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PREDICTING INVASION RISK USING MEASURES OF INTRODUCTION EFFORT AND ENVIRONMENTAL NICHE MODELS

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Abstract. The Chinese mitten crab (*Eriocheir sinensis*) is native to east Asia, is established throughout Europe, and is introduced but geographically restricted in North America. We developed and compared two separate environmental niche models using genetic algorithm for rule set prediction (GARP) and mitten crab occurrences in Asia and Europe to predict the species' potential distribution in North America. Since mitten crabs must reproduce in water with $\geq$15‰ salinity, we limited the potential North American range to freshwater habitats within the highest documented dispersal distance (1260 km) and a more restricted dispersal limit (354 km) from the sea. Applying the higher dispersal distance, both models predicted the lower Great Lakes, most of the eastern seaboard, the Gulf of Mexico and southern extent of the Mississippi River watershed, and the Pacific northwest as suitable environment for mitten crabs, but environmental match for southern states (below 35° N) was much lower for the European model. Use of the lower range with both models reduced the expected range, especially in the Great Lakes, Mississippi drainage, and inland areas of the Pacific Northwest. To estimate the risk of introduction of mitten crabs, the amount of reported ballast water discharge into major United States ports from regions in Asia and Europe with established mitten crab populations was used as an index of introduction effort. Relative risk of invasion was estimated based on a combination of environmental match and volume of unexchanged ballast water received (July 1999–December 2003) for major ports. The ports of Norfolk and Baltimore were most vulnerable to invasion and establishment, making Chesapeake Bay the most likely location to be invaded by mitten crabs in the United States. The next highest risk was predicted for Portland, Oregon. Interestingly, the port of Los Angeles/Long Beach, which has a large shipping volume, had a low risk of invasion. Ports such as Jacksonville, Florida, had a medium risk owing to small shipping volume but high environmental match. This study illustrates that the combination of environmental niche- and vector-based models can provide managers with more precise estimates of invasion risk than can either of these approaches alone.

Key words: ecological niche modeling; Eriocheir sinensis; *genetic algorithm for rule set prediction (GARP); introduced range; invasive species; native range; relative risk; risk assessment.*

Introduction

One of the most challenging problems confronting invasion biologists is the accurate identification of locations that may be successfully colonized by nonindigenous species. 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 (where a species can survive and reproduce, i.e., its ecological niche). Only in areas where both factors are present does the risk of establishment exist. Here we combined ecological niche modeling and the release of ballast water into ports in the United States to estimate the relative risk of establishment of the invasive Chinese mitten crab. This novel approach allows for spatially focused management efforts based upon port-specific risk levels.

Ecologists have sought to link invasion success to many individual factors including diversity of native species, intensity of natural or human disturbance, resource availability, habitat productivity, and the release of invading species from natural enemies (see reviews, Lodge 1993, Levine and D'Antonio 1999, Davis and Pelsor 2001, Kolar and Lodge 2002, Levine et al. 2004, Lockwood et al. 2005, Walker et al. 2005). Recent studies have established that introduction effort (i.e., the number of introduction attempts and propagules per attempt) is positively correlated with invasion success (e.g., see Drake et al. 2005, Lockwood et al. 2005,

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Ruesink 2005, Suarez et al. 2005, Drake and Lodge 2006). Drake and Lodge (2004) applied the introduction effort concept to marine coastal environments by assessing risk based upon global shipping patterns, which were assumed to be directly proportional to the volume of ballast water discharged and the number of individuals introduced. Wonham et al. (2005) explored theoretically how different scenarios of ballast water exchange would influence introduction effort and risk associated with discharges of ballast water in coastal areas.

Many other studies have demonstrated that determinants of success may be complex, affected by multiple factors simultaneously (e.g., Lonsdale 1999, Rouget and Richardson 2003, Forsyth et al. 2004, Romanuk and Kolasa 2005). For example, Cleland et al. (2004) noted that diversity of nonindigenous plants was related to both native species diversity and resource availability, while Blumenthal (2005) proposed that release from natural enemies could account for the success of invading plant species in high-resource environments.

Stage-based approaches have also been used to predict invasion success (Colautti and MacIsaac 2004). Successful establishment of a nonindigenous species depends upon its successful navigation of a series of transitions, each with independent probabilities of failure (Carlton 1985, Kolar and Lodge 2002). A transport vector must deliver a sufficient number of viable and reproductively capable propagules to an area outside of the species' historic range. These individuals must be capable of surviving ambient physical and chemical conditions, as well as interspecific interactions with residents of the community. Movement between transitions may be influenced by one or more separate or interacting factors (Colautti et al. 2006). Furthermore, different life history attributes (e.g., growth rate, environmental tolerance) may be important for different transitions. For example, Kolar and Lodge (2002) suggested that for freshwater fish species introduced to the Laurentian Great Lakes, those with high growth rates were favored at the establishment phase but performed poorly at the spread stage.

Sequential combining of different approaches to predict invasion success may provide insights beyond the capabilities offered by individual approaches. For example, Peterson (2003) observed that areas in California that should be vulnerable to Asian long-horned beetles (*Anoplophora glabripennis*), based upon current inbound ship traffic from Asian source ports, are inhospitable to the beetle's environmental needs and thus unlikely to become invaded. Peterson (2003) used genetic algorithm for rule set prediction (GARP) to determine the environmental needs of the species by matching the suite of environmental conditions associated with presence of the species in its native range with the similarity of these environmental conditions in the novel range.

Genetic algorithm for rule set prediction is an environmental niche modeling application that has been used to predict range expansion and limitation for a variety of taxa including fish, reptiles, and caribou (e.g., Raxworthy et al. 2003, Johnson and Gillingham 2005, McNyset 2005). It also has been applied to studies that seek to forecast the vulnerability of sites to establishment by nonindigenous species, based upon the degree of environmental matching between the species' native and nonnative ranges (Peterson and Vieglais 2001, Ganeshaiah et al. 2003, Arriaga et al. 2004, Drake and Bossenbroek 2004, Iguchi et al. 2004, Roura-Pascual et al. 2004, Underwood et al. 2004). The approach may be particularly useful if combined with measures of introduction effort; collectively they provide managers with information on areas where species are being introduced as well as the environmental suitability of these habitats.

The focus of our study was the Chinese mitten crab (*Eriocheir sinensis*), a species whose native range spans from 21° to 41° N and includes China, Hong Kong, and North Korea. The species is catadromous: its free-swimming planktonic larvae (duration ~43–90 days) develop predominantly in saline water and require salinity greater than 15 psu, although they spend much of the remainder of their life cycle in freshwater (Anger 1991). Adult crabs migrate back to estuaries, where they reproduce and die. This lifestyle constrains the range over which the species may establish viable populations to coastal rivers proximal and connected to brackish or salt water. Although the species is occasionally reported in solely freshwater habitats such as the Great Lakes (Nepszy and Leach 1973), there exists no evidence indicating that the crab can complete its entire life cycle in these habitats.

The crab initially invaded northern continental Europe between 1912 and 1940 and southern France between 1950 and 1960 (Herborg et al. 2003). It subsequently spread to Great Britain, the Spanish and Portuguese Atlantic coasts, and to Sweden, Finland, Poland, Estonia, and Lithuania proximal to the Baltic Sea (Silfverberg 1999, Valovirta and Eronen 2000, Ferdinand-Martinez and Carrera 2003). While it is inherently difficult to assess the most likely transport vector for a nonindigenous species, ballast water transport seems to be very important for mitten crabs. The initial introduction of mitten crabs into Europe occurred via ballast water (Herborg et al. 2003). Similarly, the most likely introductory pathways of mitten crabs into the United States are ballast water (Gollasch et al. 2002) or intentional introduction via the live seafood trade (Cohen and Carlton 1997).

Chinese mitten crabs have a very patchy distribution in North America, with reports of solitary individuals from Lakes Superior, Erie, and Ontario, the Detroit and St. Lawrence Rivers, the Mississippi River delta, and very recently in Chesapeake Bay (Nepszy and Leach 1973, de Lafontaine 2005; G. Ruiz, *unpublished manuscript*). The only locality known to support established populations of Chinese mitten crabs in North America is in San Francisco Bay and its watershed (Rudnick et al. 2003).

We combined the use of GARP with information on ship ballast water discharge patterns to predict the potential distribution of the Chinese mitten crab *Eriocheir sinensis* in North America. We developed two separate models using environmental information from the species' native range in Asia and its introduced range in Europe. We refined these predicted occurrence distributions based upon the distance of these invaded freshwater habitats to the sea in which the crab must reproduce. We used the intensity of shipping activity at major ports in the United States to identify areas most vulnerable to ballast-mediated introduction of the species. These factors were combined to determine the relative risk of invasion for each major port in the United States. Collectively, these measures provided insight into introduction effort (propagule pressure) and regions of environmental suitability, which we combined to rank the major U.S. ports in terms of risk of successful establishment of the Chinese mitten crab.

Methods

Ecological niche modeling

Genetic algorithm for rule set prediction is an iterative tool using an array of methods, including logit rule, range rule, negated range rule, and atomic rule, to identify heterogeneous rule sets describing a species' environmental niche. These rule sets represent different methods of identifying the environmental variables defining an ecological niche; single values of different variables (atomic rule), a statistically defined (95th percentile range) envelope for all variables (negated range rule), a range of some of the variables (range rule), and an adaptation of logistic regression (logit rules; for more details see Stockwell and Peters 1999). Models are constructed using species presence and geo-referenced environmental data. Here, we developed two separate sets of predictions for the potential distribution of the Chinese mitten crab based on its native Asian range (Asian model) and its invaded European range (European model). We selected 12 environmental variables with potential distributional importance based upon available data sets with global coverage. Variables considered included ground frost frequency, precipitation, wet day frequency, slope, aspect, topographic index, spring ocean surface temperature, river discharge, mean river temperature, and minimum, mean, and maximum air temperature (Appendix). These environmental layers were tested separately for their contributions to each model using multiple linear regressions (see Table 1), following Drake and Bossenbroek (2004). Environmental variables that contributed significantly to model prediction accuracy were then used to create 300 predictions using a 0.001 convergence limit and a maximum of 3000 iterations (per simulation), following the best subset procedure described by Anderson et al. (2003). We applied a <5% limit on the ratio of test data points outside the predicted range (false negatives, or omission errors) and a <50% limit for ratio of predicted suitable environments without test data points (false positives, or commission errors). Different thresholds were utilized since false negatives, representing a failure to predict actual occurrences, are a more serious problem in predicting a nonindigenous species' range than false positives, in which the species is incorrectly predicted to occur at a site and include correct predictions without presence data. The resulting 300 predictions were converted into a map of percentage of environmental match using the "Raster Calculator" in ArcMAP 9.0 (Environmental Systems Research Institute [ESRI], Redlands, California, USA). We applied hierarchical partitioning analysis of environmental layers used in the final model to identify coverages that were most important to accurate predictions. Hierarchical partitioning is based on an additional GARP prediction that uses all possible combinations of the environmental coverages used in the model and tests their effect on the overall predictive accuracy (Peterson and Cohoon 1999).

In order to distinguish between freshwater habitats in which mitten crabs can survive vs. those in which they can establish (i.e., return to the sea to reproduce), we developed a dispersal distance layer in the ecological niche model. We measured the distance between locations of reported occurrence and the nearest body of water with ≥15 psu salinity using the European data set and the "Spatial Analyst" tool in ArcMAP 9.0. This dispersal distance was calculated as the shortest path downstream following the river course. Where distances were measured across large water bodies with ≤15 psu salinity (Eastern Baltic Sea), the shortest possible route was taken. The maximum distance of reported occurrence was 1260 km from the sea (≥15 psu; Fig. 1). We also identified the 90th percentile (354 km) for the distribution of inland dispersal distances in Europe (Fig. 1). This limit was selected since it is not known whether crabs are established at the most distal sites for which they are reported in Europe, but they are established at the 90th percentile distance. We applied the 1260-km and 354-km distances as separate cut-off points for maximum expected dispersal distances for crabs in major North American rivers. The resulting layers identified waterways that are suitable for survival and are within established dispersal distance limits based upon the crab's European distribution. This procedure precluded habitats in inland states (see Figs. 2a and 3a) that otherwise conformed with GARP model predictions.

Ship vector traffic to U.S. ports

We refined our analysis further by identifying rivers that are most at risk of mitten crab establishment associated with commercial shipping, using a proxy of introduction effort. Chinese mitten crabs have been found in ballast water (Peters 1933, Gollasch et al. 2002), and we have assumed here that propagule

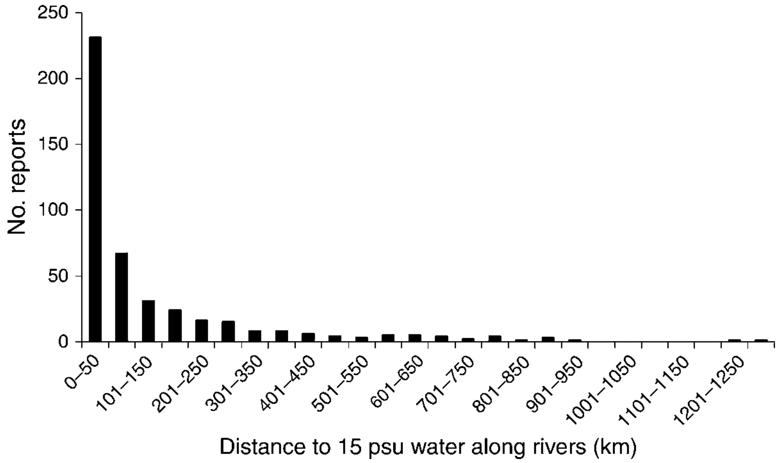

FIG. 1. Distribution of Chinese mitten crab dispersal distances in Europe. Dispersal distance is calculated as the distance from the freshwater point of occurrence to the nearest site with sufficient salinity (15 psu) for crabs to reproduce successfully. Distances were measured along rivers using ArcGIS (Environmental Systems Research Institute, Redlands, California, USA).

pressure is proportional to the volume of ballast water discharged that originated from foreign ports within the natural or introduced range of mitten crabs. We used records of ballast water discharge for the period 1 July 1999 through 31 December 2003 for ships entering the United States, which are self-reported by ships and collected and maintained by the Smithsonian Environmental Research Center (e.g., Verling et al. 2005). We considered only those ships that loaded ballast water in China or Europe and that had not exchanged ballast water while en route to U.S. destination ports. Ballast water exchange can dramatically reduce propagule pressure owing to discharge of planktonic larval (zoea, megalopa) crabs or to osmotic stress if they remain in the ships' ballast tanks (see Choi et al. 2005, Wonham et al. 2005). We also excluded vessel traffic that originated in the Mediterranean Sea as mitten crabs are not reported from this region. We assume that survival rate of ballast-borne crabs is invariant across source regions, although the actual risk posed by ships visiting from Asian ports may be reduced by the longer voyage durations and the greater mortality associated with longer trips (Verling et al. 2005).

We determined mean level of environmental suitability for major watersheds within the 354-km dispersal limit associated with U.S. ports using the "Spatial Analyst" tool in ArcMAP 9.0. This procedure allowed us to combine the total amount of ballast water received and the percentage of environmental match to develop an overall risk assessment for North American freshwater habitats.

Estimating relative risk

We defined risk of establishment as the product of propagule pressure (P) and individual probability of survival (S), risk $= PS$. Therefore, if propagule pressure or the probability of mitten crab survival is zero, the risk of establishment is zero at a specific port. This measure of risk can be further justified mechanistically as a binomial survival process from which the metric of risk is the expectation of the number of surviving individuals. Propagule pressure, P, is a measure of the number of individuals entering a location. Survival, S, is an individual probability. The binomial survival formulation assumes individuals act independently. Future investigations could consider the influence of non-independent survival such that groups of individuals have different individual probabilities of survival depending on group size (Lockwood et al. 2005). Additionally, biotic factors such as competition, biodiversity, and enemy release may be incorporated into the estimates of the probability of survival (Levine et al. 2004). From the GARP analysis we were able to quantify the percentage of environmental match (GARP%) between source (European or Asian populations of mitten crabs) and potential destination locations (U.S. ports). We assumed that the percentage of environmental match is correlated with the probability of a mitten crab surviving and eventually reproducing in the destination. From the 13 ports considered in our study, the volume of ships' ballast water was recorded for a 4.5-year period. While this is not a direct measure of the propagule pressure, we can assume the volume (V) of ballast water is proportional to the propagule pressure, $P = \alpha V$. It is crucial to note that other factors, such as inoculation frequency, may be influential on the formulation of establishment risk. While we did not include them in this study due to data limitations, future projects could consider the influence of these features and their influence on the risk formulation. Given these limitations, we reformulated risk for a port x, $\text{Risk}_x = \alpha V_x \times \text{GARP\%}_x$. Because GARP% does not capture the actual probability of survival, we could not calculate the probability of establishment per se. However, if the GARP scores were similar between two locations (A and B), we could formulate a relative risk:

$$R = \frac{(\alpha V_A \times \mathrm{GARP}\%_A)}{(\alpha V_B \times \mathrm{GARP}\%_B)}.$$

If the GARP% scores were similar ($\mathrm{GARP}\%_A \sim \mathrm{GARP}\%_B$) and α was also assumed constant, our measure of relative risk between two locations was simply the proportion of ballast volume introduced, (V_A/V_B). In order to allow comparisons between ports of similar environmental match, they were divided into five groups according to their GARP scores: high, 100–85; medium-high, 84–50; medium-low, 49–15; low, 14–0. If the GARP scores were not similar (i.e., the ports are in different groups), then relative risk comparisons were likely not valid owing to the unknown relationship between GARP scores and survival rate.

Results

Ecological niche modeling

The GARP model developed for the native Asian range retained the following layers, each of which significantly improved model fit: precipitation (in millimeters), wet day index (number of days of precipitation), minimum, mean and maximum air temperatures (in degrees Celsius), and compound topographic index (wetness index based on flow accumulation and slope; Table 1). Hierarchical partitioning revealed that the most important contributors to model accuracy were maximum temperature, compound topographic index, minimum temperature, and precipitation level (Table 1). By contrast, the GARP model based upon the European distribution retained minimum, mean, and maximum temperature, wet day index, precipitation, topographic index, and river discharge (Table 1). Of these, temperature and wet day index were the most important contributors to model fit.

Despite differences in the importance of different environmental variables in development of Asian and European models, both sets of models yielded similar predictions of potential ranges for mitten crabs in North America (Figs. 2 and 3). The only exception to this generality was for models run without consideration of dispersal distance to the sea, i.e., models that considered only environmental and not reproductive suitability (Figs. 2A and 3A). For example, the Asian model predicted widespread environmental suitability throughout the eastern, central, and Pacific Northwest sections of the United States (Fig. 2A), whereas the European model had much lower suitability overall and particularly so for most central and western areas (Fig. 3A). The only two areas for which the European model predicted higher environmental suitability are the northern Great Lakes and along the West Coast north of Vancouver Island. Some of the areas highlighted in the Asian model (e.g., South Dakota, Nebraska) as providing suitable environmental conditions for mitten crabs are far inland from the sea and thus beyond all reported dispersal distances characteristic of the species (Fig. 1).

Table 1. Hierarchical partitioning of environmental variables that contributed significantly to the development of the predictive genetic algorithm for rule set prediction (GARP) models of mitten crab presence in Asia or Europe.

Factor	Contribution to model accuracy (%): Asian GARP models	Contribution to model accuracy (%): European GARP models
Maximum temperature (°C)	34	15
Mean temperature (°C)	4	22
Minimum temperature (°C)	10	33
Wet day index (no. days of precipitation)	8	16
Topographic index (wetness index based on flow accumulation and slope)	27	1
Precipitation (mm/d)	9	7
River discharge (km^3/yr)	···	3

Note: Importance of each retained environmental variable is given as the relative percentage contribution to model accuracy.

Asian and European models that considered dispersal distance to the sea typically had a high degree of similarity in predicted range of mitten crabs. The Asian model with broad dispersal (1260 km) had a reduced distribution relative to the unrestricted dispersal Asian model (Fig. 2B), particularly in central parts of the continent. The crab's expected distribution with the 1260-km dispersal limitation was restricted to the eastern seaboard from southern Nova Scotia to central Florida, in the Gulf of Mexico from central Florida to Corpus Christi, Texas, and in the Pacific Northwest from San Francisco Bay to southwestern British Columbia. Inland distribution along the eastern seaboard was constrained by the Appalachian mountains (Fig. 2A).

The European model with broad dispersal (1260 km) resembled that of its Asian counterpart, although environmental matching was typically lower and particularly so in the southern United States (Figs. 2B and 3B). The lower Great Lakes and upper St. Lawrence River were predicted as environmentally suitable by both Asian and European models with broad dispersal distance. In the Pacific Northwest, highly suitable environments were generally farther north into British Columbia (including Vancouver Island) in the European model, whereas the Asian model predicted greater inland penetration in Washington, Oregon, and California.

With the more stringent dispersal limit of 354 km, consistent with the 90th percentile of observations of mitten crabs in Europe (Fig. 1), the predicted occurrence of mitten crabs with the Asian model decreased in three areas: the lower Great Lakes and upper St. Lawrence River, central sections of the Mississippi watershed, and interior areas of Washington, Idaho, northeastern California, and northwestern Nevada (Fig. 2C). Similarly, European models with constrained dispersal (Fig. 3B, C) had the same range restrictions relative to the broad dispersal models as was noted above for the Asian models (Fig. 2B, C).

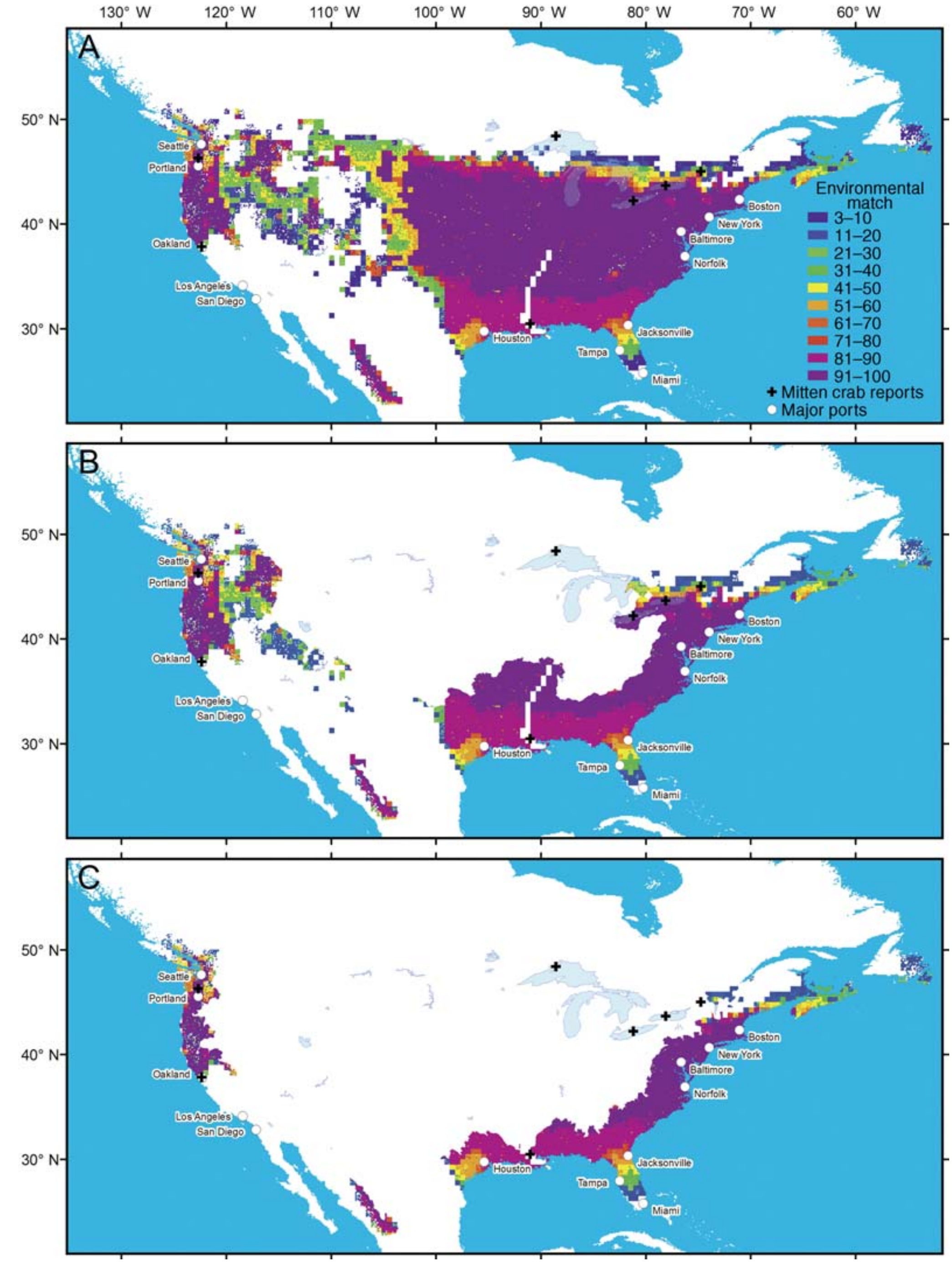

FIG. 2. Predicted occurrence of Chinese mitten crabs in North America based on the ecological niche models developed using environmental data for Asian sites of crab presence. Included in the models are (A) no dispersal limitation or (B) limitation based upon maximum (1260 km) or (C) 90th percentile (354 km) of reported crab dispersal distance in Europe (see Fig. 3). Dispersal distances are measured from the inland location to the nearest site with salinity ≥15 psu. Stars indicate occurrence reports of mitten crabs in North America; the only North American site known to have an established population is San Francisco Bay. Labels indicate U.S. ports for which ballast water discharge data were obtained to estimate introduction effort.

Relative risk to U.S. ports

The volume of non-exchanged ballast water that originated at sites in Europe or China and was discharged into the United States varies considerably among ports (Table 2) and years (not shown). Not surprisingly, ports along the eastern seaboard receive non-exchanged ballast water mainly from European donor ports, whereas those in the west receive it mainly

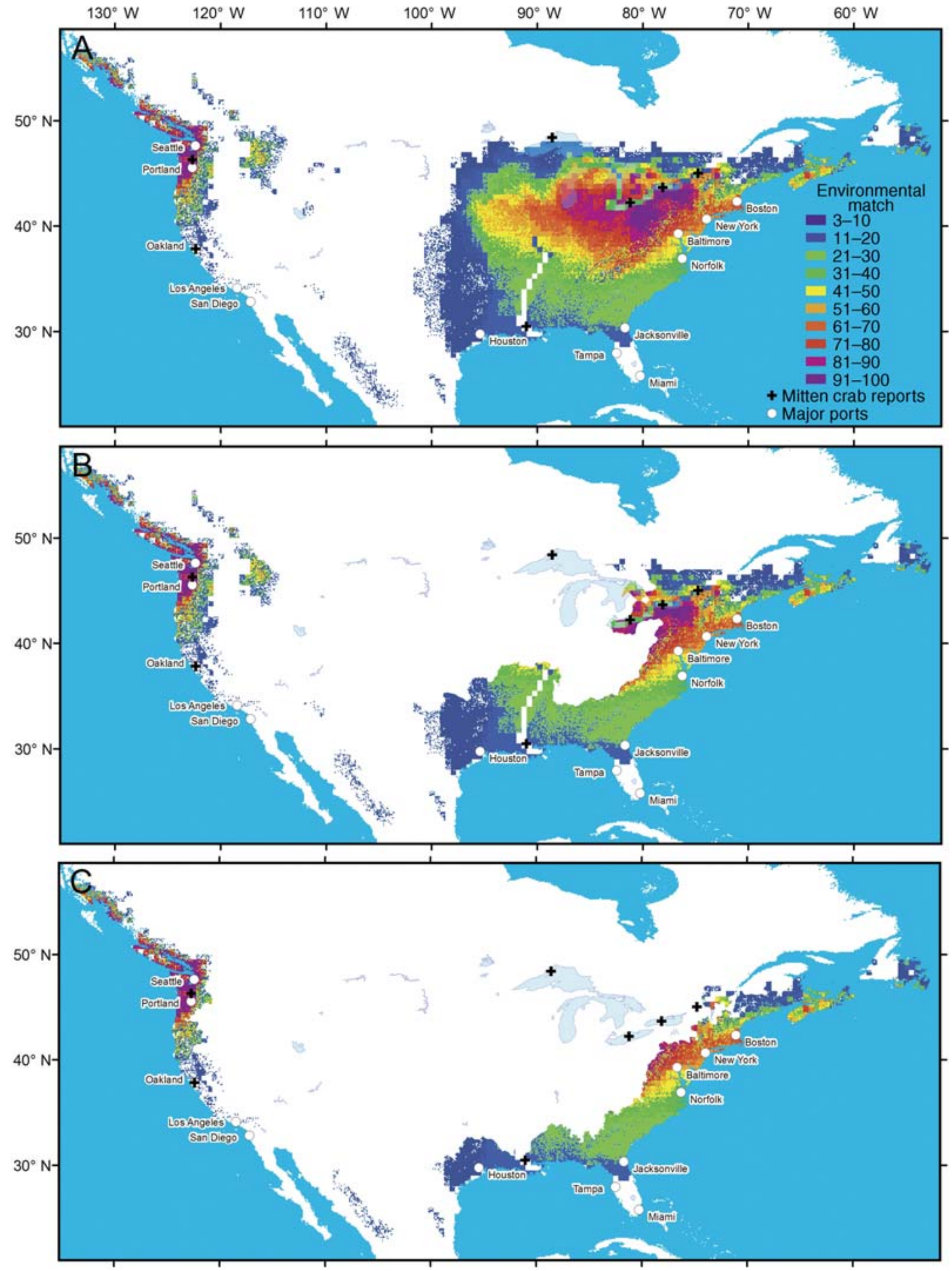

FIG. 3. Predicted occurrence of Chinese mitten crabs in North America based upon the ecological niche models developed using environmental data for European sites of crab presence. Included in the models are (A) no dispersal limitation or (B) limitation based upon maximum (1260 km) or (C) 90th percentile (354 km) of reported crab dispersal distance in Europe.

from China. The port of Norfolk, Virgninia, received more unexchanged ballast water from sites inhabited by mitten crabs than all of the other major ports in the contiguous United States combined (Table 2).

The ports of Norfolk and Baltimore were most vulnerable to introduction and establishment of Chinese mitten crabs. These areas were the only ports in the high-risk group in the Asian model and were also associated with the highest relative risk in the European model (Tables 2 and 3). These areas were at risk because they receive a high volume of ballast water from risky sources (i.e., propagule pressure) and had high environmental

TABLE 2. Relative risk of invasion of the major ports in the United States based on environmental matching levels estimated by the Asian model (based on the native Asian distribution).

Group and port	Asian model Mean	SD	Ballast volume (Mg)	Relative risk
High				
Norfolk, Virginia	98	8	365 427	4.8
Baltimore, Maryland	98	8	76 160	1
Medium/high				
Portland, Oregon	67	34	65 465	160.6
Houston, Texas	80	12	24 836	60.9
New York, New York	84	31	21 019	51.6
Seattle, Washington	68	37	13 266	32.6
Tampa, Florida	59	19	1021	2.5
Jacksonville, Florida	75	19	408	1
Medium/low				
San Francisco–Oakland, California	33	44	21 718	5.7
Boston, Massachusetts	49	44	3792	1
Low				
Los Angeles–Long Beach, California	0	0	30 458	21.7
Miami, Florida	13	13	1402	1
NA				
San Diego, California	0	0	0	···

Notes: Environmental match mean scores estimated the degree of environmental compatibility (range 0–100%) for that port's watershed (to a distance of 354 km upstream of the port) based upon 300 simulations. The risk proportionality was based on the ratio of ballast water received and only applies within a group of ports of similar environmental match.

suitability. The relative risk of Norfolk becoming invaded was 4.8 times higher than that of Baltimore. The port of Portland had the third highest risk of invasion; it had the highest relative risk within the medium-high environmental match group in the Asian model, and the third highest in the European model. While a direct comparison of the relative risk between Portland and Norfolk and Baltimore was not possible for the Asian model (except that it is higher for the latter two), the risk was only slightly lower for Portland (4.9) than Baltimore (5.7) in the European model. However, it is also important to note that the ports of Baltimore and Norfolk occur within Chesapeake Bay and are ~280 km apart. Other ports such as New York and Seattle had a lower risk of establishment as they had

TABLE 3. Relative risk of invasion of the major ports in the United States based on habitat-matching levels estimated by the European model (based on the invaded European distribution).

Group and port	European model Mean	SD	Ballast volume (Mg)	Relative risk
Medium-high				
Norfolk, Virginia	53	17	365 427	27.5
Baltimore, Maryland	69	16	76 160	5.7
Portland, Oregon	63	36	65 465	4.9
New York, New York	51	18	21 019	1.6
Seattle, Washington	74	31	13 266	1
Medium-low				
Boston, Massachusetts	25	21	3792	9.3
Tampa, Florida	15	9	1021	2.5
Jacksonville, Florida	21	7	408	1
Low				
Los Angeles–Long Beach, California	0	1	30 458	21.7
Houston, Texas	9	5	24 836	17.7
San Francisco–Oakland, California	2	3	21 718	15.5
Miami, Florida	0	2	1402	1
NA				
San Diego, California	0	0	0	···

Notes: Environmental match mean scores estimated the degree of environmental compatibility (range 0–100%) for that port's watershed (to a distance of 354 km upstream of the port) based upon 300 simulations. The risk proportionality was based on the ratio of ballast water received and only applies within a group of ports of similar environmental match.

moderate ballast discharge volumes and medium-high or medium-low environmental matches (Tables 2 and 3). Other ports were expected to have a much lower risk of mitten crab establishment, either because low discharge volumes limit propagule pressure and/or because inhospitable conditions limit survival of introduced individuals. For example, risk of establishment in the Asian model for the ports of Los Angeles–Long Beach and Miami appeared to be very low owing to an inhospitable environment, despite the fact that these areas received moderate volumes of unexchanged ballast water from invaded source ports. A few ports, including Tampa and Jacksonville, were vulnerable to establishment of mitten crabs based upon environmental matching. However, as they received little unexchanged ballast water from invaded source regions, their relative risk was very low (Tables 2 and 3). The risk level for San Francisco–Oakland harbor was in the medium-low category for the Asian model and low in the European model (Tables 2 and 3).

Discussion

Combining environmental matching and vector transport

The relative risk assessment presented here allows a focused management program at the most effective point of the invasion process, the pre-establishment phase (Ricciardi and Atkinson 2004, Jeschke and Strayer 2005). Our approach combined reported quantities of ballast water discharge (as a proxy for propagule pressure) with environmental matching to establish relative invasion risk for different U.S. ports. Norfolk, Baltimore, and Portland have the greatest relative risk of introduction and establishment of Chinese mitten crabs since they receive the greatest volumes of ballast water from source regions known to support the species and have the highest environmental match for both models (Tables 2 and 3). Additionally, the ports of Norfolk and Baltimore are both located in Chesapeake Bay, further increasing the overall risk for this area.

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 (e.g., Wonham et al. 2000, Kolar and Lodge 2002, Rouget and Richardson 2003, Forsyth et al. 2004). Genetic algorithm for rule set prediction modeling can accurately predict the occurrence of mitten crabs. The same Asian model used here was validated using the European distribution (L. M. Herborg, *unpublished manuscript*). Eighty-four percent of reports in Europe occurred in areas predicted as suitable by >80% of Asian GARP models and only 4% occurred in areas predicted suitable by <50% of Asian models. However, 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. Our results highlight the advantage of combining environmental matching, measures of propagule pressure, and limitations imposed by the species' catadromous life cycle for estimating establishment risk. For example, central portions of the United States outside of the maximum known dispersal capability of mitten crabs were nevertheless predicted as environmentally suitable (e.g., Figs. 2A and 3A) for the species. Similarly, the combined port system of Los Angeles–Long Beach received relatively high volumes of ballast discharge from key source regions (Table 2) and has considerable risk to establishment of Chinese mitten crabs based solely on propagule supply. However, when combined with information on environmental matching, our analysis indicated that this port system had a low risk of invasion (Tables 2 and 3). Jacksonville and Tampa were coastal cities with moderate environmental matches based upon the Asian model; however, they receive very little ballast water discharge from possible donor regions. If, however, other potential vectors of mitten crab introduction, including seafood imports (Cohen and Carlton 1997), were to introduce this species to these areas, both port areas could seemingly be colonized successfully. Alternatively, these ports could be vulnerable if the founding population were genetically differentiated (e.g., directional selection) from that in the source and better adapted to prevailing conditions in these areas (e.g., McMahon 1996, Lee and Petersen 2002).

The approach used here has advantages over methods that only assess vector transport (e.g., Drake and Lodge 2004, Leung et al. 2004, MacIsaac et al. 2004). In order to estimate propagule supply via ballast water discharge, detailed knowledge is required of ballast practices of ships arriving in focal ports of interest (Verling et al. 2005). Vectors transmitting nonindigenous species and the pathways between sources and destinations are important for an understanding of the invasion process (Hilliard et al. 1997). This is consistent with a propagule-pressure-based approach to risk assessment, which is supported by empirical evidence for an array of species (e.g., Rouget and Richardson 2003, Forsyth et al. 2004, Lockwood et al. 2005, Suarez et al. 2005).

European vs. Asian model

The Asian and European models, when combined with dispersal constraints, provided quite similar predicted ranges for mitten crabs in North America. Despite this, these models differed with respect to environmental suitability of coastal areas in the southeastern United States (Figs. 2 and 3). These differences are likely attributable to distribution differences in Europe and Asia. The crab is native to Asia, and thus its reported distribution there is relatively complete. Conversely, despite an invasion history in northern Europe that extends back as far as 1912 (Peters 1933), the species is still colonizing localities in southern Europe along the Atlantic coastline. Had colonization of southern Europe been more complete, inclusion of these sites into our European GARP model would almost certainly extend the projected distribution of mitten crabs farther south in the United States. If management decisions required selection of either of the Asian or European model predictions for the southeastern United States, we would err on the side of caution and opt for the former model since it had higher environmental matching for this region. The higher environmental match of western Canada in the European model is restricted to a very narrow strip along the coastline, rendering establishment of mitten crabs in this area very unlikely. Mitten crab distribution is also expanding in Great Britain and in coastal areas around the Baltic Sea. Northern range expansion in Europe would not influence projected distribution in the coterminous United States.

North American mitten crab reports

Our models allow us to compare expected distributions of mitten crabs with reported occurrences in the Chesapeake Bay, Great Lakes, lower Mississippi River, and San Francisco Bay (established population; Fig. 2A). The recent discovery of mitten crabs in Chesapeake Bay close to the port of Baltimore (G. M. Ruiz, *unpublished manuscript*) is consistent with our predictions that this region has the greatest relative risk of invasion (Tables 2 and 3). While suitability for survival in both models was predicted to be very high for all areas where crabs have been found in the lower Great Lakes (Figs. 2A and 3A), one mitten crab was found on a hydro intake screen in Lake Superior at Thunder Bay, Ontario (R. Eberhardt, *personal communication*). This location is proximal to an area with 7–11% environmental suitability according to the European model (Fig. 3A), but is outside the zone of suitability in the Asian model (Fig. 2A). Both Asian and European models suggest very low suitability for the Mississippi River; however these projections are likely artefacts of the manner in which the models were constructed. Both models included compound topographic index, which is in part related to river discharge. In addition, the European model also included river discharge directly (Table 1). Neither European nor Asian models incorporated rivers with flow rates as high as that of the Mississippi River, and thus this environment was assessed as unsuitable. Considering that live mitten crabs have been recorded from the lower Mississippi River and that adjacent areas are highly suitable environmentally (Figs. 2 and 3), we contend that the crabs may be capable of establishing in this watershed. San Francisco Bay–Oakland lies at a split point for environmental coverage in the Asian model. Some areas of this watershed were suitable for establishment whereas others were not, thus accounting for the high standard deviation (Tables 2 and 3) for this region. The European model predicted that this environment was unsuitable, although considering the limited southern distribution in Europe this prediction may not be reliable. Clearly, the fact that the crab is established in San Francisco Bay illustrates that suitable conditions exist in at least some areas. Our models identified this region as having a relatively low risk of invasion (Tables 2 and 3) due both to low propagule pressure and low environmental match. However, this outcome may be affected by several factors. Shipping patterns are changing, and past propagule supply by ships may have been greater, especially prior to ballast water treatment, which was implemented in the late 1990s. In addition, alternative introduction vectors could increase propagule pressure to the Bay, leading to a higher invasion risk. Genetic analysis of the San Francisco Bay population has suggested that it originated from Europe (Hanfling et al. 2002), while ballast water discharged into the Bay during the 1999–2003 period all originated from Asia. Thus, introduction via the live seafood trade may have been responsible for this population (Webb et al. 2003).

Risk of secondary ballast water transport

Our study does not include secondary transport of mitten crabs from San Francisco–Oakland to other North American ports. This problem appears to be inconsequential, considering that ballast water from San Francisco–Oakland is mainly released into Valdez Port, Alaska, which lies 4° N of environmentally suitable areas (Fig. 3). It seems that secondary spread presently poses a very small risk of larval transport, as the volume of ballast water released at locations with environmental suitability along the West Coast is very limited. Other potentially important secondary transport mechanisms such as hull fouling or pelagic larval dispersal from San Francisco Bay are outside the scope of this study.

Future developments

There remain several areas to consider in the application and further advancements of this predictive tool. First, these models do not address biotic interactions or the integrative ability of this species in recipient communities. If predators attack colonizing crabs, then establishment success could be further reduced. Second, shipping and ballast discharge patterns are highly dynamic, which obviously affects vector-based predictions. This is particularly true for ballast water treatment, which is now practiced on some ships and is rapidly evolving throughout the world. Also the frequency of ballast water exchange has increased dramatically in recent years (Miller et al. 2004). Because our analysis is based on the discharge volume of untreated ballast from 1999 to 2003, changes in ballast discharge volumes can affect the ability of our analyses to be representative of past or future patterns. Thus, such risk analyses address explicitly a specific time frame. Third, our current modeling of suitable conditions includes primarily water quality characteristics. Although this data set provides a conservative estimate of potential geographic range, other habitat characteristics (e.g., benthic substrate type, physical structure, vegetation cover, etc.) may provide improved resolution. These data exist for several bodies of water, but they are not yet readily available in aggregate or standardized fashion, constraining use in current applications.

Conclusions

Here we have developed an approach that uses a proxy for introduction effort combined with models that identify environmental suitability to predict vulnerability of North American coastal habitats to invasion by Chinese mitten crabs. Collectively, these models identify where Chinese mitten crabs are being introduced and where they are most likely to survive. Such information could be used for a focused management program, which for example could encourage mid-ocean ballast water exchange for ships arriving from risk areas in Europe and Asia to the ports of Norfolk, Baltimore, and Portland. Monitoring efforts could also focus on these high-risk ports to detect early signs of establishment similar to those developed for high-risk areas associated with commercial and recreational shipping in Australia and New Zealand (Hewitt and Martin 1996, Hewitt et al. 2004). As shipping patterns change, the risk level would require frequent reevaluation. Additionally, the inclusion of secondary transport from invaded sites such as San Francisco Bay, as well as an estimate of propagule pressure from illegal shipments of mitten crabs for the seafood trade, could be included.

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APPENDIX

A table showing the source of environmental coverages used in the predictions (*Ecological Archives* A017-028-A1).