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PRIMARY RESEARCH PAPER

Is *Gammarus tigrinus* (Crustacea, Amphipoda) becoming cosmopolitan through shipping? Predicting its potential invasive range using ecological niche modeling

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Abstract While the intensity of global shipping has increased dramatically over the last decades, species exchange between continents has likewise intensified. Ballast water of ships is recognized playing a major role in this process. Many of the larger sea ports have become bridgeheads for invasions. Ecological niche modeling is used to investigate the potential invasive range and high invasive risk ports of the North American amphipod *Gammarus tigrinus*. Sixty-two occurrences of *G. tigrinus* in its native range (North America) and 34 environmental data sets were compiled. Data on dispersal distances were used via ecological niche modeling to analyze the invasive potential of *G. tigrinus*. The invasive risk of large ports was analyzed according to modeling result, as well as their salinity in the main oceanic routes of the world. *G. tigrinus* had a rapid range extension on the British Isles and in the rest of Western Europe. Now it is invading the countries surrounding the Baltic Sea. Worldwide it has a vast potential invasive range. It has a high invasive risk for many large ports along the main oceanic routes, among which the ports of Shanghai, Buenos Aires and Montevideo have the highest invasive risk. *G. tigrinus* may become cosmopolitan through shipping, and this possibility is increasing. Particular emphasis should be placed on preventing human-mediated dispersal. Ports may be the first places *G. tigrinus* invades. This study can identify high invasive risk ports, especially those at risk of introduced North America species. More importantly, the water of large ports should be monitored regularly for exotic aquatic organisms that may survive temporarily or permanently.

Keywords Ballast water · Amphipods · Invasive range · Human-mediated dispersal

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Introduction

Transportation is increasingly being recognized as the major species dispersion vector. Globalization of international trade has promoted numerous biological invasions and the rate at which species are being transported is unprecedented (Levine & D' Antonio, 2003; Perrings et al., 2005). Around 7,000 marine and coastal species travel across the world's oceans every day (Battle, 2009). Eighty-four percent of the world's marine regions reported invasive species in 2008, with shipping being a major reason for their spread (www.wwf.org). Invasive marine and freshwater species are being spread around the world in ship's ballast water, damaging industries and natural resources (Dunstan & Bax, 2008). Ballast water is probably the most important mechanism where aquatic invasions are concerned (Cohen, 1998). Although many organisms cannot survive the dark and often dirty conditions in ballast tanks for a long period, the increased speed of modern vessels has improved the survival rate of species and individuals in transoceanic transports (Costello et al., 2007). For an invasive species a matching habitat may facilitate a successful invasion (Stohlgren et al., 2006).

Animals must obey the same ecological "rules" in invaded ranges as they do in native ranges, and knowledge of the ecological characteristics of native ranges may give indications for potential dispersion localities. A sizeable body of evidence is accumulating to support the idea that, at least on a coarse spatial scale, ecological shifts rarely accompany species invasions (Richardson & McMahon, 1992; Higgins et al., 1999; Iguchi et al., 2004; Robertson et al., 2004). However, accurate prediction of future species distributions is challenging. This requires knowledge of the number of individuals introduced into a particular area over time (i.e., propagule pressure), as well as measures of environmental suitability. Only if both these criteria are met, can successful invasions take place (Herborg et al., 2007a).

The Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell & Noble, 1992; Stockwell & Peters, 1999) is a system that has excellent capabilities for delineating ecological niches and predicting the geographic distributions of species. GARP has been utilized to predict potential distributions of invasive species, such as Zebra Mussels (*Dreissena polymorpha*) in the western USA (Drake & Bossenbroek, 2004), Chinese mitten crabs (*Eriocheir sinensis*) in Europe and USA (Herborg et al., 2007a, b), *Anoplophora glabripennis* in North America (Peterson & Pereira, 2004), *Barred Owl* in North America (Peterson & Robins, 2003), and *Quadrastichus erythrinaw* worldwide (Li et al., 2006).

The gammarid *Gammarus tigrinus* Sexton, 1939 is a widespread species that occurs principally in estuaries of the northwestern Atlantic and is distributed from the St. Lawrence River in Quebec to Florida (Bousfield, 1958, 1973). It is dominant in intertidal and subtidal benthic habitats including reeds, algae, hard or soft substratum, and sand (Bousfield, 1958, 1973; van Maren, 1978). In its native range, this euryhaline species lives in both fresh and brackish water (Bousfield, 1973), whereas in coastal waters it is restricted to shallow lagoons, bays, and estuaries. Being a bottom dwelling omnivore, *G. tigrinus* is relatively tolerant to pollution and has a much greater reproductive capacity in oligohaline waters than many native gammarid species (Pinkster, 1975; Pinkster et al., 1977). The species is able to form populations in a wide range of inland and coastal ecosystems in temperate regions. Unlike some epiphytic amphipods, *G. tigrinus* is unlikely to disperse by algal rafting (Myers, 1993). Its distribution showed a continuous rather than fragmented pattern. There is a high risk of further expansions to the various lakes of Eastern Europe via inland canal–river systems, which may lead to unforeseeable changes in aquatic communities (Berezina, 2007).

It was introduced into British waters by ballast water in 1931 (Sexton & Cooper, 1939), then spread to similar habitats in Western Europe and, most recently, to Eastern Europe, the Baltic Sea, and the Laurentian Great Lakes (Kelly et al., 2006b). The spread of this amphipod in European continental waters was accelerated by its intentional release into the tributary of the German River Weser in 1957 (Schmitz, 1960). In the Netherlands, this species was first recorded from the IJsselmeer in 1964 (Pinkster, 1975) and in 1975 reached the south-western part of the Baltic Sea (Schlei Fjord) probably via the "Nord-Ostsee-Kanal" (Bulnheim, 1976). After two decades, its rapid spread in German waters along the southern Baltic coastline was noticed (Rudolph, 1994; Zettler, 1995) and soon the species was found in Szczecin Lagoon (Gruszka, 1995), Puck Bay (Gruszka, 2002) and the Vistula Lagoon (Jażdżewski & Konopacka, 2000). The latter water body was the northern limit of the species in the Baltic until its occurrence in the Gulf of Riga (Kotta, 2005) and along the Finnish coast in 2003 (harbors of Hamina in the Gulf of Finland and Turku in the northern Baltic) (Pienimäki et al., 2004). *Gammarus tigrinus* was discovered in the Lithuanian part of Curonian Lagoon in September 2004 (Daunys & Zettler, 2006). In 2006, it was found in the easternmost part of Baltic Sea (Neva Estuary) and may well have been transported there with ballast waters from the Finnish area of the Gulf of Finland (Berezina, 2007). Dispersion in the last decade was extremely rapid in Eastern Europe. In South America, it was found in the Gulf of Paria, and the Orinoco Delta, Venezuela (Capelo et al., 2004; Martín & Díaz, 2007). The initial introduction of *G. tigrinus* into Europe via ballast water (Sexton & Cooper, 1939) confirmed its survival during transportation in ballast tanks. The comparison of life history traits indicated that *G. tigrinus* has a high tolerance toward salinity changes (0–25 PSU) and human degradation of the environment and is well adapted to withstand predation (Grabowski et al., 2007a, b). Concurrent with the invasion of *G. tigrinus*, the diversity of native gammarids has declined (Herkül & Kotta 2007). *Gammarus tigirnus* is not only restricted to near port water bodies, but is also widespread in inland water systems. At present, it is difficult to foresee natural pressures which may limit the spread or establishment of the alien *G. tigrinus.*

The global shipping industry has developed rapidly, and most of the maritime traffic (85%) takes place in the northern hemisphere (Corbett et al., 1999; Endresen et al., 2003). The international sea borne cargo statistics indicate that the USA, Europe and East Asia are the main export regions of ballast water by crude oil carriers. The pattern is different for bulk vessels where the most important export areas of ballast water are Asia and Europe while the importing regions are North and South America, Australia and Asia.

In the present study, we have collected the distribution data of *G. tigrinus* in both native ranges and introduced ranges. On the basis of the distribution data, we used the GARP models to predict the potential distribution of *G. tigrinus* and to identify areas most vulnerable to future invasion. Predicting future ranges of nonindigenous species using only environmental niche models may provide misleading forecasts since many areas suitable for colonization may lack appropriate vectors to transmit the species to these locations (Herborg et al., 2007a). In particular, we combined the result of ecological niche modeling (ENM) and salinity for some larger ports in the potential invasive regions and the main ocean routes of the world to analyze the invasive potential of *G. tigrinus*.

Methods

Species data

We compiled a database of the distribution of *G. tigrinus* in its native range (North America) and non-native range (Europe and Venezuela) from the Global Biodiversity Information Facility (Anonymity, 2009) and papers (Daunys & Zettler, 2006; Kelly et al., 2006a, b; Berezina, 2007; Martín & Díaz, 2007; Piscart et al., 2007; Arbačiauskas, 2008). In the Netherlands, it had a large number of records for *G. tigrinus*, so we only selected some localities at random. The detailed invasive distribution and history of *G. tigrinus* were listed in Table 1. A total of 127 distinct, spatially unique locations that had at least 1 min difference in coordinates (Levine & D' Antonio, 2003) were identified (Appendix 1). Distributional records were available from the UK, Germany, Northern Ireland, the Netherlands, Poland, Russia, Finland, France, Estonia, Latvia, and Lithuania. Records with unspecified or unknown localities were not considered; the remaining records were plotted on maps and inspected visually to detect obvious errors using ArcMap (9.0). For ENM analyses, occurrence locations were considered only once, with no weighting to account for multiple cases at single locations.

Geographic data

Environmental data sets input into GARP came from three principal sources. (1) January and July average maximum and minimum temperature, January and July average precipitation and 19 other factors related to bioclimatic data were obtained from global land area interpolation of climate point data (1950–2000) at a spatial resolution of 2.5 arc-min (http://www.worldclim.org) (Table 2, No. 1–25); (2) Other climatic data averaged over the period 1961–1990, including data layer summarizing wet days, water vapor pressure and solar radiation were drawn from the Intergovernmental Panel on Climate Change (http://www.ipcc.ch) (Table 2, No. 26–28); (3) Landsurface data summarizing elevation, aspect, flow

Table 1 Historical invasion of *Gammarus tigrinus* in nonnative range (*EU* Europe, *NA* North America, *SA* South America)

Continent	Country	Water body	First report	Transport vector	Source
NA	Canada	Laurentian Great Lakes	2002		Kelly et al. (2006b)
EU	Estonian	Kõiguste Bay	2003		Herkül & Kotta (2007)
EU	Finland	Gulf of Finland	2003	Ballast water	Pienimäki et al. (2004)
EU	Finland	Turku	2003	Ballast water	Pienimäki et al. (2004)
EU	France	Brittany			Piscart et al. (2007)
EU	France	Meurthe River	2002		Piscart et al. (2005)
EU	France	Moselle River	1999		Devin et al. (2001)
EU	Germany	Schlei estuary	1975	Intentional release	Bulnheim (1976)
EU	Germany	Mecklenburg area	1994	Intentional release	Rudolph (1994)
EU	Germany	Weser River	1957	Intentional release	Schmitz (1960)
EU	Ireland	Lough Neagh; Bann River	1931	Ballast water	Sexton & Cooper (1939)
EU	Latvia	Gulf of Riga	2003		Kotta (2005)
EU	Lithuanian	Curonian Lagoon	2004		Daunys & Zettler (2006)
EU	Luxembourg	Moselle (Germany-Luxembourg border near D-Nennig)	1991	Intentional release	Massard & Gaby (1992)
EU	The Netherlands	Ijsselmeer	1960	Intentional release	Nijssen & Stock (1966)
EU	Poland	Szczecin Lagoon	1988	Ballast water	Gruszka (1995)
EU	Poland	Puck Bay	2002		Szaniawska et al. (2003)
EU	Poland	Vistula Lagoon	1998	Ballast water	Jażdżewski & Konopacka (2000)
EU	Russia	Neva Estuary	2006	Ballast water	Berezina (2007)
EU	Russia	Kaliningrad province			Ezhova et al. (2005)
EU	England	Frodsham Marsh	1931	Ballast water	Sexton & Cooper (1939)
SA	Venezuela	Orinoco Delta; Gulf of Paria		Ballast water	Capelo et al. (2004)

accumulation, flow direction, slope, and topographic index were obtained from the U.S. Geological Survey's Hydro-1K data set (http://edcdaac.usgs.gov/gtopo30/hydro) (Table 2, No. 28–34). All 34 environmental data sets were resampled to 0.1° for analysis to match the approximate resolution of occurrence data.

Ecological niche modeling

Ecological niches and potential geographic distributions were modeled using the GARP (http://www.lifemapper.org/desktopgarp). GARP is an application that builds ENM based on nonrandom associations between known occurrence points for species and sets of raster GIS coverages describing ecological landscapes (Gaubert et al., 2006). It is a widely applied environmental niche modeling application that uses raster-based environmental and biological information to predict a suitable habitat for a given species (Herborg et al., 2007a).

In order to reduce environmental coverage sets to just those coverages that provide highest predictive accuracy, we used a jackknife manipulation and analysis to test the effect of different environmental layers on prediction precision. Sets of geographical coverages were reduced to an optimal 24 ecological dimensions in the final model (Peterson & Cohoon, 1999; Zhu et al., 2007) (Table 2, Variables included in the final analysis is indicated with a $\surd$).

In our model, we used 62 unique occurrence points from the native distribution of *G. tigrinus* to develop the algorithm. The GARP model selected nonrandom associations between environmental layers and presence of *G. tigrinus* in its native range with a genetic algorithm. The algorithm develops a set of conditional

Table 2 Description of environmental variables in the coverage set

	Description	Included
1	Annual mean temperature	
2	Mean diurnal range (mean of monthly (max temp − min temp))	√
3	Isothermality (P2/P7) (*100)	√
4	Temperature seasonality (standard deviation * 100)	√
5	Max temperature of warmest month	
6	Min temperature of coldest month	
7	Temperature annual range (P5–P6)	
8	Mean temperature of wettest quarter	
9	Mean temperature of driest quarter	√
10	Mean temperature of warmest quarter	√
11	Mean temperature of coldest quarter	√
12	Annual precipitation	√
13	Precipitation of wettest month	
14	Precipitation of driest month	√
15	Precipitation seasonality (coefficient of variation)	
16	Precipitation of wettest quarter	√
17	Precipitation of driest quarter	√
18	Precipitation of warmest quarter	
19	Precipitation of coldest quarter	√
20	January average maximum temperature	√
21	January average minimum temperature	√
22	July average maximum temperature	√
23	July average minimum temperature	√
24	January average precipitation	√
25	July average precipitation	
26	Wet days (number of days of precipitation)	√
27	Water vapour pressure	
28	Solar radiation	√
29	Elevation	√
30	Aspect (direction of the slope)	√
31	Flow accumulation (the amount of upstream area draining into each cell, drainage area)	√
32	Flow direction	√
33	Slope (maximum change in elevation between each cell and its eight neighbours)	√
34	Topographic index	√

Variables included in the final analysis are indicated with a √

rules from an available range (i.e., atomic rule, logistic regression), then iteratively improves the solution by testing and selecting rules on random subsets of available data (Stockwell & Peters, 1999). Presence data are randomly divided by the GARP program into 80% training and 20% validation data. Models were generated with a maximum of 10,000 iterations and a 0.001 convergence limit. The final prediction maps were produced by summing these 10 high-quality models (Anderson et al., 2003). This approach selects models with a false negative rate (omission error) of <5% and a false positive rate (commission error) of <50%. The intersection of all the 10 best-subset models generated a final map with values ranging from 0 to 10 (10 for regions where all the predicted niche models present; 0 for regions of niche absence). Color gradations are used to indicate the proportion of times out of 10 that specific areas were included in the predicted distribution of *G. tigrinus*.

Dispersal limitation

The high invasive risk range of the alien freshwater invertebrates through ballast water mainly spread along coastal areas. *G. tigrinus* is an extremely euryoecious species and characteristic to shallow water habitats (Grabowski et al., 2007a). In order to distinguish the higher invasive potential range, we developed a dispersal distance layer in the ecological niche model (Herborg et al., 2007a). We measured the distance between locations of reported occurrence and the nearest coastline and identified the 90th percentile (306 km) for the distribution of inland dispersal distances in Europe and Venezuela (Fig. 1). The coastline of Europe is rather irregular, the invasive regions are not very far from the coasts. Therefore, our model does not have limiting dispersal distances in Europe. This limit was selected since it is not known whether *G. tigrinus* were established at the most distant sites for which they are reported in Europe and Venezuela, but they are established at the 90th percentile distance. We applied the 306 km distances as separate cut-off points for maximum expected dispersal distances for *G. tigrinus* in their native and some potential invasive ranges. The resulting layers identified waterways that are suitable for survival and are within established dispersal distance limits based on the *G. tigrinus*'s native distribution.

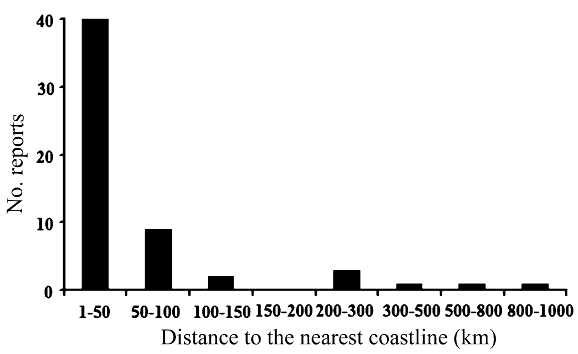

Fig. 1 Dispersal distances of *G. tigrinus* in nonnative range. Dispersal distance is calculated as the distance from the freshwater point of occurrence to the nearest coastline. Distances were measured using DIVA-GIS software

Ports and ocean route

We selected some major ports in the regions within the potential invasive range of *G. tigrinus* according to our model, because these major ports receive large amounts of ballast water that may carry nonindigenous aquatic invertebrates. We did not consider the ports of Europe, because the area is surrounded by the Atlantic Ocean, the Baltic Sea, the Mediterranean Sea and the Black Sea, possessing abundant ports. These ports have short dispersal distances between them and more importantly they had a longer history of invasions. In addition, we considered the salinity of port water (World Ocean Data 2005, www.nodc.noaa.gov) and the main oceanic routes in the world, because these routes connect larger ports with a high invasion or dispersal potential.

Results

Potential distribution range

From the results of our model it may be concluded that *G. tigrinus* has a wide potential invasive range worldwide (Fig. 2A). Major areas with potential invasions are the central west coast of North America, the north coast of the Mediterranean Sea, East Asia, the estuary of the River Plate in South America, the regions Rio de Janeiro in Brazil, the coastal areas of Gulf of Guinea in Africa, and the southeast coastal areas of Australia. The main ocean routes play an important role in transmitting exotic aquatic species through ballast water. Most of the maritime traffic (85%) takes place in the northern hemisphere, specifically over the north Atlantic and north Pacific Oceans (Corbett et al., 1999; Endresen et al., 2003). The North Atlantic shipping lines between North America and Western Europe are amongst the busiest maritime traffic lines, which may have had great influence on the dispersion of *G. tigrinus* over Europe (Fig. 2B). East Asia has a high potential for the invasion of *G. tigrinus* as a result of maritime trade with North America and Europe where the *G. tigrinus* is already a widely distributed species. Within this range, *G. tigrinus* is most likely to invade coastal areas which in China may be in the provinces of Guangxi, Guangdong, Fujian, Zhejiang, Jiangsu, Shandong, and Liaoning province (Liaodong Peninsula), in Russia the Vladivostok

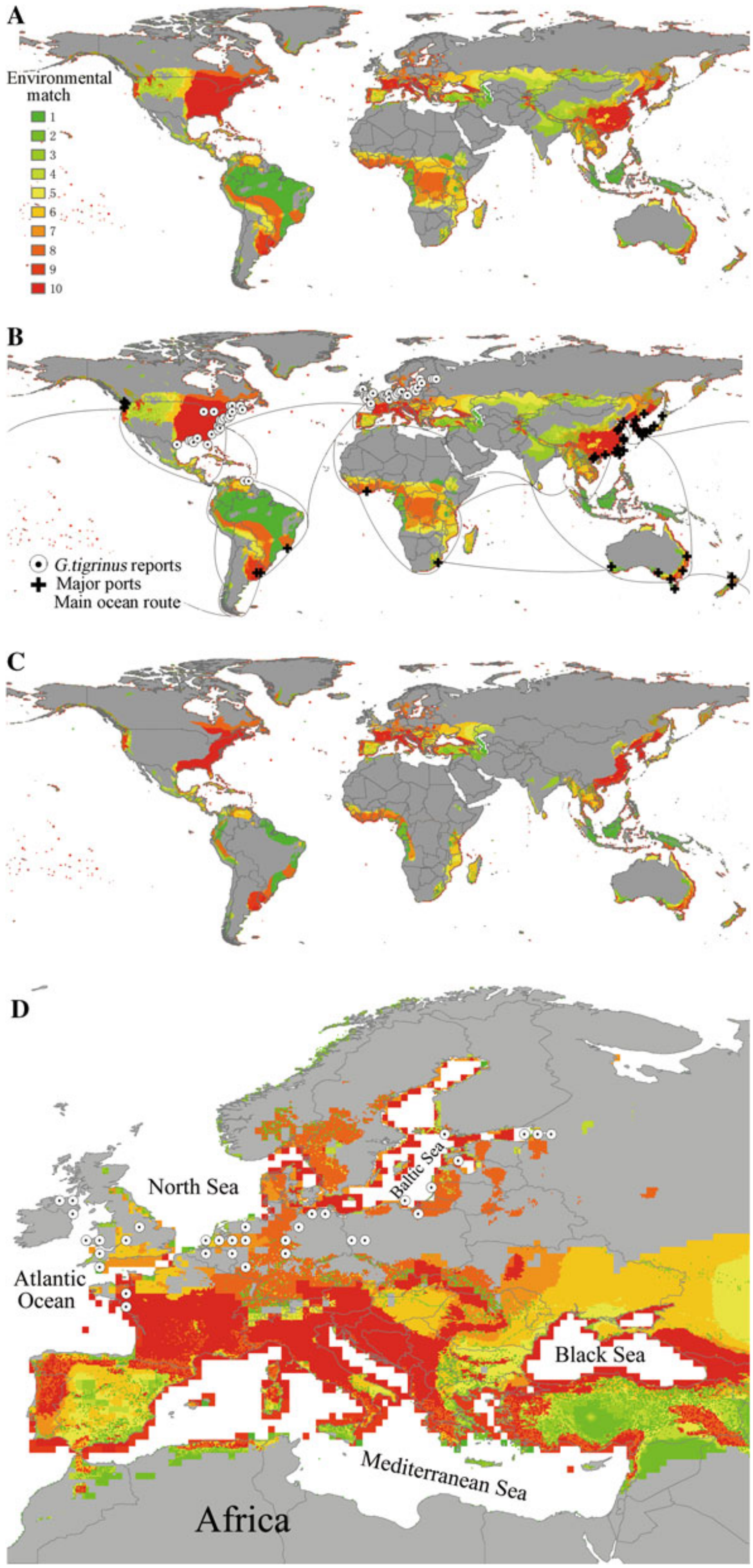

Fig. 2 Predicted occurrence of *G. tigrinus* based on the ecological niche models developed using environmental data for North American sites of *G. tigrinus* presence. Included in the models are **A** no dispersal limitations or **B** addition of the main ocean routes in the world or **C** limitation based upon 90th percentile (306 km) of reported *G. tigrinus* dispersal distance in nonnative range or **D** the potential invasive range of *G. tigrinus* in Europe. Dispersal distances are measured from the inland location to the nearest coastline. Dot circles indicate occurrence reports of *G. tigrinus* and crosses indicate some large ports which located in the potential invasive range

region, Korean Peninsula, and southwest Japan (Fig. 2C). The Gulf of Guinea, the coastal areas of Tanzania and Kenya, and the southeast of Madagascar were also predicted as potentially suitable areas as they have medium–high environmental matches.

In Europe, our model indicates a high invasive potential in the Balkan Peninsula, Apennine Peninsula, and Asia Minor Peninsula, especially the northern coastal areas of the Mediterranean Sea and regions surrounding the Black Sea (Fig. 2D).

Potential risk to ports

Adult *G. tigrinus* tolerated the 30 and 45 PSU sodium chloride treatments for 12–24 h. (Santagata et al., 2008). The salinity of sea water is approximately 36 PSU, yet the salinity of most ports is lower because of input from inland water (Table 3). *Gammarus tigrinus* has a high invasive risk in Chinese coastal ports and the ports of Buenos Aires and Montevideo (30.42 PSU; Table 3). Shanghai port has the lowest salinity (29.54 PSU) indicating that it may have the highest invasive risk for *G. tigrinus* and other aquatic organism with a similar niche preference. Ocean ports are not suitable for the survival of *G. tigrinus* because of the species limited tolerance of salinity (0–25 PSU). Thus, the species is likely to disperse from the port to inland water systems, especially in estuaries.

Discussion

Ecological niche modeling provides valuable insight into the potential distribution of many nonindigenous species (Peterson, 2003). It can identify areas at risk of invasion, which can focus subsequent management efforts to maximize efficacy. More generally, this study demonstrates the anticipatory capacity of the ENM tools we used. Indeed, even species that have not yet invaded can be evaluated as to their invasive potential, and risks can thus be evaluated proactively (Peterson, 2003). Although certainly not 100% correct in its predictions, the ENM approach offers some information where little or none was available before. This predictive and proactive approach can be used on a broad scale to prioritize use of limited resources in control and prevention of species' invasions

Table 3 Ports that have a high potential invasive risk for *Gammarus tigrinus* as determined by our model

Countries	Ports	Invasive risk	Salinity (PSU)
Argentina	Buenos Aires	High	30.42
Australia	Adelaide	High	35.66
	Brisbane	High	35.45
	Hobart	High	35.02
	Melbourne	High	35.44
	Perth	Medium–high	35.64
	Sydney	High	35.62
Brazil	Rio de Janeiro	Medium–high	36.22
Canada	Vancouver	High	31.56
China	Dalian	High	31.20
	Fangchenggang	High	32.73
	Fuzhou	High	33.42
	Guangzhou	High	33.67
	Kaohsiung	High	33.95
	Keelung	High	34.40
	Lianyungang	High	31.62
	Ningbo	High	31.85
	Qingdao	High	31.62
	Shanghai	High	29.54
	Xiamen	High	33.84
Cote d'Ivoire	Abidjan	Medium–high	34.64
Japan	Fukuoka	Medium–high	33.85
	Fukuyama	Medium–high	34.49
	Hakodate	Medium–high	33.33
	Hiroshima	Medium–high	33.85
	Kagoshima	Medium–high	34.54
	Kanazawa	Medium–high	33.83
	Kawasaki	Medium–high	34.43
	Kobe	Medium–high	34.34
New Zealand	Auckland	Medium–high	35.49
	Wellington	Medium–high	34.98
North Korea	Hungnam	High	33.52
Russia	Vladivostok	High	33.80

Table 3 continued

Countries	Ports	Invasive risk	Salinity (PSU)
South Africa	Durban	Medium–high	35.36
South Korea	Busan	High	33.70
	Inchon	High	32.22
Uruguay	Montevideo	High	30.42
USA	Portland	High	30.80
	San Francisco	High	33.18
	Seattle	High	31.50
Vietnam	Haiphong	High	32.09

Salinity data from World Ocean Data 2005, www.nodc.noaa.gov

(Peterson et al., 2007). GARP is a widely used approach that had succeeded in predicting species' distributions accurately in several cases (Peterson & Robins, 2003; Drake & Bossenbroek, 2004; Gaubert et al., 2006). Collectively, these results indicate that GARP models provide valuable insights into potential ranges of nonindigenous species, and this information can be harnessed for the development of management strategies to prevent future invasions (Herborg et al., 2007a). Our GARP model successfully predicted the high potential invasive risk ranges of *G. tigrinus*, and revealed that most of Europe and East Asia and South America are vulnerable to invasion by *G. tigrinus*.

With the development of the technology, large ships which are used in the ocean shipping accelerated the invasion of aquatic invertebrates transmitted in ballast water. These invasive species reduced the native biological diversity, and as a result of strong environmental tolerance invasive species even became dominant groups in nonnative regions by replacement of native species. Many studies have demonstrated that survival of nonindigenous species depends on the degree of environmental similarity between donor and recipient regions, thereby implicating the importance of physiological tolerance to conditions in the introduced environment (Wonham et al., 2000; Kolar & Lodge, 2002; Rouget & Richardson, 2003; Forsyth et al., 2004).

Environmental niche models may yield misleading forecasts of the future ranges of nonindigenous species because successful invasions require a pathway to the potential invasive range. Our results highlight the advantage of combining environmental matching and distribution of larger ports in the marine transportation. *Gammarus tigrinus* survived at higher temperatures in more ion-rich, polluted waters than the indigenous gammarids, indicating a wider physiological tolerance and thus a higher competitive ability in these waters (Wijnhoven et al., 2003). Domestic water containing more chemical substances may also increase salinity, which may have facilitated the invasion of *G. tigrinus* of upstream stretches of river systems.

Our predictions of potential distribution of *G. tigrinus* can provide a strong basis for identifying areas where detection efforts would be most effective and beneficial. In Europe, *G. tigrinus* might have invaded regions of Baltic Sea rapidly because of lower seawater salinity (<10 PSU). Some regions of Western European area where *G. tigrinus* is found are in relatively low risk from the GARP prediction based on environmental matching. However, as these regions have great maritime trade with native range of *G. tigrinus*, and received large volume of ballast water from invaded source regions. They have high invasive risk, and *G. tigrinus* may expand further into regions susceptible to its invasion. Identification of such sites would help in formulating measures to contain its spread. Canals connecting rivers are important pathways for invaders, especially as they connect formerly separated biogeographical regions (Bij de Vaate et al., 2002). In general, the genus of *Gammarus* is considered widespread in the northern hemisphere but since *G. tigrinus* was found in the Gulf of Paria and Orinoco Delta in Venezuela (latitude <10°N) (Capelo et al., 2004), it may well cross the equator by ballast water. The Orinoco Delta has rich oil resources and most Venezuelan oil export is to the USA. The invasive *G. tigrinus* introduced to Orinoco Delta may be a result of this oil trade. Our study suggests that East Asia might be at high risk of invasion by *G. tigrinus* and other potentially harmful organisms because this area is the focus of intense shipping activity and receives large volume of ballast water. One area in particular is the Yangtze River estuary, which makes it highly susceptible to introductions through intense trading activity. Shanghai is one of the world's financial centers, and the large ports of Shanghai and Ningbo are located on the Yangtze River estuary. Invasive alien freshwater species may quickly disperse to all lower and middle reaches of the Yangtze River after a successful invasion of the ports.

This study also indicates the invasive potential of other freshwater invertebrates with niche preferences similar to *G. tigrinus*. Because suitable habitats for this species are present on the major continents, particular emphasis should be placed on preventing human-mediated dispersal, especially by ballast water discharges and intentional introductions. The current recommended methods for controlling the introduction of nonindigenous species involve the open ocean exchange of ballast water and the elimination of organisms using chemicals (IMO, 2003; Santagata et al., 2008). This study can assist in detecting specific high invasive risk ports, especially those at high risk of invasions from North America. The further dispersal of *G. tigrinus* from ports to inland water systems is currently possible, which may result in unforeseeable consequences for ecosystem stability. Efforts should focus on preventing the introduction of exotic aquatic species in these ports. More importantly, high invasive risk ports should have their waters monitored regularly for exotic aquatic organisms; alien species from other countries and continents may survive in these ports either temporarily or permanently.

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