Predicting the Range of Chinese Mitten Crabs in Europe

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Abstract: *Ecological niche modeling provides a means for predicting the potential future distribution of a nonindigenous species based on environmental characteristics of the species' native range. We applied this method to the Chinese mitten crab* (Eriocheir sinensis)*, a catadromous crustacean with a long history of invasion in Europe. We used genetic algorithm for rule-set prediction to predict the potential European distribution of mitten crab based on its distribution in 42 locations in its native Asia. The climatic variables, air temperature, number of days, amount of precipitation, and wetness index, contributed significantly to predictions of native distribution limits. Although the genetic algorithm for rule-set prediction model was developed for the native range, the species' extensive distribution in Europe (*n = 434*) allowed independent validation of the predictions. Application of the model to Europe was successful, with 84% of occurrences in regions predicted to be suitable by >80% of the models and <4% of occurrences in areas predicted suitable by <50% of the models (mainly along the northern range). At the watershed scale, areas with established mitten crab populations had significantly higher habitat matching than sites that were not invaded. The independent validation of the Asian-based model by the European distribution revealed that predictions were highly accurate. The model also identified large areas of Europe, particularly along the Mediterranean coast, as vulnerable to future invasion. These predictions can be used to develop strategies to control the spread of mitten crab by preventing introductions into vulnerable areas.*

Keywords: Chinese mitten crab, ecological niche modeling, *Eriocheir sinensis*, genetic algorithm for rule-set prediction, habitat matching, nonindigenous species, species dispersal

Predicción de la Distribución de *Eriocheir sinensis* en Europa

Resumen: *El modelado del nicho ecológico proporciona un medio para la predicción de la distribución potencial futura de una especie no nativa con base en características ambientales del rango de distribución nativo de la especie. Aplicamos este método a* Eriocheir sinensis*, un crustáceo catádromo con una larga historia de invasión en Europa. Utilizamos GARP (algoritmo genético para la predicción de conjunto de reglas) para predecir la distribución potencial en Europa del crustáceo con base en 42 localidades en su nativa Asia. Las variables climáticas temperatura del aire, número de días y cantidad de precipitación e índice de humedad contribuyeron significativamente a la predicción de los límites de distribución nativa. Aunque el modelo GARP fue desarrollado para el rango de distribución nativo, la distribución extensiva de la especie en Europa (*n = 434*) permitió la validación independiente de las predicciones. La aplicación del modelo en Europa fue exitoso, con 84% de ocurrencias en regiones pronosticadas como adecuadas por >80% de los modelos y*

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<4% de ocurrencias en regiones pronosticadas como adecuadas por <50% de los modelos (principalmente a lo largo del rango norteño). A escala de cuenca hidrológica, las áreas con poblaciones establecidas de Eriocheir sinensis *tenían significativamente mayor número de sitios concordantes que no estaban invadidos. La validación independiente del modelo basado en Asia por la distribución europea reveló que las predicciones eran altamente precisas. El modelo también identificó que extensas áreas de Europa, particularmente a lo largo de la costa Mediterránea, son vulnerables a invasiones futuras. Estas predicciones pueden ser utilizadas para desarrollar estrategias para controlar la expansión de* Eriocheir sinensis *mediante la prevención de introducciones en áreas vulnerables.*

Palabras Clave: algoritmo genético para la predicción de conjunto de reglas, concordancia de hábitats, dispersión de especies, *Eriocheir sinensis*, especies no nativas, modelado del nicho ecológico

Introduction

Predicting spread is an essential aspect of nonindigenous species management, particularly if the species is associated with adverse effects on recipient ecosystems or native species. Such forecasts provide important information in the assessment of ongoing invasions or for identification of areas that are likely to be invaded next. Numerous methodologies used to predict the occurrence and potential range of nonindigenous species focus on life history attributes (e.g., Kolar & Lodge 2002) or on vectors that link invaded sources with uninvaded destinations (e.g., MacIsaac et al. 2004; Verling et al. 2005). Another methodology, ecological niche modeling, seeks to predict the potential range of nonindigenous species based on distribution data in the native range and a range of environmental variables in both areas (reviewed in Peterson 2003). This latter approach can be combined with vector-based predictions to identify areas at risk from nonindigenous species (Herborg et al. 2007*b*).

The genetic algorithm for rule-set prediction (GARP) is a widely applied environmental niche modeling application that uses raster-based environmental and biological information to predict suitable habitat for a given species. The GARP has been used to predict potential range limits for a variety of nonindigenous species (Peterson & Vieglais 2001; Arriaga et al. 2004; Drake & Bossenbroek 2004; Roura-Pascual et al. 2004). Nevertheless, a potential problem with the use of GARP and other environmental niche modeling procedures is that validation of the model prediction based on an independent range is rarely conducted, usually because of a lack of distribution data on the ranges of introduced species (but see Peterson & Robins 2003; Arriaga et al. 2004; Iguchi et al. 2004; Roura-Pascual et al. 2004).

Here, we focused on the Chinese mitten crab (*Eriocheir sinensis*), a catadromous crustacean whose native range extends from the Vietnamese–Chinese border into North Korea (21°N–41°N). It reproduces in brackish and marine estuaries, where its pelagic larvae settle (Anger 1991) and later move upstream. Juveniles may migrate up to 750 km upstream in rivers, where they mature (Herborg et al. 2003). Once the crabs reach sexual maturity they migrate back to estuaries to reproduce and die (Peters 1938).

The Chinese mitten crab is rapidly expanding its worldwide distribution. It was first reported in Europe in 1912 in northern Germany (Peters 1933) and spread thereafter along the North and Baltic Sea coastlines, eventually reaching southern France by the 1950s and the United Kingdom by the 1970s (see Herborg et al. 2003, 2005). Recent southern range expansions include spread along the Spanish and Portuguese Atlantic coast in the rivers Tagus (Cabral & Costa 1999), Guadalquivir (R. Ferreo-Rodriguez, personal communication), and Mino (8.8129°W 41.9238°N) (Ferdinand-Martinez & Carrera 2003). Recent northward spread has occurred in Great Britain, along the Estonian and Lithuanian Baltic coastlines (J. Kotta et al., personal communications), into the Finnish lake district (Silfverberg 1999; Valovirta & Eronen 2000), and into Lake Mälaren, Sweden (P. Vidlund, personal communication). A population has recently established in San Francisco Bay (Rudnick et al. 2003), and additional finds have occurred elsewhere in North America. The most likely vectors for such long-distance dispersal of mitten crabs are either ballast water or intentional introduction to establish a food fishery (Cohen & Carlton 1997; Hänfling et al. 2002; Herborg et al. 2007*a*)

Mitten crabs have a number of adverse ecological and socioeconomic impacts on the systems they invade. The crab causes riverbank erosion due to burrowing activity and preys on surface-dwelling invertebrates, possibly competing with native invertebrates and fish (Peters 1933; Dutton & Conroy 1998; Rudnick & Resh 2005). In fact, in certain areas of San Francisco Bay and Dutch estuaries commercial trawl fishers have been unable to haul in nets because of the weight of mitten crab catches (Ingle 1986; Veldhuizen & Stanish 1999). The range of adverse impacts associated with mitten crabs have earned the species a place on the "100 of the world's worst nonindigenous species" list published by the Invasive Species Specialist Group (Lowe et al. 2000).

Given the range of ecologic and economic impacts of the mitten crab in areas where it has been introduced, it is important to predict the potential distribution of Chinese mitten crabs in Europe. We have a unique, high-resolution data set of the distribution of *E. sinensis* in both its native range (Asia) and introduced range (Europe). We used this data set to develop a GARP model based on a series of variables in the crab's native range. We validated the model's ability to predict the crab's distribution in Europe and identified areas most vulnerable to future invasion.

Methods

Distribution Database

We compiled a database of the distribution of the Chinese mitten crab in its native range from the literature (Shen 1932; Sakai 1976; Dai 1991; Chen et al. 1995; Guo et al. 1997; Ng et al. 1999; Tang et al. 2003). Reports were obtained for major rivers along the Chinese coastline and for sites up to 300 km upstream. We used data only for fresh and brackish water habitats; thus, our results cannot be extrapolated to coastal, marine habitats. Although the focus of our work was the mitten crab, we also included reports for *E. hepuensis* because molecular analyses suggest that they may be the same species (Lu et al. 2000; Chu et al. 2003; Tang et al. 2003). We included these reports to increase the number of reports within our prediction.

A second database was compiled for the introduced range of Chinese mitten crabs in Europe. These data were obtained from literature reports (see Herborg et al. 2003, 2005) and from personal interviews with scientists working on marine or estuarine systems and/or aquatic nonindigenous species. We classified mitten crab reports based on the abundance of crabs in each of these systems over at least 5 years to determine whether populations were established (>10 individuals/year or presence of ovigerous females) or not established (Table 1).

GARP Distribution Modeling

We used the GARP modeling application to generate a predictive model of mitten crab distribution. A key aspect of ecological niche modeling is the selection of appropriate environmental data layers. In this study an array of aquatic and terrestrial layers was tested for their contribution to the model (see Table 2 for more details). Environmental variables were selected based on our knowledge of mitten crab biology, and potential factors that could influence environmental suitability. Some data were available as coverage for the entire study area (e.g., annual air temperature minimums, means and maximums; precipitation, digital elevation, river discharge), whereas other data were generated from specific data points (i.e., river temperature, watershed size).

The GARP model selected nonrandom associations between environmental layers and presence of the mitten crab in its native range with a genetic algorithm. Absence data are not incorporated into this approach. The algorithm selects a single method from an available range (atomic rule, BIOCLIM rules, logistic regression, range rules) and creates random rules, which are then iteratively improved through combination, point deletion, and crossing over (Stockwell & Peters 1999; Roura-Pascual et al. 2004). Presence data are randomly divided by the

Table 1. Rivers and canals with established Chinese mitten crab populations in Europe.*

Country	*Water body*	*Latitude*	*Longitude*	*First report*	*Source*
France	Seine River	49.4522	0.1579	1946	Petit & Mizoule 1974; T. Vincent, personal communication
Germany	Havel River, tributary of the Elbe	52.4524	13.2421	1924	Peters 1933; Paepke 1984
Germany	Elbe River	51.7948	12.9551	1914	Peters 1933; Paepke 1984; Tittizer et al. 2000
Germany	Ems River	52.9762	7.3567	1929	Peters 1933; Tittizer et al. 2000
Germany	Rhine River	47.9614	7.6131	1931	Kamps 1937; Tittizer et al. 2000
Germany	Weser River	51.4609	9.5916	1912	Peters 1933; Tittizer et al. 2000
Netherlands	Meuse/Maas River	51.5585	4.0004	1931	Kamps 1937; Wolff & Sandee 1971; K. Wouters, personal communication
Netherlands	Schelde River	51.3823	4.2222	1931	Kamps 1937; Wouters 2002; K. Wouters, personal communication 2005
Poland	Vistula River	19.3710	54.3219	1932	Peters 1933; Normant & Skora 2002
Poland	Odra River	53.4919	14.6094	1929	Peters 1933; Jażdżewski & Konopaoka 1993; Normant et al. 2000; M. Normant, personal communication
Portugal	Tagus/Tajo River	39.4271	−8.3110	1988	Cabral & Costa 1999
Spain	Guadalquivir River	37.4059	−5.9371	1997	Cuesta et al. 2004
Sweden	Lake Mälaren	59.4159	17.5272	1994	P. Vidlund, personal communication
United Kingdom	Thames River	51.4841	−0.3401	1973	Ingle 1986; Clark et al. 1998

**The geographical coordinates represent the estuary of each body of water. The sources listed include the first and most recent reports. Four watersheds are reported with more than one established population.*

Table 2. Environmental coverages tested for their contribution to predictive accuracy of the model of mitten crab invasion

Variable	*Grid size*	*Source*
Maximum annual temperature, °C*	0.5° × 0.5°	climate research unit global climate data set:
Mean annual temperature, °C*	0.5° × 0.5°	http://ipcc-ddc.cru.uea.ac.uk/obs/get_30yr_means.html
Minimum annual temperature, °C*	0.5° × 0.5°	
Wet-day frequency (no. of days of precipitation/year)*	0.5° × 0.5°	
Precipitation, mm/day*	0.5° × 0.5°	U.S. geological survey Hydro1k elevation derived database:
Topographic index (wetness index based on flow accumulation and slope)*	1 × 1 km	http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html
Elevation	1 × 1 km	
River discharge, km^3/a	0.5° × 0.5°	Xenopoulos et al. 2005
Mean river temperature, °C	10 × 10 km	generated from the global environment monitoring system: http://www.gemswater.org/publications/index-e.html
Watershed size	10 × 10 km	generated from the Atlas of the World Water Balance: http://www.crwr.utexas.edu/gis/gishydro99/atlas/Atlas.htm#describe

*Included in the GARP model predicting the potential range of Chinese mitten crabs in Europe.

GARP program into 80% training and 20% validation data, and the level of prediction accuracy is assessed for the native range by comparing the ratio of test data points outside the predicted range (false negatives or omission errors) with test points within the predicted range and the ratio of pseudo-absence points in predicted suitable environment (false positives or commission errors) with pseudo-absence points in unsuitable environment. Commission errors may occur with incorrect predictions, undersampling, natural dispersal barriers, or because the species has had insufficient time to disperse to a particular site (Stockwell & Peters 1999; Roura-Pascual et al. 2004).

In our model we used 42 sites from the native distribution of the mitten crab to develop the algorithm; results were then projected and validated based on the European data set. We used multiple regression analysis to test the effect of different environmental layers on prediction precision. As measures of model accuracy, we used the effect of each environmental layer on the extrinsic omission and commission error (Anderson et al. 2003; Drake & Bossenbroek 2004). Layer selection is critical because some layers deemed important through ecological knowledge of the system can actually decrease model quality. For example, in our model, the inclusion of maximum and minimum river temperature reduced model accuracy for predicting mitten crab occurrence relative to a similar model without these variables. We applied hierarchical partitioning analysis to the GARP prediction with all possible combinations of environmental layers used in the final model to identify variables that contributed most to the final model (Peterson & Cohoon 1999).

Models were generated with a maximum of 3000 iterations and a 0.001 convergence limit, or until 100 accurate predictions were obtained, which follows the best subset method (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% (see above).

To test the predictive ability of our model, we used our independent data set for mitten crab occurrence in Europe. Each of the best-subset layers provided coverage estimates for Europe ranging from 0 (unsuitable habitat) to 1 (suitable habitat). Three separate models with 100 best subsets each were generated and compared. Because of their high similarity, the resulting 3 × 100 best-subset layers were averaged with the Raster Calculator tool in ArcMAP 9.0. Values in the resulting habitat-matching layer ranged from 0 to 100 for each raster cell of coverage and represented the percentage of models that predicted a particular cell as suitable habitat. To test the quality of this prediction, the habitat-matching level was extracted for all reports of mitten crabs in inland sites in Europe ($n = 434$) with ArcMAP 9.0. Because this data set was not used to generate the model, it provided an independent validation test of model performance. To determine model accuracy, we compared the number of reports in areas where <80% of the models predicted suitable habitat versus the number of reports in areas predicted suitable by >80% of the models with a chi-square test.

As a separate assessment of model prediction accuracy, we compared the habitat suitability predicted for watersheds with and without established mitten crab populations. We used a Mann–Whitney *U* test to contrast habitat-match values for European watersheds with ($n = 10$) and without ($n = 86$) established mitten crab populations (Table 1). Given that mitten crabs may occupy a watershed anywhere from its headwaters to its marine terminus, habitat matching at the watershed level seems appropriate.

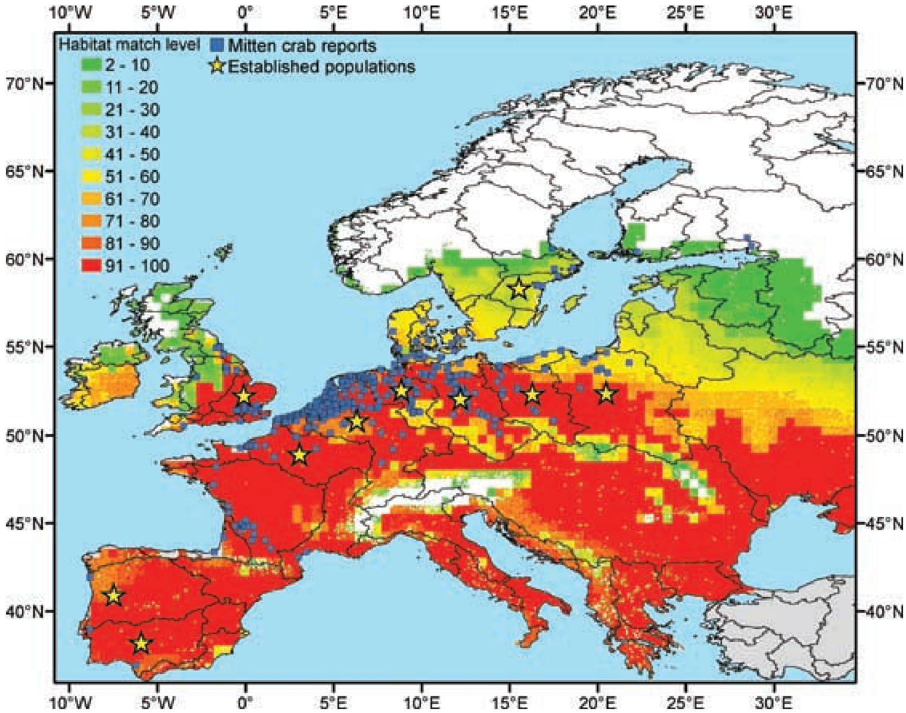

*Figure 1. Percentage (habitat-match levels) of models that identified an area as suitable for the Chinese mitten crab in its introduced range in Europe based on an environmental niche model developed with environmental data from its native range. Blue squares indicate actual mitten crab reports (*n *= 434), which were used as an independent test of the quality of the GARP model's predictions. Watersheds containing established populations are highlighted with a yellow star. Turkey and some coastal areas in northern Spain, France, Russia (Kaliningrad), and western Lithuania were not included in the model (gray shading).*

Results

The GARP model developed for the native distribution of mitten crabs in Asia retained the following layers, which significantly contributed to model fit: precipitation; wet-day frequency; minimum, mean, and maximum air temperatures; and topographic index, or wetness index (Table 2). Hierarchical partitioning indicated that the most important variables affecting model accuracy in the native range were topographic index, maximum temperature, and wet-day frequency.

The GARP model developed for the Chinese mitten crab in Asia predicted the known distribution in Europe very well (Fig. 1). Only 3.7% of reports were at sites predicted by <50% habitat-match models, whereas 84% of occurrence reports were at sites predicted as suitable habitat by >80% of GARP models. This occurrence distribution was significantly nonrandom, indicating a very high predictive ability of the model (df $=1$, $\chi^2 = 87$; $p < 0.0001$; Fig. 2).

Watersheds with established mitten crab populations had significantly higher predicted suitable habitat than those without (Mann–Whitney, df $= 85$, $W = 712$, $p < 0.0005$; Table 1; Fig. 1). For example, 9 out of 10 watersheds that contained mitten crab populations were predicted by ≥75% of models, whereas only 14 of 76 watersheds without crab populations were predicted at this level of sensitivity. Most of the latter sites are located along the Mediterranean Sea.

The only region where the GARP model failed to predict mitten crab populations well was in freshwater systems along Baltic Sea coastlines of Sweden, Finland, and Russia. Here, the model typically predicted low habitat matching, although the species has been reported in the Gulf of Finland, the Swedish Baltic Sea, and is established in Lake Mälaren, Sweden. All of these locations were predicted by <60% of habitat match models.

Discussion

Environmental niche modeling provides valuable insights into the potential distributions of many nonindigenous species (Peterson 2003). It can identify areas at risk of invasion, which can focus subsequent management efforts to maximize efficacy. For example, GARP provided input into management efforts aimed at identifying areas at risk of zebra mussel (*Dreissena polymorpha*) invasion in the western United States (Drake & Bossenbroek 2004). Our GARP model successfully predicted both the native and introduced ranges of mitten crabs.

Although a recent study reports that GARP's ability to predict species' distributions is exceeded under some conditions by a number of other modeling procedures (Elith et al. 2006), it is a widely used approach that had succeeded in predicting species' distributions accurately in several cases (Peterson & Robins 2003; Iguchi et al. 2004; Ruora-Pascual et al. 2004). 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.

Our GARP model revealed that most of Europe is vulnerable to invasion by Chinese mitten crabs. Eighty-four

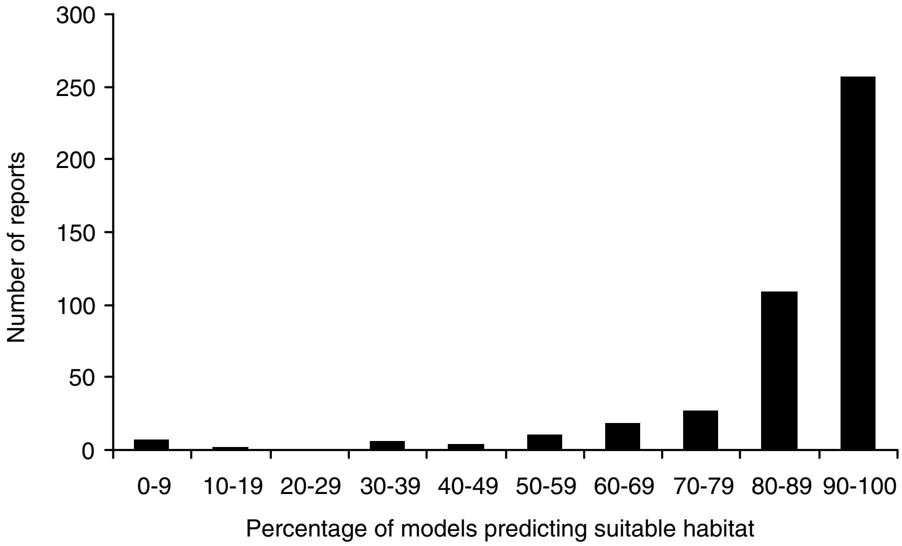

Figure 2. Validation of the GARP prediction of mitten crab invasion in Europe. The number of mitten crab reports found in each category of predicted level of habitat match are from Fig. 1.

percent of occurrences in Europe were in areas where habitat matching exceeded 80%, and very few occurrences were recorded in areas with poor habitat matching. Considering that much of the continent appears to constitute suitable habitat for this species, particular emphasis should be placed on preventing human-mediated dispersal—especially by ballast water discharges or intentional introductions—to suitable habitats where the species is not established presently. We identified a number of reports indicating the presence, but not establishment, of Chinese mitten crabs in European watersheds, where the GARP model predicted suitable conditions for establishment. Additional time will be required to determine whether these invasions succeed. Nevertheless, considering the high habitat matching for these localities, we view these occurrences as indicating likely establishment. Our model indicated that rivers flowing into the Mediterranean Sea appear to be highly suitable for the establishment of the mitten crab; thus, particular emphasis should be placed on preventing its introduction to this region.

Areas deemed unsuitable for the establishment of mitten crabs were principally located in northernmost Scandinavia, the eastern Baltic Sea (Karelia, Russia), and in mountainous areas (Fig. 1). Although the GARP model predicted that the area surrounding Lake Mälaren should have a relatively low likelihood of crab establishment (only 45% of models predicted suitable habitat), the species is reported to be established in the lake. Similarly, individual reports of mitten crab occurrence exist for the Finnish Baltic coast (Fig. 1).

These reports have to be considered in the context of the catadromous life cycle of this species. Considering that the mitten crab requires at least 15‰ salinity for larval survival (Anger 1991), crabs from the Lake Mälaren population would be required to migrate 700 km to the Kattegat–Baltic Sea connection, which is the nearest location in the Baltic Sea containing appropriate salinity conditions. A migration of this distance is possible because crabs have been reported up to 750 km inland (Herborg et al. 2003) and downstream migration rates of 400 km/year have been recorded (Panning 1938). Individual mitten crabs in coastal Finnish waters are even farther (1300 km) removed from the Kattegat–Baltic Sea connection, suggesting that the crab is either capable of extremely long-distance migrations, is introduced regularly to this location by humans, or can reproduce at lower-than-expected salinity. The latter possibility is consistent with a report of ovigerous mitten crabs in the River Odra, Poland, where the salinity of the Baltic Sea is only 8.3‰ (M. Normant, personal communication). Clearly, further research is required to establish the lower salinity requirement for successful reproduction in this species. If the crab is capable of successfully reproducing in lower-salinity waters, migration distances around the Baltic Sea could be much lower than those considered here, increasing suitable habitat in and around the Baltic Sea greatly.

We did not incorporate salinity in our model for several reasons. We were concerned with invasion of freshwater habitats, where salinity is very low; use of coastal salinities would have meant projecting them inland with uncertain consequences. Furthermore, although nearshore salinity data have a high resolution for Europe, such data are extremely limited for the Chinese coastline.

The accuracy of predictions for the northern European boundary may be compromised by the available data for the Asian range. For example, it is possible that populations along the northern edge of the native distribution have been undersampled or underreported in the scientific literature, considering that the area covers North Korea and eastern Siberia. If this is the case, inclusion of additional reports from areas with a cooler climate in Asia could influence the projected northern range in Europe. Nevertheless, a disproportionate number of European reports derive from central European countries, consistent with expectations from Asia.

Other factors could cause the introduced and native ranges to differ because the latter encompasses the realized niche rather than the more extensive fundamental niche. Accordingly, the release from predators, competitors, or parasites could allow a nonindigenous species to occupy a wider ecological niche than in its native range.

The continued expansion of Chinese mitten crab distribution in Europe suggests that the availability of propagules for further range expansion may also be increasing. Because this species has a biphasic life cycle, with pelagic larvae and benthic adults, numerous natural and human-mediated dispersal mechanisms may contribute to range extension. These mechanisms include advective movement of larvae; the transfer of larvae, juveniles, or adults in ballast water; natural dispersal and/or the human transfer of adults in the live food trade. As this species' distribution expands, development of programs to control the spread will become increasingly difficult to implement. Advective movements are virtually impossible to manage, although dispersal by both ballast water and intentional stocking can be controlled via legislative means.

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