substantial variation around the 77-year average time until spread beyond the basin. Our model does not explain this variation. Seventy-seven years can only be viewed as a rough estimate of the time elapsed between a species discovery in the GL and its spread beyond the basin. Our classification model suggests that a valuable future analysis would be to investigate the actual time elapsed between the discovery of a beachhead NIS in the GL and the first report of its discovery elsewhere in North America. Furthermore, future work should also investigate the mechanisms associated with our statistical model’s indication of a 77-year time lag before spread beyond the GL basin. Possible mechanisms could include suitability of available vectors and the frequency of their movements, proximity to suitable out-of-basin habitat, occurrence of major weather events (e.g., 100-year floods that provide temporary inter-basin hydrologic connections), and species' life history traits. Understanding these mechanisms may explain the time lags associated with spread beyond the GL basin and could help to distinguish between beachhead NIS that are likely to spread rapidly and those that are less likely to spread.

Several beachhead NIS have in fact established populations outside the GL basin in many fewer than 77 years since their discovery in the GL. Nearly all of these relatively rapid dispersers came to the GL via ballast water release. The same traits that facilitated these species' inter-continental transport by ships may have contributed to their quick dispersal beyond the basin. For example, planktonic veligers of dreissenid mussels are easily pumped into ballast tanks. Veligers are also easily dispersed in moving water that connects the GL to one another and to other watersheds (e.g., the Chicago Sanitary and Ship Canal that connects the GL to the Mississippi River basin) (Griffiths et al. 1991). Future studies could investigate if and how the actual time elapsed until spread beyond the GL basin depends on the traits of beachhead NIS. Such studies could identify likely-to-spread species that are currently confined to the GL, suggesting priorities for increased containment efforts (Vander Zanden and Olden 2008).

The Great Lakes as a gathering place

Gathering place NIS in the GL basin currently outnumber beachhead NIS. These NIS, new to the GL basin, were, by definition, already established elsewhere in North America before arriving in the GL. Key vectors for introducing gathering place NIS are authorized release, unauthorized release, and canals (Table 1). Compared to shipping, these non-shipping vectors have received less attention from scientists, managers, and policy-makers. However, recent studies highlight the risks that NIS established elsewhere in North America pose to the GL (Duggan et al. 2006; Cohen et al. 2007; Keller and Lodge 2007; Drake and Mandrak 2010; Veraldi et al. 2011; Gordon et al. 2012). For example, Cohen et al. (2007) demonstrates that aquarium dumping exerts substantial propagule pressure on the GL from a potentially invasive aquatic plant. This and similar studies indicate that non-shipping vectors are likely to transmit NIS established elsewhere in North America to the GL.

Recognizing that the majority of NIS in the GL were established elsewhere in North America prior to being discovered in the GL and that non-shipping vectors introduce most of these gathering place species to the GL has two important implications. First, improvements in regional coordination of the management of non-shipping vectors may be crucial to prevent additional invasive species from entering the GL basin. Regional coordination could improve the current patchwork of state-by-state regulations, a patchwork that affords protection only as strong as its weakest regulation (Peters and Lodge 2009). For the non-shipping vectors considered here, state regulations vary widely as to their stringency and level of enforcement (Peters and Lodge 2009). This finding is consistent with recent conservation plans that identified improving regional consistency of regulations as a top priority for preventing future invasions to the GL (Thomas et al. 2009; Pearsall et al. 2012). Notably, the 2012 renewal of the Great Lakes Water Quality Agreement (GLWQA) between the United States and Canada includes an annex (Annex 6) that specifically addresses aquatic invasive species. This annex represents a binational commitment to consistent and coordinated regulations with respect to aquatic invasive species, with an emphasis on prevention.

The second implication is that risk assessments of species already in North America, but not yet in the GL basin, may provide valuable information for prioritizing management actions to block the most harmful species. As of 2012, there were 394 freshwater NIS (not including plants) documented in North America (NAS 2013). Fewer than 100 of these 394 species are currently found in the GL (GLANSIS 2013). Thus, it is likely that new NIS in the GL will come from among those already established elsewhere in North America. Predictions of which of these nearly 300 freshwater NIS (i.e., those in North America, but not yet in the GL) are most likely to disrupt GL ecosystems could guide efforts to prevent future high-impact invasions. Risk assessments may need to consider how projected changes in climate in the GL region may improve the habitat suitability for NIS whose northern non-native range boundary currently falls south of the GL (Magnuson et al. 1997; Kling et al. 2003). Such risk assessments would enable the development of early detection and rapid response programs tailored to the species, taxonomic groups, or introduction vectors most likely to inflict harm. The need for risk assessments also applies to species endemic to regions of North America other than the GL basin.

One vector that has already drawn such attention is canals, several of which connect the GL basin to other watersheds (Ashworth 1986; Annin 2006). Canals appear to be an important vector for species established elsewhere in North America to enter the GL. Indeed, by definition, species that entered the GL via canals were already established elsewhere in North America. A future analysis could examine the vectors of introduction to North America of species that have spread throughout the continent via canals. Several species native to North America, but not to the GL basin, have entered the GL via canals (Mills et al. 1993b; Ricciardi 2006). Conversely, canals facilitate the spread of species away from the GL (Mari et al. 2011). In both respects, the connection of the GL to the Mississippi River drainage via the Chicago Ship and Sanitary Canal (CSSC) is of major importance. For instance, round goby (*Neogobius melanostomus*) has spread from the GL to colonize the Mississippi River drainage via the CSSC (Irons et al. 2006). Bighead and silver carp (*Hypothalmichthys nobilis* and *H. molitrix*, respectively) are high-profile examples of NIS first established in North America outside of the GL basin that now threaten to enter the GL via the CSSC (Hinterthuer 2012; Jerde et al. 2013). The establishment of these species may cause substantial disruption of GL food webs and ecosystems (Irons et al. 2007; Langseth et al. 2012). Thus, canals are likely to be an increasingly important vector for species to and from the GL in the future.

Conclusion

The GL are both a beachhead for NIS establishing initial populations in North America, and a gathering place for NIS dispersing into the GL from other parts of North America. Ballast water release has introduced the most beachhead NIS, while authorized release, unauthorized release, and canals have introduced the most gathering place NIS.

More broadly, this paper suggests that investigating the invasion history and subsequent spread of NIS established in an ecosystem or region may reveal key vectors and patterns of introduction. Identifying these vectors and patterns can help to guide management actions to prevent new invasions into that ecosystem or region and those originating from it. Future studies could compare the GL to other locations in North America to consider the relative importance of each as beachheads and gathering places for NIS on the continent.

Our management recommendations, all of which are consistent with the established binational policy goal to prevent future harm from invasions in the GL basin (Annex 6 of the GLWQA), demonstrate the value of this approach: (1) seek regional coordination of vector regulations, (2) conduct risk assessments of NIS that are already in North America but not yet in the GL to prioritize management actions, (3) maintain ballast water regulations that prevent species novel to North America from being introduced to the GL, and (4) increase systematic surveillance to rigorously measure the effectiveness of management actions.

Acknowledgements

The NOAA National Sea Grant Program (Award No. NA16RG2283) through the Illinois-Indiana Sea Grant College Program (Subaward No. 2003-06727-10) and the NOAA Center for Sponsored Coastal Ocean Research awards NA09NOS 4780192 and NA10NOS4780218 funded this research. A Schmitt Graduate Research Fellowship from the University of Notre Dame and a research fellowship from the Center for Aquatic Conservation at the University of Notre Dame also partially supported JDR. An intergovernmental personnel agreement between the U.S. Forest Service and the University of Notre Dame facilitated the completion of this project. Thanks to C. Jerde, R. Keller, J. Peters, J. Wilson, M. Wittmann, and several anonymous reviewers for helpful comments. This is a publication of the Notre Dame Environmental Change Initiative.

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Supplementary material

The following supplementary material is available for this article.

Appendix 1. List of 182 nonindigenous species (NIS) established in the Great Lakes (GL) basin.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2013/Supplements/AI_2013_Rothlisberger_Lodge_Supplement.pdf