



Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network

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ABSTRACT

Aim Some nations, and the International Maritime Organization, are moving towards requirements for managing ballast water to reduce the number of alien species transported and released. These and other measures will be most efficient when targeted at ships posing the greatest risks. Here, we analyse world-wide ship movements and port environmental conditions to explore how these risk components differ across arriving ships.

Location Global, with a case study of the Laurentian Great Lakes.

Methods We gathered salinity and temperature data for all global shipping ports, and data for all global ship movements during a 12-month period. We applied these data to the Laurentian Great Lakes to determine which global ports may donate new species to the Great Lakes via ship traffic, and which are most environmentally similar to the Great Lakes.

Results We show that ships regularly travel to the Great Lakes from all major coastal, and many inland, regions of the world. Most global ports, and thus the species in them, are separated from the Great Lakes by no more than two ship voyages. Combined with a measure of environmental similarity among global ports, we identify ship routes likely to transport species adapted for survival in the Great Lakes and global regions that may be the source of increasing future invasions.

Main conclusions The Great Lakes account for a small fraction of global shipping yet are closely connected to all other ports, and the species in them, by the shipping network. Our methods and data allow risks from individual ships to be ranked so that management activities can be targeted at ships most likely to introduce new invaders. Because our data sets are global, they could be applied to ship arrivals at any global port.

Keywords

Ballast water, biological invasions, environmental matching, great lakes, port, vector.

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INTRODUCTION

Networks of human trade and travel transport plants, animals and pathogens across the globe (Lodge *et al.*, 2006). Analysing traffic patterns across these networks – such as speed of travel and number of organisms transported – illuminates potential management strategies to halt or slow the spread of invasive species and epidemic diseases (Wilson *et al.*, 2009). For example, the global airline network is routinely considered

when investigating the spread of diseases such as SARS and influenza (Lessler *et al.*, 2009). Shipping forms a network that spans the globe and introduces many economically and environmentally harmful invasive species, including human diseases such as cholera (McCarthy & Khambaty, 1994; Kaluza *et al.*, 2010). Current management approaches target individual ships, but few analyses of this network have been conducted and little is known about the variation in invasion risk among individual ships. Thus, the effectiveness of current

management strategies aimed at preventing ship-borne invasions is unknown (Ricciardi, 2006; Costello *et al.*, 2007; Barry *et al.*, 2008).

What is known is that shipping is the dominant global vector for unintentional translocation of non-native marine species (Molnar *et al.*, 2008) and of euryhaline and freshwater species to many freshwater regions (Ricciardi, 2006). Ships transport non-native species in their ballast tanks and attached to hulls as fouling organisms (Drake & Lodge, 2007; Sylvester & MacIsaac, 2010). To reduce the probability of invasion, some countries require arriving ships to replace coastal ballast water with water drawn offshore (ballast water exchange, BWE) to remove coastal organisms. In addition, the International Maritime Organization (IMO), an agency of the United Nations, adopted in 2004 the *International Convention for the Control and Management of Ships' Ballast Water and Sediments* (Gollasch *et al.*, 2007). This convention, which is yet to be ratified, sets standards for the density of organisms that can be discharged in ships' ballast water. BWE and the IMO standards are each based on the premise that reducing the concentration of live organisms in ballast tanks will reduce the number of invasions. The extent to which either approach actually reduces invasion rates is unknown (Ricciardi, 2006; Costello *et al.*, 2007; Gollasch *et al.*, 2007; Ruiz & Reid, 2007; Dunstan & Bax, 2008; Johnston *et al.*, 2009), and neither approach addresses hull-fouling.

The biology of invasions from the shipping vector is poorly understood. For example, the number and condition of individuals required to found reproducing populations, the effect of voyage length on organism survival and the effect of oceanic water on survival of freshwater organisms attached to ship hulls are each probably important determinants of invasion success but remain largely unknown. On top of this, basic information about the shipping network, such as the level of connectedness among ports across the global shipping network, is poorly resolved. Finally, we note that although ships can move species in a number of ways, including in ballast tanks and as hull-fouling organisms, the relative contribution of each sub-vector to the total number of invasions is unknown (Fofonoff *et al.*, 2003; Ruiz & Reid, 2007).

In the face of this uncertainty, decisions need to be made about how to target limited management resources. It has been argued that assessments based on integrated analyses of the ports recently visited by a ship and the likelihood that organisms collected there could survive in subsequent ports could inform more cost-effective management strategies (Endresen *et al.*, 2004; Barry *et al.*, 2008). Here, we use global databases of ship traffic and port environmental conditions to assess the chance that individual arriving ships will contain organisms capable of surviving in the recipient port. Specifically, we evaluate two components of invasion risk posed by the global shipping network. First, arriving ships pose risks based partly on the ports recently visited and the organisms that may have become entrained in ballast or attached to hulls. Second, the global shipping network presents risks when

invasive species use ports as 'stepping-stones' in a sequence of invasions in which an invader spreads from its endemic area to other ports that become the origins for further spread.

As a case study, we consider the Laurentian Great Lakes, which comprise 20% of the world's surface freshwater, provide drinking water to more than 33 million people in two countries (NRC (National Research Council), 2008) and support what are possibly the world's largest freshwater recreational and commercial fisheries. The Great Lakes ecosystem is also one of the most invaded freshwater ecoregions in the world (Mills *et al.*, 1993), and a region where debate over policy to prevent shipping invasions continues to have national and international influence (NRC (National Research Council), 2008). We base our analyses on known positive relationships between probability of species establishment and (1) the number of organisms released and (2) the environmental similarity between source and recipient ecosystems (Hayes & Barry, 2008). In the absence of better information, we assume that the number of organisms released from ballast and hull-fouling is proportional to the number of ship visits to the Great Lakes and estimate environmental similarity as a function of salinity and temperature differences between source ports and the Great Lakes. We evaluate the global distribution of these risk components, presenting previously unanalysed data on global ship traffic, new data for temperature and salinity in all global ports and analyses combining these two components of invasion risk. This study is the first comprehensive analysis to combine global ship traffic and global port environmental data. It builds upon the work of Kaluza *et al.* (2010) who investigated the movement patterns of different classes of ships. We work with similar shipping data, combine it with global environmental data and apply it to a focused geographic region. We demonstrate an approach, and provide the data, that could be applied to any port to assess the likelihood that individual ships will release species that could become invasive.

METHODS

Global shipping network

We obtained port locations and ship voyage data from Lloyd's Maritime Intelligence Unit (LMIU, New York, NY, USA). LMIU manages the global data collected by the Lloyd's of London Agency Network, which gathers information from c. 1200 local agents who observe port arrivals and departures directly, and additionally gather data from written port records. This is the only global data set of ship traffic and is the standard data source for government and business applications.

The data obtained from LMIU gave locations for 6651 ports globally and records for c. 1.55 million ship voyages (arrival and departure port) during the period 1 May 2005, through 30 April 2006. To assess connectedness of the Great Lakes to global ports, we began by defining the Greater Great Lakes Ecosystem (GGLE) as all connected water bodies from the city

of Quebec (ports of Quebec City, Lauzon, Levis) on the St. Lawrence River upstream to, and including, the five Great Lakes (Ontario, Erie, Huron, Michigan, Superior) and Lake St. Clair. The GGLE is entirely freshwater and interconnected by both flowing water and ship traffic. To assess connectedness of the GGLE to other aquatic ecoregions, we traced the recent voyage history of all ships entering this region from places outside. We designate ports that were the origin of non-stop voyages that began outside and ended inside the GGLE as 'primary ports'. Since hull-fouling organisms and organisms entrained in ballast tanks may remain viable for multiple voyages, particularly if ballast has not recently been discharged, we tracked all ships that visited the GGLE backward through their shipping histories to identify ports with secondary (i.e., ports visited by ships immediately before primary ports), tertiary and quaternary connections to the GGLE. For some ships, we did not have data to trace all higher-level connections because those voyages occurred before 1 May 2005. In these cases, we included all information in the data set.

Many species are now established in ports beyond their native range. We define a 'stepping-stone' invasion to have occurred when individuals first become established beyond their native range and are then introduced to the GGLE from this non-native population. To assess how the shipping network can lead to stepping-stone invasions among ports, we began with primary ports from the previous analysis. Next, we identified all remaining global ports that were connected to primary ports by non-stop shipping traffic, regardless of whether those ships ever called on GGLE ports. These are termed '2-step' ports (i.e., a maximum of two separate ship voyages connects them to the Great Lakes). The same process was followed to identify 3-, 4- and 5-step ports.

Environmental distance

Because the chance of harm from an alien species is positively related to its ability to thrive in the target ecosystem of interest, it is essential to compare environmental conditions in the port of arrival to conditions in recently visited ports (Endresen *et al.*, 2004; Barry *et al.*, 2008). We chose to model environmental similarity based on salinity and temperature for several reasons. First, salinity and temperature tolerances are known to be two of the strongest determinants of aquatic species range (e.g., Van den Hoek, 1982; Berezina, 2003; Barry *et al.*, 2008). Second, salinity and temperature data can feasibly be gathered or estimated for all global ports. Finally, Barry *et al.* (2008) recently reviewed existing tools for calculating aquatic environmental similarity. They concluded that only environmental variables known to be strongly associated with species survival should be used and suggested temperature and salinity as the most appropriate variables.

We obtained measured or estimated values for salinity, mean temperature during the warmest month, mean temperature during the coldest month and annual average temperature (all at water surface) for each of the 6651 global ports in the LMIU database. The three temperature variables were used because

although average annual temperature gives a good indication of general global climate zone (e.g., temperate versus tropical), maximum and minimum temperatures can also be strong determinants of species range (Van den Hoek, 1982). A single salinity value was used for each port because most have stable salinities (i.e., marine or freshwater) and because it was not possible to estimate the magnitude of fluctuations at estuarine ports, which have daily and seasonal salinity fluctuations.

Salinity values were derived using one of four methods depending on port location. First, ports on an ocean shoreline were assigned a value from the World Ocean Atlas (WOA; Boyer *et al.*, 2005). Second, for ports located in estuaries or rivers within 100 km of the coast, we constructed a statistical model to estimate salinity. Training data came from a study of salinity dynamics in 15 estuaries of the US South Atlantic drainages (Orlando *et al.*, 1994). For the points with directly measured salinity data ($n = 49$), we calculated the distance inland and the discharge/width ratio of the waterway. These were used as training variables in a generalized additive model (GAM) (see Table S1 in Supporting Information for full training data). Both variables were significant (distance inland $P < 0.001$; discharge/width $P < 0.01$) and the model performed well ($R^2 = 0.677$). We applied the model to global ports within 100 km of the coast (but see exceptions below). Distance inland (river distance, not straight line) and river width were measured from GIS maps, discharge was taken from Alcamo *et al.* (2003). Third, the model just described classified all ports located more than 100 km inland as fully freshwater. Instead of running the model for these ports, they were simply designated freshwater.

Fourth, because the training data for the GAM came from estuaries that flowed into the Atlantic, which has > 30 ppt salinity, the model was not appropriate for application to rivers that flowed into lower-salinity waterbodies (e.g., the Black Sea). For these ports ($n = 329$), we assigned the salinity of the nearest WOA record (i.e., the mouth of the river). This is likely to be an overestimate in some cases, but because most of the ports in question are located near the river mouth, we believe that, in the absence of better data, it is the most reasonable assumption. An alternative assumption is that these are all freshwater ports. We tested this alternative by setting salinity in these 329 ports to 0 and recalculating environmental distance to the GGLE (see below for environmental distance methods).

Water temperatures (annual average, average during warmest month, average during coldest month) were derived using one of three methods depending on port location. First, ports on ocean shorelines were assigned temperature values directly from the WOA. Second, we developed a regression model for estimating water temperature at ports on inland waterways (mostly large rivers). Average monthly water temperatures were obtained from the United Nations Global Environmental Monitoring System database (<http://gemswater.org>) and the United States Geological Survey for 89 inland locations throughout the world. Following established methods (Mohseni

et al., 1998; Caissie, 2006), we regressed (five-parameter Weibull model) mean monthly water temperature against mean monthly air temperatures from the Climatic Research Unit (New *et al.*, 2002) at those sites ($n = 1068$; $R^2 = 0.96$). This regression model was used to estimate temperatures at inland ports (see Table S2).

Third, large lakes are morphologically and hydrologically very different to rivers and have different temperature dynamics. We used satellite-derived Advanced Very High Resolution Radiometer (AVHRR; Schwab *et al.*, 1999) imagery to determine water temperature for ports in the Laurentian Great Lakes. We obtained one image for the 15th day of the month for 11 years (1995–2005 inclusive). Monthly water temperatures for each Great Lakes port were the average from this 11-year data set. Annual mean temperatures were the average from all months.

The four environmental variables (salinity plus three temperature variables) were each transformed to mean 0 and standard deviation of 1. As a measure of environmental distance to the GGLE we calculated the Euclidean distance, in four-dimensional space (salinity plus three temperature dimensions), from all global ports to the average salinity and temperature values of the 164 ports located within the GGLE.

We conducted a sensitivity analysis to determine the relative effect of each variable on the environmental similarity measure. To do this, we sequentially dropped each variable

from the model and recalculated environmental distance of the GGLE from all global ports (i.e., four scenarios). Additionally, we calculated environmental similarity based only on mean annual temperature and salinity. Because dropping variables change the dimensionality of the Euclidean distance measure (and thus necessarily reduces the distance), it is not appropriate to report results as average change in environmental similarity for each port. Instead, we scaled the output from each analysis to mean 0 and standard deviation 1 and report the average change (\pm SD) across all global ports from the full model to each smaller model. To give a more intuitive measure of change, we also ranked all ports according to their environmental similarity and report the average change in rank (\pm SD) from the full model to each reduced model.

Combining environmental distance and ship traffic

Ports that were the source of primary ship movement to the Great Lakes were organized by global region (mostly continents). Number of arriving ships was plotted against environmental distance for each port to identify those regions most likely to be donating species that could survive in the GGLE. Russian ports were included in 'Europe' because all Russian ports with primary connections to the GGLE were in the far west of that country. Central America included the Caribbean. The Canary Islands were included with Africa.

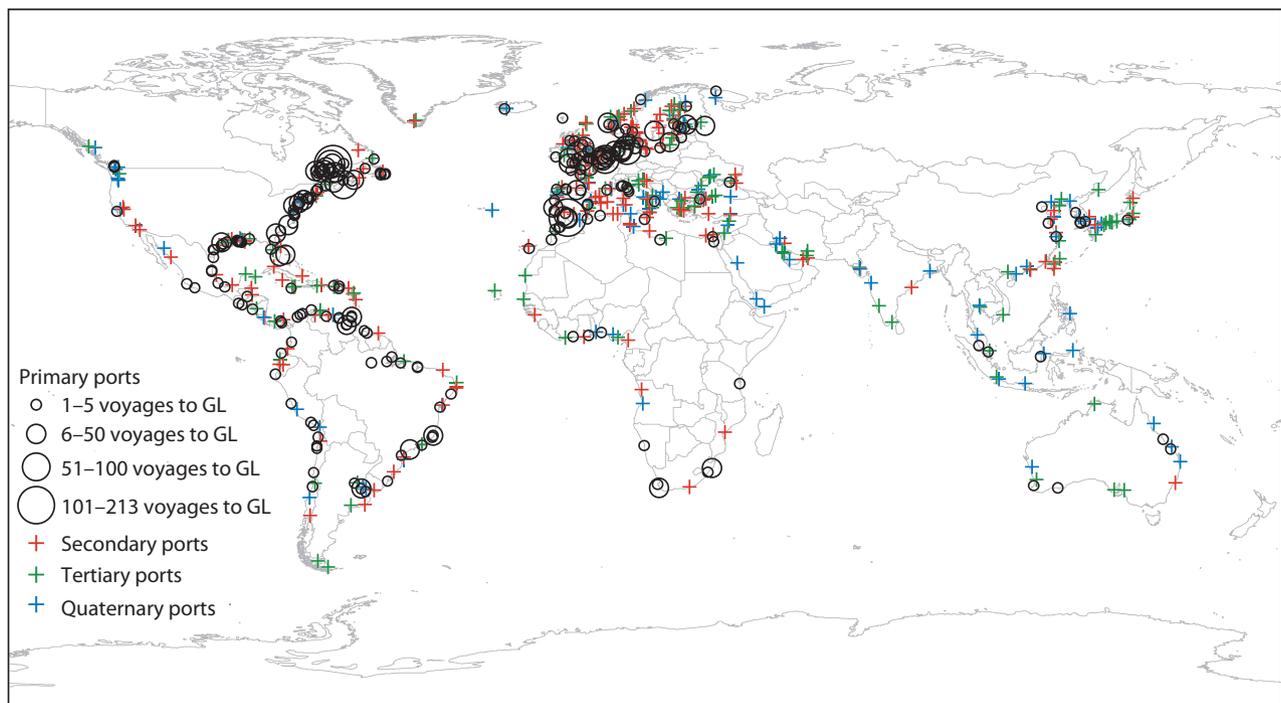


Figure 1 Global map showing ports that were connected to the Greater Great Lakes Ecosystem (GGLE) by primary, secondary, tertiary and quaternary ship voyages during 1 year (May 2005–April 2006). Circles are for primary ports and sized by the number of ship voyages from that port to the GGLE; crosses are coloured for the higher degree of separation ports (and for simplicity do not indicate the number of vessels). Ports falling into multiple categories (e.g., a port could be primary for one ship, but secondary for another) are shown with their lowest degree of separation.

RESULTS

The GGLE contains 52 of the 3522 global ports that received ship visits between 1 May 2005, and 30 April 2006. A total of 1821 ship voyages, originating from 274 ports, entered the GGLE (Fig. 1). These voyages were made by 716 individual ships, with most entering once ($n = 413$), and a maximum number of entries of 18. Ports of departure were concentrated in Western Europe and the Eastern Seaboards of North and South America, but include ports from most temperate and tropical coastlines, and several inland regions, of the world. Many voyages originated at ports immediately outside the GGLE. Including consideration of secondary, tertiary and quaternary ports shows that the GGLE is connected by ship voyages to all major coastal, and many inland, regions of the world (Fig. 1).

The stepping-stone analysis began with the 274 primary ports from the previous analysis (Fig. 2a) and shows that well over half ($n = 2456$) of the world's 3522 active ports during 2005–06 were separated from the GGLE by no more than two separate ship voyages (Fig. 2b). Considering 3- (Fig. 2c), 4- and 5-step (Fig. 2d) ports added 686, 9 and 45 ports, respectively, that could have been involved in stepping-stone invasions to the GGLE during the year of study. No active global port was separated from the GGLE by more than 5 steps during 2005–06. (Separation of all global ports from GGLE is given in Table S3, and full global ship traffic data in Table S4).

Environmental distance of ports from the GGLE ranged from 0.11 to 5.06 (Fig. 3). An $R^2 = 0.54$ for the linear

regression of salinity against environmental distance demonstrates that the distance metric is driven roughly equally by temperature and salinity. Ports with an environmental distance of 1 may have salinity as high as 15 ppt and average annual temperatures in the range of 1–15 °C. Marine ports (salinity > 32 ppt) score at least 2.3 (see Figs S1 & S2). (Full environmental data for all global ports are in Table S3; Table S5).

The greatest concentration of ports most environmentally similar to the GGLE is in Western Europe and the Baltic Sea (Fig. 3). Combined with the shipping data, environmental distance measures allow us to identify the ports and regions that are most likely to have been the source of new non-native species from direct shipping traffic during 2005–06 (Fig. 4). For example, the Western Europe and Baltic Sea regions are both similar and highly connected by shipping to the GGLE. The relative risk from secondary and higher-order ports, and from stepping-stone ports, is unknown and is not represented in Fig. 4.

Sensitivity analysis revealed salinity to be the most influential variable in the environmental similarity calculations (average absolute change across all 6487 global ports in scaled score (\pm SD) when salinity is dropped = 0.38 ± 0.24). Dropping average temperature during coldest month (0.19 ± 0.13), average annual temperature (0.14 ± 0.09) and average temperature during warmest month (0.11 ± 0.13) had less impact. The model based only on average annual temperature and salinity produced an intermediate change (0.24 ± 0.15). Changes in port rankings mirrored changes in environmental similarity scores: removing salinity had the greatest impact

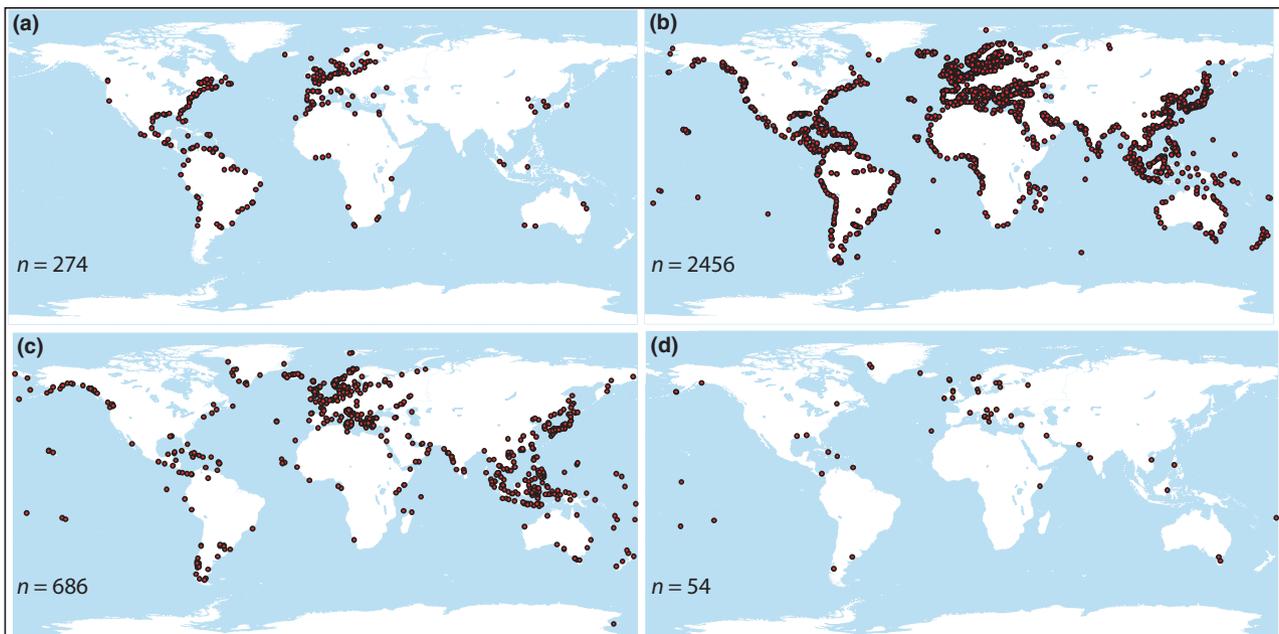


Figure 2 Potential for ‘stepping-stone’ invasions to the Greater Great Lakes Ecosystem (GGLE). A total of 274 ports were separated from the GGLE by a single ship voyage during 1 year [May 2005–April 2006 (Panel a)]. Two-step ports, those connected to 1-step ports by a single ship voyage, but not directly connected to the GGLE, are shown in Panel b. Three-step (Panel c), 4-step and 5-step (combined in Panel d) ports were assessed following this pattern.

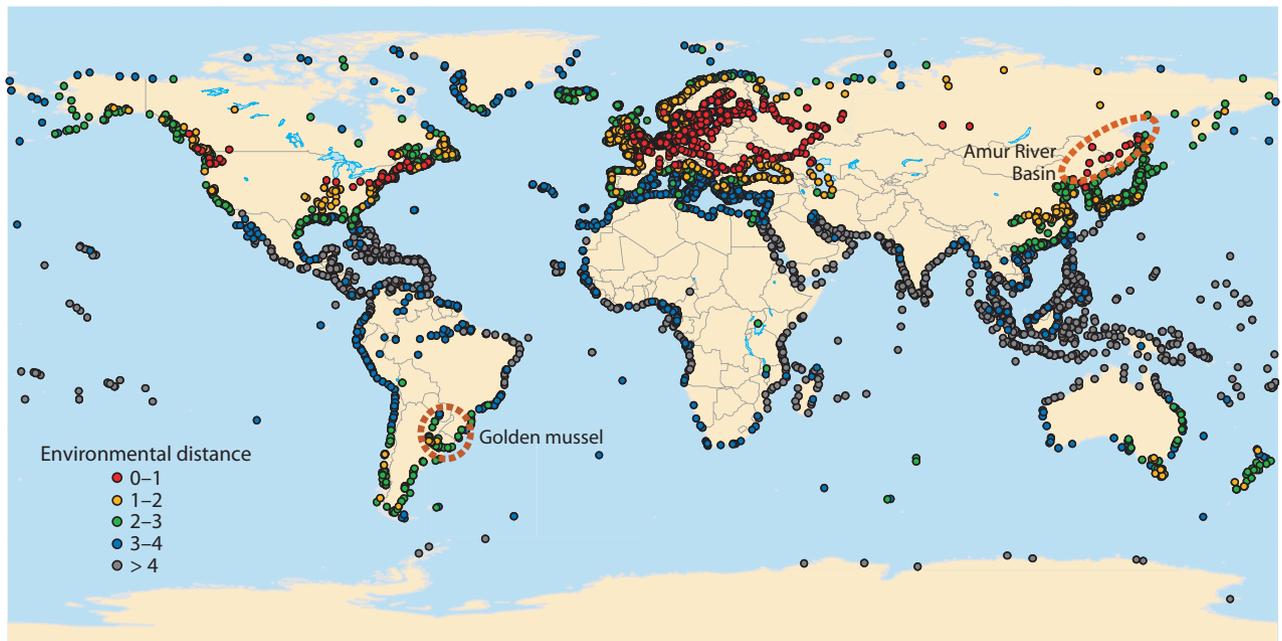


Figure 3 Environmental distance of global ports from the Greater Great Lakes Ecosystem. This index is based on salinity and temperature, with lower numbers indicating ports that are more similar. As examples of high-risk ports, the locations of South American ports invaded by the golden mussel, and ports along the Amur River, are indicated.

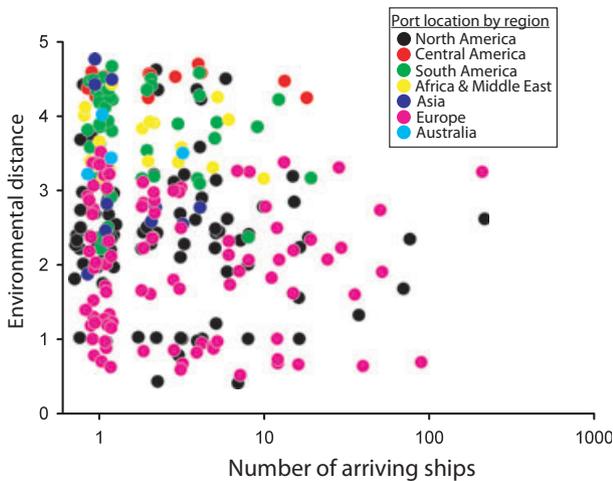


Figure 4 Ship traffic and environmental distance from ports with direct traffic to the Greater Great Lakes Ecosystem (GGLE) during 1 year (May 2005–April 2006). Each point is a port, arranged by the number of ships travelling directly from that port to the Great Lakes, and the environmental distance of the port from the GGLE. Port region is indicated by colour. A small amount of random scatter along the x-axis was introduced to prevent symbol overlap.

(average change in rank of all 6487 global ports (\pm SD) = 587 ± 537), and removal of other variables had less impact (average temperature during coolest month 262 ± 324 ; average temperature during warmest month 210 ± 257 ; average annual temperature 180 ± 204). The model based only on average annual temperature and salinity was again intermediate (361 ± 374).

Changing the assumption used for the 329 ports on rivers that flowed into non-marine waterbodies had a large impact on environmental distance scores for those ports. Again, the results were scaled to mean 0 and standard deviation 1 because adjusting the input data for the environmental similarity calculation changed all scores. As would be expected, environmental distance for all 329 ports declined (i.e., their salinity declined to 0, making them more similar to the GGLE). The average magnitude of decline in scaled score was 0.98, corresponding to an average change in rank of 1114 ± 557 . Average absolute change in scaled score for all other ports was 0.07.

DISCUSSION

The GGLE is connected to all major coastal regions by the global shipping network. In the short term, there is the possibility of receiving non-indigenous aquatic species from most major port regions of the world because individual ships are visiting the GGLE soon after visiting other regions (Fig. 1). Over the longer term, invasive species are likely to continue to spread elsewhere, increasing the probability of stepping-stone invasions to the Great Lakes because more arriving ships will have visited the expanded ranges of invaders (Fig. 2). Although only *c.* 0.1% of all ship voyages during the study year ended in the GGLE, the shipping network makes it possible that new invasive species could arrive in the Great Lakes from virtually any freshwater port world-wide.

Since 1993, all ships that reported carrying ballast water have been required to conduct BWE before entering the Great

Lakes. Results suggest that BWE reduces the concentration of live organisms in ballast by 80–95% (Ruiz & Reid, 2007). This undoubtedly reduces the likelihood of new invasions in the Great Lakes, but the extent of that reduction is unknown and management activities to mitigate invasion risk (e.g., by the U.S. Coast Guard) continue. In combination with reports from arriving ships about recently visited ports, where ballast has been collected, and any management activities carried out, the environmental data set presented here could be used to target management activities at vessels posing the greatest risks. This may include preventing all discharge of ballast, even after BWE, for particularly high-risk vessels, or refusing entry to ships if it is considered that their hull-fouling communities pose a sufficiently large risk.

Ports most likely to contain species that could establish in the GGLE (i.e., those with low environmental distance) are globally distributed, with the highest concentration in Western Europe. Consistent with patterns of ship traffic and environmental conditions, about 50–60% of aquatic alien species discovered in the Great Lakes since the opening of the St. Lawrence Seaway in 1959 are native to Europe and/or the Ponto-Caspian Basin (Mills *et al.*, 1993; Ricciardi, 2001). European freshwaters are highly interconnected through rivers and canals from the Ponto-Caspian Basin in the east as far west as the Atlantic coast, and north to the Baltic Sea (bij de Vaate *et al.*, 2002). This region has been the source of many of the most damaging Great Lakes invaders, including zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussel, round goby (*Neogobius melanostomus*) and spiny water-flea (*Bythotrephes longimanus*). Several additional potential invaders of concern (Ricciardi & Rasmussen, 1998; Kolar & Lodge, 2002) are already well distributed throughout the region. These include the amphipods *Dikerogammarus villosus* and *Corophium curvispinum*, and the monkey goby fish (*Neogobius fluviatilis*). Because the GGLE was connected to many environmentally similar European and Baltic Sea ports during 2005–06, these species may pose a particular risk in the near future, or may already be established in the GGLE but not yet detected.

Our analyses point out other regions of high environmental similarity (Fig. 3 red ports) that in the 2005–06 study year had relatively low ship connection to the Great Lakes and have not been the source of many previous invaders. The Amur River Basin, for example, of north-eastern China and south-eastern Russia is environmentally similar to the Great Lakes and contains the native ranges of a number of species already invasive elsewhere around the world, including the fishes Amur goby (*Rhinogobius lindbergi*) and Chinese false gudgeon (*Abbottina rivularis*) (Neely *et al.*, 2008), and the Chinese pond mussel (*Anodonta woodiana*; Watters, 1997). These species could be introduced by shipping either directly from their native range or via a stepping-stone process. Although shipping connections from the Amur Basin to GGLE are currently relatively weak, they are likely to increase along with total trade with China (Jenkins & Mooney, 2006), potentially exposing the GGLE to many new species beyond the three just

mentioned. Other regions of high similarity but relatively low shipping connection include the North American Pacific Northwest and western Russia (Fig. 3).

Ports that are less similar to the GGLE may also pose a risk if they contain species with broad environmental tolerances. The golden mussel (*Limnoperna fortunei*) is native to East Asia, is established as an invader in Japan, Korea, Taiwan and Hong Kong, and has been expanding its range in South America since it was first recorded there in 1991 (Darrigran & Damborenea, 2005; Karatayev *et al.*, 2007). Although South American ports within the invaded range of golden mussel are less similar to the Great Lakes than many European ports (Fig. 3), this is driven by temperature differences, over which the golden mussel has broad tolerance (Karatayev *et al.*, 2007). The eleven direct shipping voyages we documented from invaded South American ports to the GGLE, and the potential for invasions from higher-degree and stepping-stone ports, indicate that despite higher environmental distance scores, these ports may be the source of future GGLE invasions because of the broadly tolerant species established there.

International and many national policies to reduce ship-borne invasions are moving in the direction of mandating the same management steps on every ship (e.g., BWE, IMO regulations). Concurrently, some nations (e.g., Australia; Barry *et al.*, 2008) and individual US states are employing risk management, monitoring and/or enforcement approaches that depend in part on ship-specific risk assessments (NRC, 2008). Compared to other approaches for assessing the risk of individual ships (see Barry *et al.*, 2008 for a review), the data and procedures described here can be deployed rapidly, are based on data collected consistently across the globe and are transparent. Because our salinity and temperature data are global in scope, they can be used to assess the environmental distance from any port or port region to all other global ports. This could improve current management strategies by allowing rapid assessments of individual ship risk based on voyage history.

Sensitivity analyses revealed that salinity has roughly the same effect on the environmental similarity metric as the three temperature variables combined and that removing salinity has a larger effect on environmental similarity scores and port rankings than removing other variables. We also tested the assumption that ports on rivers flowing into waterbodies with salinity < 30 ppt should be assigned the salinity value of the nearest WOA cell. The alternative assumption was that these ports should be classified as freshwater. For the ports involved ($n = 329$), the difference in environmental similarity from these alternative assumptions is large; the average rank of the ports (by distance from the GGLE, out of the 6487 non-GGLE ports) dropped by 1114 places under the freshwater assumption. Although we believe that the former assumption (i.e., closest WOA cell) is the most accurate, this result indicates that better estimates of salinity for these ports may lead to changes in their ranking. Until better data are available, it may be prudent for managers to treat the total risks from these ports as

being greater than suggested by their environmental similarity score.

Several limitations of our approach should be kept in mind. First, our methods for determining inland salinities and temperatures (i.e., the regression models) are based on relatively small data sets. In particular, the only data available for parameterizing the salinity model (i.e., the model used for ports within 100 km of the coast) came from a small region and may not apply equally across the globe. Also, determining the distance inland for the salinity model needed to be carried out for many hundreds of fjords and bays, each with its own annual, seasonal and daily water regimes. This has likely led to some errors. Second, our data set does not include information about where ballast was taken on by ships, or actual ballast discharges into the GGLE. No data sets are available that give both ballast discharge volume and information about the multiple recent voyages of ships. Hence, in our analyses, we used the simplifying assumption that all vessels were equally likely to discharge ballast. Third, we do not know the extent of inter-annual variation in ship movements. It is possible that our results would be different if we had used data for other years. Finally, we did not separate the risks from hull-fouling and ballast water. The relative invasion risk from each is unknown (Fofonoff *et al.*, 2003). These last three issues would be overcome in future management applications. Management would be on a ship-by-ship basis, and information could be requested from ship captains about ports recently visited, where ballast was collected, whether BWE was performed, and where the ship next planned to discharge ballast. Activities to reduce the possibility of invasion could be based on this additional information and the environmental similarity of recently visited ports.

We conclude by noting that with so little ship traffic, it is striking that the GGLE is nevertheless connected to most active global ports by no more than two ship voyages, and all global ports by no more than five voyages. The integration of even busier ports into the global shipping network is likely far greater. Exposure of any port to invasion risks will change as species invade new ports, as new ports are added to the network and as the number of ships and their routes change. Decisions affecting these changes are generally made without any consideration of invasion risks, especially the risks to ports on the other side of the world. This emphasizes that effective management of shipping invasions will require global coordination. The IMO regulations, if ratified, will be an important step, but will not come fully into effect until at least 2016. They may inadequately address ballast water invasion risks, and they do not address risks from hull-fouling organisms (Gollasch *et al.*, 2007). The ship- and port-based assessments presented here are a new application of network analysis that layers a human system of nodes (i.e., ports) and edges (i.e., ship routes) over global environmental conditions to estimate the potential for species transport and establishment. As well as advancing our knowledge of how human and environmental networks interact (Cumming *et al.*, 2010), it provides a rapid method for estimating which arriving ships

pose the greatest risks. This information could reduce invasion rates if used to target inspection, enforcement and management efforts at those ships most likely to introduce new invaders.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Graphical analysis of environmental distance scores.

Figure S2 Graphical analysis of environmental distance scores.

Table S1 Training data for salinity model.

Table S2 Training data for temperature model.

Table S3 Full port data, including separation from GGLE and environmental distance.

Table S4 Global shipping data.

Table S5 Data used to calculate salinity for ports within 100 km of coast.

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BIOSKETCH

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