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A simple range expansion model of multiple pathways: the case of nonindigenous green crab *Carcinus aestuarii* in Japanese waters

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Abstract Forecasting the range expansion of non-indigenous organisms enables effective quarantine and the development of pre-arrival countermeasures, as well as raises public and scientific concerns among the general public. Here, we present an approach to forecasting the range expansion of the nonindigenous green crab *Carcinus* in Japanese waters, with consideration of the human-mediated shipping and natural dispersal. Two types of shipping, namely, primary transport to Japan via long-distance ocean-going shipping and secondary transport within Japan via short-distance coastal shipping, were considered. The presence and absence of the crab in 50-km shoreline segments were obtained at 5 year intervals from 1985 to 2005, based on observation records by professional and amateur naturalists. Two types of dispersal kernel, namely, conventional logistic regression and a multiplicative immigration model considering multiple pathways explicitly, were compared. The multiplicative immigration model gave significantly better results. Natural dispersal was the most significant factor, in spite of its low expansion rate: secondary transport by coastal shipping was the second. Transport by international ocean-going shipping was not statistically significant, suggesting quite a small immigration probability of the crab by long voyages. Stochastic simulations forecasted that the crab will invade most of the coasts of western Japan along the Pacific Ocean and Seto Inland Sea by 2055, and will become widespread all over the country by 2205. Quarantine scenarios to eliminate transport by vessels revealed that preventing crab transport by domestic coastal vessels may delay the arrival of crabs in Hokkaido and the northern Japan area by 700 years at maximum.

Introduction

The human-mediated introduction of marine nonindigenous species (NISs) beyond their natural ranges has been of great public and scientific concerns because of its serious impacts on native marine biodiversity and industries. Forecasting the range expansion of nonindigenous marine organisms enables effective quarantine and pre-arrival countermeasures, and raises concerns among the general public. Through such forecasting, we can determine quarantine areas including regions where

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NISs will arrive in the near future (sometimes already established but not yet detected), and thus concentrate much effort for the early-detection and emergency control of areas where NISs will soon appear. We can also start planning for the timely reduction in damage just before invasion, and design a map that will accurately show the spread of the distribution range; this will raise much concern among the general public, which is necessary for obtaining public consensus on countermeasures.

Various mathematical models for predicting range expansion have been developed and applied to the study of many invasive species in the terrestrial and freshwater ecosystems (Lubina and Levin 1988; Shigesada and Kawasaki 1997; Grosholz 1996). The first step in the development of range expansion models is to study population growth and diffusion in a spatially homogenous area (e.g., Skellam 1951). The second step is to consider population dynamics with a spatially realistic habitat-patch distribution using a geographical information system (GIS) (e.g., Lurz et al. 2001; Broadfoot et al. 2001), however; much effort is necessary to obtain population parameters. Another step is to simplify the model by applying metapopulation dynamics dealing with presence or absence of organisms in unit-habitats to the prediction of range expansion (e.g., Koike 2006; Facon and David 2006), which requires essential information, namely, the habitat patch distribution and an organism's distribution maps for different years (Hanski 1998). As the next step in the metapopulation approach, various pathways through human-mediated transport are considered here together with natural dispersal (Ruiz et al. 1997; Wasson et al. 2001; Vander Zanden and Olden 2008). In the present paper, we propose an immigration kernel that multiplies probabilities by such various pathways instead of a conventional logistic function (Havel et al. 2002; Komuro and Koike 2005). A similar multiplicative model has been developed to consider habitat quality and a propagule arrival (Leung and Mandrak 2007; Fukasawa et al. 2009). However, we simultaneously consider multiple pathways in our model.

The green crab of the genus *Carcinus*, native to Europe and North Africa, has been receiving much attention because of its success as a global invasive predator in coastal ecosystems (Grosholz and Ruiz 1995). It has been invaded in eastern North America

(Carlton and Cohen 2003), western North America (Cohen et al. 1995), South Africa (Le Roux et al. 1990), Australia (Thresher et al. 2003) and Argentina (Hidalgo et al. 2005). The green crab was first recorded in 1984 within the bay of Tokyo Metropolitan area in Japan (Sakai 1986; Muraoka 1996), and subsequently found in isolated coasts of large cities (Fig. 1). Future range expansion and damage are now an issue of concern.

The green crab is a large littoral species that lives for 4–6 years (Furota et al. 1999; Yamada et al. 2005). It belongs to the swimming crab family Portunidae. However, it lacks swimming legs suggesting the lesser swimming ability of adults of this species than of adults of species of other genera. It has a planktonic stage in its ontogeny. For the species, ballast water and hull fouling has been considered as the major medium for introduction (Carlton and Cohen 2003); however, Otani (2004, 2006) considered only hull fouling as the major pathway.

Two species are recognized in the genus; the Atlantic green crab *Carcinus maenas* (Linneus 1758) native to Atlantic Europe and northwest Africa, and the Mediterranean green crab *Carcinus aestuarii* Nardo 1847 (old name *C. mediterraneus* Czerniavsky 1884) native to the Mediterranean Sea, Black Sea and the Sea of Azov (Almaça 1989; Yamada and Hauck 2001; Roman and Palumbi 2004). There is some mixing of the two species near the Strait in Morocco (Clark et al. 2001). Invaded crab populations other than those in Japan (Pacific and Atlantic North America, Australia, Africa, etc.) have been identified as *C. maenas*. All of the Japanese invaded crab population has been identified as *C. aestuarii* based on morphology (Yamada and Hauck 2001), although some *C. maenas* genes have been found based on genetic analysis (Geller et al. 1997; Bagely and Geller 2001; Darling et al. 2008). In this study, we call the Japanese crab population to be *C. aestuarii*, because of morphology and major part of genetic composition is common to *C. aestuarii* (Darling et al. 2008).

Green crabs are omnivorous predator (Chen et al. 2004) feeding on many resources including Asian date mussel, *Musculista senhousia* (Mistri 2004). It has caused a serious negative impact on commercial fisheries (Morgan et al. 1980; Cohen et al. 1995; Lafferty and Kuris 1996; Grosholz and Ruiz 1995, 1996). A rapid phenotypic change in prey intertidal snails with the occurrence of this predator (Vermeij

Fig. 1 Sites where *Carcinus aeatuarii* was discovered in Japan from 1984 (first record, asterisk) to 2008. Only older records are plotted for the locations where the species was found more than once. The figure was drawn from the records by Watanabe (1995, 1997, 2000), Nabeshima et al. (1997), Tamura (1999), Chen et al. (2003), Iwasaki et al. (2004a), and Doi et al. (2009). *HK* Hokkaido Island, *HS* Honshu Island, *SK* Shikoku Island, *KS* Kyushu Island
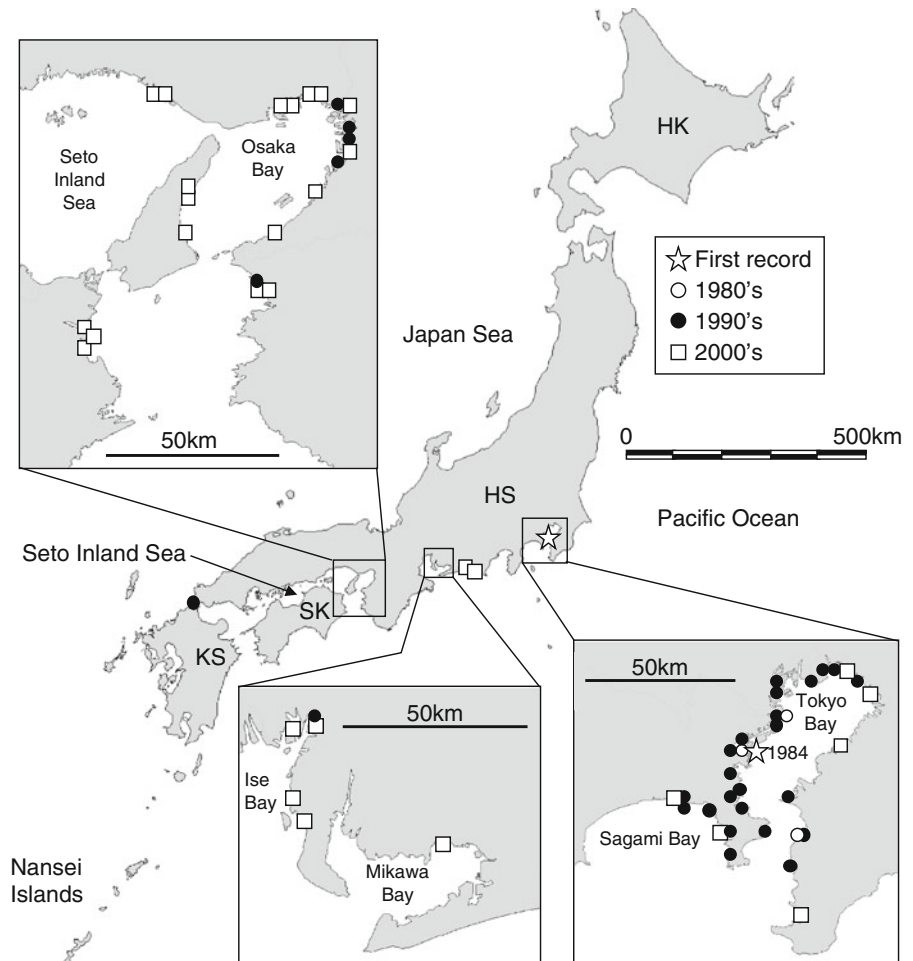
1982; Seeley 1986; Trussell 2000) suggests a strong impact on native ecosystems, although the total effect on native ecosystems has not yet been elucidated (de Rivera et al. 2005).

Adult crabs live in shores, and larvae spread as planktons. The propagules of such marine organisms (e.g., larvae in ballast water, and adults or juveniles in hull fouling) transported via shipping can be repeatedly supplied to major ports (Drake and Lodge 2005; Costello et al. 2007; Jerde and Lewis 2007). Natural range expansion often starts from such major ports, and secondary transport via domestic shipping can also occur from such areas. Range expansion models should include such human-mediated transport together with natural dispersal (Ruiz and Carlton 2003).

Here, we present a metapopulation approach to the prediction of range expansion of the crab assuming a 50-km coastal line as a "unit-habitat" to record the presence or absence of the green crab (Fig. 2). The range expansion of the crab introduced into Japanese waters is forecasted based on the 50-km coastal segments. In this approach, we develop a model including both natural dispersal along the shoreline and human-mediated transport via shipping as factors promoting such range expansion. Then we examine the effects of human-mediated transport on future range expansion to assess the validity of quarantine.

Materials and methods

Potential environmental tolerance

To infer the potential distribution range of *C. aestuarii* in Japan, the maximum and minimum seawater temperatures at the surface were compared between 25 native locations (3 locations in the Sea of Azov, 4 in the Black Sea, 18 in the Mediterranean Sea) and 38
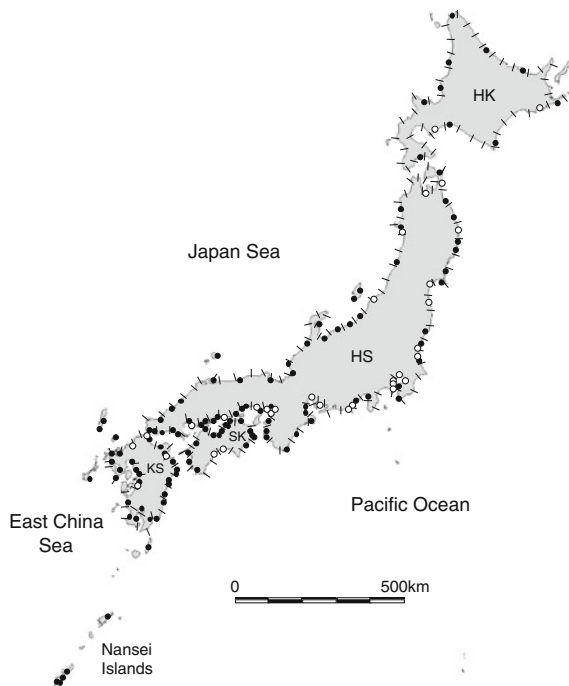
Fig. 2 Locations of 185 50-km shoreline segments and 166 major ports (*circles*) including 33 ports where ocean-going vessels carrying imports from the countries along Mediterranean Sea called in 2005 (*open circles*). For abbreviations, see Fig. 1

Fig. 3 Thermal matching of *Carcinus aestuarii* between the native regions (*open symbols*) and Japan (*closed symbols*). A *bold dotted area* indicates the range of thermal regime suitable for the survival of *C. aestuarii* based on Mediterranean data. *EHI* Eastern Hokkaido Island, *Nansei* Nansei Islands

locations in Japan (8 locations on the Hokkaido Island, 25 on the Honshu, Shikoku and Kyusyu Islands, and 5 on the Nansei Islands; Japan Oceanographic Data Center (2008), http://www.jodc.go.jp/index_j.htm). Then the average annual maximum and minimum seawater temperatures for 41 years from 1962 to 2003 in the native locations and for 97 years from 1906 to 2003 in Japan were calculated.

The average maximum and minimum temperatures in the native regions showed ranges of 20–30°C and 0–20°C, respectively (Fig. 3). The thermal ranges on the western Hokkaido island and on the Honshu, Shikoku, Kyushu Islands in Japan were within that for the native regions. The thermal conditions at four locations on the eastern Hokkaido Island (EHI in Fig. 3, east of 143°E) and at five locations on the Nansei Islands (Nansei in Fig. 3, south of 31°N) were outside the native thermal range. On the eastern Hokkaido Island, however, the Mediterranean mussel *Mytilus galloprovincialis*, whose native region (i.e., Sea of Azov, Black Sea and Mediterranean Sea, Gosling 1992) is similar to
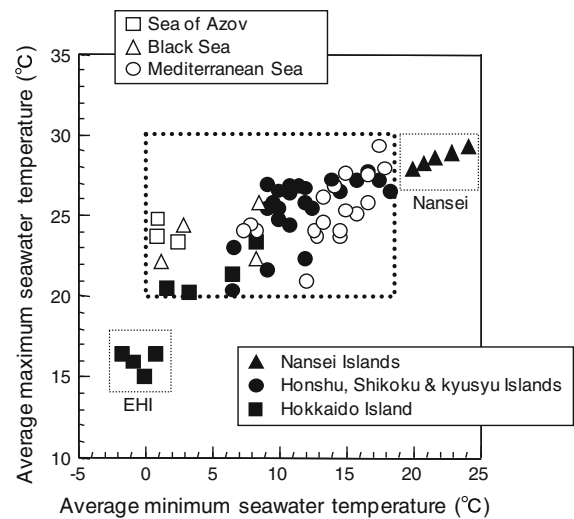
that of *C. aestuarii*, has become widespread after the 1990s (Iwasaki et al. 2004a; Iwasaki 2006). The northern ends of the native ranges of *M. galloprovincialis* and *C. aestualii* in the Mediterranean area is limited by the European Continent, and such Mediterranean species have not yet tried to expanded their distribution into lower-temperature areas. The potential coldest limit of the closely related *C. maenas* covers the Hokkaido Island (Carlton and Cohen 2003), and the potential range of distribution for *C. aestualii* likely includes the eastern Hokkaido Island. Thus we included all of Hokkaido Island, except the Nansei Islands, for the regions covered for forecasting.

Historical range expansion in Japan

We used published data on historical distribution (Takeda and Horikoshi 1993; Watanabe 1995, 1997, 2000; Nabeshima et al. 1997; Tamura 1999; Chen et al. 2003; Iwasaki et al. 2004a, b; Iwasaki 2006; Doi et al. 2009). The data was based on observations by professional and amateur zoologists collecting marine invertebrates. Since their observations cover almost all the shores in Japan, we assumed that the area where the crab was not found to be not immigrated. The existence of the crab was summarized in 50-km

coastal segments (Fig. 2) for every 5 years from 1985 to 2005. Data before 1985 was not included because people scarcely knew about the green crab at that time, and we were concerned that the observation effort by naturalist might be quite smaller than that in the years after 1984 when the crab was first record in Japan.

Trade activity

Data on the ocean-going shipping volume and coastal shipping volume in metric ton in 2005 were obtained from the Annual Statistical Report 2005 on Imports and Coastwise Vessel Transport, which was published by the Transport Research and Statistics Office, Information Security, Research and Statistics Division, Ministry of Land, Infrastructure and Transport (2008) (http://toukei.mlit.go.jp/saisintoukei.html#ryuudou). The statistical report was the latest available at the time of our study, We considered cargo vessels (including bulk carriers, container ships and tankers) only, because such cargo vessels are dominant, more than 4 times greater than other types of vessels in total gross tonnage, both in ocean-going and coastal shipping in Japan (Ministry of Land, Infrastructure and Transport 2000–2005, http://toukei.mlit.go.jp/k-toukei/01/01a0 pdf.html). Imports via ocean-going shipping were those transported from 13 countries around the Mediterranean Sea, Spain, France, Italy, Croatia, Greece, Turkey, Cyprus, Syria, Israel, Egypt, Tunisia, Algeria and Morocco. We could not distinguish Mediterranean Sea side and Atlantic Sea side in Spain and France. Shipping from all these countries were summed and assigned to 50-km segments to which destination ports in Japan belong. We did not consider other countries because *C. aestuarii* is only found in the Mediterranean area, except for the invaded populations in Japan. The coastal shipping volumes for all of the 166 major ports in Japan (Fig. 2) were summarized into a segment × segment matrix.

Immigration models

A 50-km coastal line was considered as unit-habitat for recording the presence or absence of crabs in the metapopulation model (Fig. 2). *C. aestuarii* inhabits wave-sheltered shores near or within bays or estuaries in its native region (Yamada and Hauck 2001) and Japan (Furota and Kinoshita 2004; Doi et al. 2009). In Japan, generally, a 50-km coastal line contains both small capes and bays, and each segment contains a potentially suitable site for the crab. Thus, we considered no differences in habitat suitability among 50-km segments.

In the logistic immigration kernel, the incidence probability p of the crab in a 50-km coastal segment was determined using the logistic equation,

$$p = \frac{\exp(ax + by + cz + d)}{1 + \exp(ax + by + cz + d)} \tag{1}$$

where x is the distance (m) from the nearest source habitat considering natural range expansion. A source habitat is a 50-km segment already inhabited by the crab. The distance was measured as a center-to-center distance between segments travelled on the sea. y is the weight of cargo (metric ton) carried by coastal vessels between major ports in Japan (coastal shipping volume) as a proxy of propagule pressure via secondary transport from an invaded location to an uninvaded location in Japan. z is the weight of import cargo (metric ton) carried by ocean-going vessels from the Mediterranean Sea to ports in Japan (ocean-going shipping) as a proxy of propagule pressure via repeated primary transport from the source region. a, b, c and d are regression constants ($a \leq 0$).

In the multiplicative kernel, the incidence probability of the crab in a 50-km coastal segment is

$$p = d(1 - f), \tag{2}$$

where f is the probability that the crab failed to arrive at the segment via all the pathways simultaneously and d ($0 \leq d \leq 1$) is a regression constant. d can be a function of habitat quality (Fukasawa et al. 2009); however, we considered it as a constant, since we used a large spatial scale, that is, a unit-habitat including at least several suitable sites in it. The probability that all pathways fail in causing immigration is the product of three probabilities: that immigration by natural dispersal does not occur, that immigration by domestic transport does not occur, and that immigration by international transport does not occur.

$$p = d\left\{1 - (1 - I_n)(1 - I_d)(1 - I_g)\right\} \tag{3}$$

Here, I_n is the immigration probability by natural dispersal, I_d is that by domestic shipping, and I_g is that by international shipping. We consider natural immigration as a negative exponential function of the distance from the nearest source segment.

$$I_n = \exp(ax) \tag{4}$$

Here, a ($a \leq 0$) is the regression constant determining the shape of the immigration kernel. Negative exponential function has often been used for the immigration kernel (e.g., Fukasawa et al. 2009). We assume a saturating curve for the relations between immigration probability and shipping volume (Fig. 4);

$$I_d = 1 - \exp(by)$$

and

$$I_g = 1 - \exp(cz), \tag{5}$$

where b ($b \leq 0$) and c ($c \leq 0$) are regression constants. If the shipping volumes (y and z) are sufficiently large, the immigration probabilities (I_d and I_g) are close to unity. The overall incidence probability is written as,

$$p = d[1 - \{1 - \exp(ax)\} \exp(by) \exp(cz)] \tag{6}$$

!In both immigration kernels, the presence or absence of the crab in 50-km coastal segments was used as dependent variable, and all parameters were determined by the maximum likelihood method (e.g. Sokal and Rohlf 1995) using Solver of Microsoft Excel with randomized initial values. Akaike's Information Criteria (AIC, Akaike 1974) were used for model selection, considering all combinations of pathways. AIC represents goodness of fit, and smaller AIC means the better fitting with fewer parameters. We combined all periods of 5 year interval to a dataset, and obtained the average dispersal rate from 1985 to 2005.

Standard deviations of parameters were determined with the bootstrap method (Efron and Tibshirani 1993). In bootstrapping the trials to determine a parameter set with a randomly re-sampled dataset was iterated 20 times, and each trials gave slightly different parameter values due to difference in stochastically re-sampled data. The standard deviation (SD) of parameters by different trials were calculated.

Simulations

Future range was predicted by simulation. The crab distribution in 2005 was used as the initial state. The probability that the crab is present in each 50-km coastal segment after 5 years was calculated using Eq. 6, and the presence or absence was determined stochastically using random numbers. The crab range expansion was simulated using GIS software developed by one of the authors (Koike 2009, Minna de GIS, http://www13.ocn.ne.jp/~minnagis/). The center-to-center distance between 50-km coastal segments travelled on the sea was determined as a distance matrix using the same GIS software. Shipping volume by vessels in 2005 was used throughout the simulation.

In order to evaluate the accuracy of prediction, we iterated bootstrap-trials based on parameter sets obtained from re-sampled datasets. In each bootstrap-trials we iterated 100 simulations using a given parameter set, and invasion probability of each segment was obtained. We calculated the standard deviation (SD) of the invasion probability within boot strapping. Small SD means reliable prediction.

To assess the effectiveness of quarantine to slow down range expansion, a simulation under the assumption that no artificial immigration by shipping occurs, was carried out. It may be quite difficult to stop natural range expansion, however; we can start studies on the methods to prevent unintentional crab transport by shipping, if artificial transport contributed greatly to the range expansion.

Fig. 4 Estimated natural immigration probability $d \exp(ax)$ in Eq. 4 and the human-mediated immigration probability by coastal shipping, $d[1 - \exp(by)]$, in Eq. 5 of *C. aestuarii* in Japan based on the distribution data from 1985 to 2005. *Curves* were drawn based on the parameters on Table 1
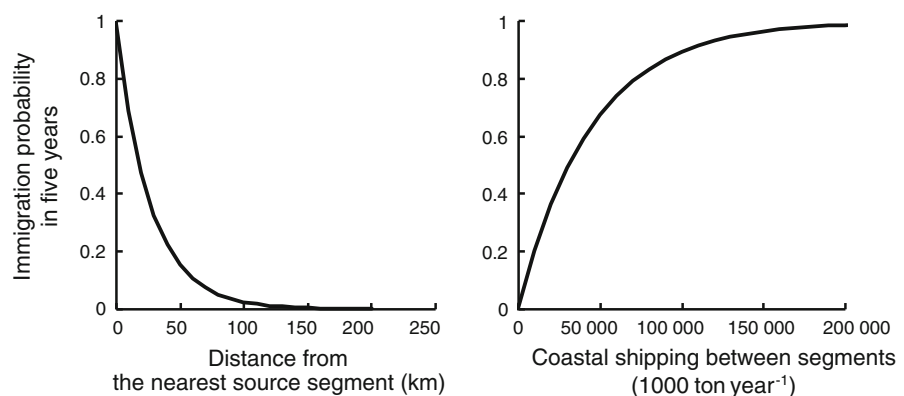
In order to assess natural range expansion rate, we simulated range expansion in a hypothetical straight coast. We assumed straight coast with two-hundred 50-km coastal segments, and the crab started to spread from the one end of the hypothetical coast. The average range expansion rate of distribution front (where invasion probability = 0.95) was measured by simulation.

Results

Pathways

Considering immigration probability by various pathways explicitly, the multiplicative model (Eq. 6) was significantly better than the logistic model (Eq. 1) (Table 1), and we used the multiplicative model in the latter part of the study. The distance from the nearest source population was highly significant (Table 1). Its ΔAIC, indicating the magnitude of effects on the regression when the variable is excluded from the regression equation, was highest among the three independent variables. Coastal domestic shipping was also significant, and its ΔAIC was relatively high. Ocean-going shipping was not significant in the variable selection. These results indicate that natural dispersal along the shoreline was the most important factor in range expansion in the past, and that secondary domestic transport via coastal shipping was also significant. Primary transport of the crab from its native region via ocean-going shipping was statistically not detected at least between 1985 and 2005.

The distance-dependent natural immigration probability was 2.37% for 5 years in a vacant segment 100 km distant from the source area (Fig. 4, calculated from Table 1). It was less than 1% when the distance exceeded 200 km. When the total coastal shipping volume from the infested area was 5,000,000 ton year^{-1}, it resulted in a new artificial immigration probability of 10.6% for 5 years (Fig. 4, calculated from Table 1). The immigration probability was less than 1% when the shipping volume was less than approximately 500,000 ton year^{-1}.

Simulations and significance of quarantine

In the simulation, the green crab first spread on the southern coasts of the western Honshu Island and on the coasts around the Seto Inland Sea (Fig. 5). Then it immigrated to some major ports on the Hokkaido Island and northern Honshu Island, which it has not yet infested as of 2006. Then a gradual range expansion occurred from these major ports.

By 2015, the probability of invasion will exceed 10% in 40 currently uninvaded segments on the southern coasts of the western Honshu Island and on the coasts around the Seto Inland Sea. By 2030, the green crab will invade those coasts with a probability higher than 40%, and infest large ports on the Hokkaido Island at a probability of 82%. The probability of invasion in large ports in the central Japan Sea will become 29%. By 2055, ca 50 years from now, the crab will spread from several large ports, and inhabit nearly half of the number of the segments (81/185) at a probability higher than 50%.

Table 1 Result of parameter estimation for the logistic model (Eq. 1) and the multiplicative immigration model (Eq. 6) of three independent variables on the range expansion of the noindigenous green crab *Carcinus aestuarii* in Japan from 1985 to 2005

Variable	Logistic kernel AIC = 153.17		Multiplicative kernel AIC = 106.80		
	Parameter	ΔAIC*	Parameter	SD	ΔAIC*
Regression constant (d)	−1.559	–	0.9995	4.67×10^{-5}	–
Shortest distance from invaded segment (a)	-6.488×10^{-6}	51.53	-3.75×10^{-5}	8.79×10^{-6}	178.72
Coastal shipping volume (b)	1.945×10^{-7}	9.42	-2.20×10^{-8}	6.42×10^{-9}	57.20
Ocean-goings shipping volume from Mediterranean region (c)	4.338×10^{-6}	1.28	–	–	–

Smaller AIC (Akaike's Information Criteria) means the better fitting. ΔAIC indicates the magnitude of effects on AIC when the variable is excluded from the regression equation, and the larger ΔAIC means that the independent variable is more important. Standard deviation (SD) of the variable was determined by the bootstrap method
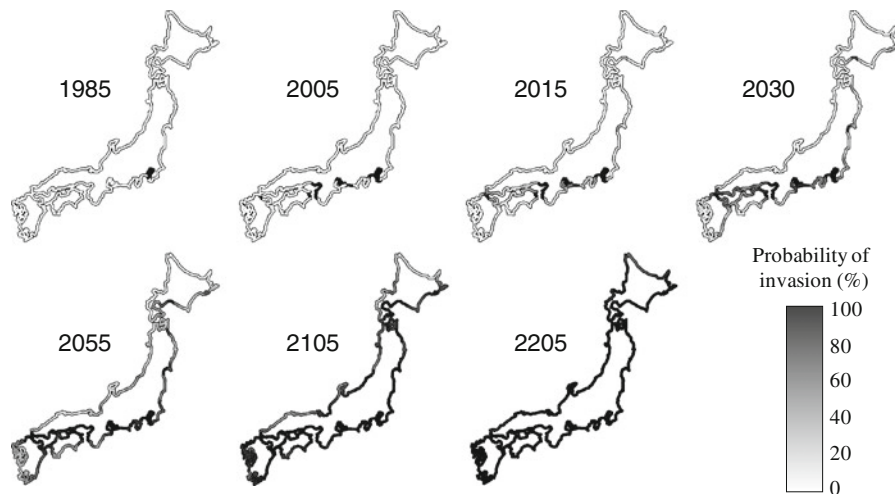
Fig. 5 Forecast of range expansion of *Carcinus aeatuarii* using a model considering two pathways: natural range expansion represented by nearest distance, and human-mediated shipping represented by coastal shipping volume. The average incidence in 100 iterated simulations is shown

Fig. 6 Uncertainty of *Carcinus aeatuarii* range expansion simulation in Japan. Standard deviation (SD) of simulated invasion probability by a bootstrap method was shown
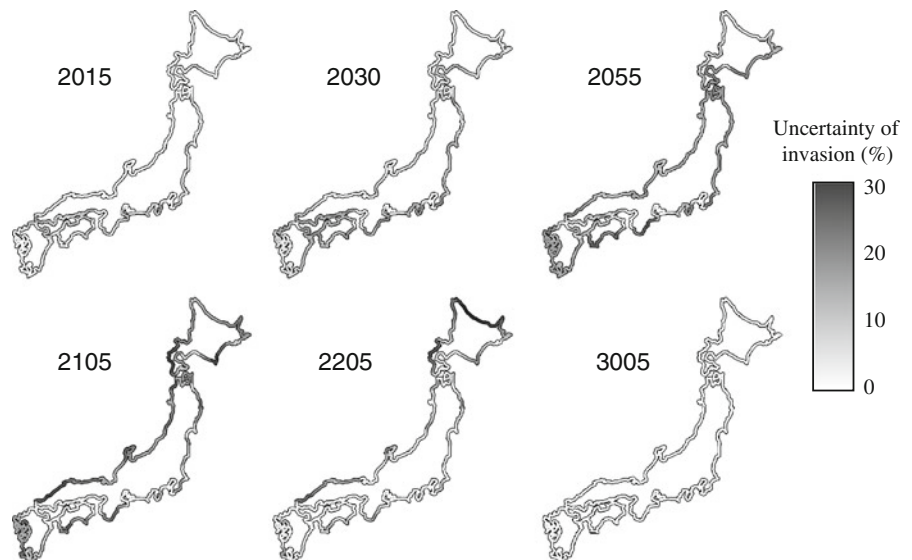

Almost all the coasts in Japan (159/185 segments) will be invaded with a probability higher than 50% by 2105, about 100 years from now. By 2205, all potentially inhabitable Japanese coasts will be invaded by the green crab with a probability higher than 60%, which will then exceed 95% by 2305, about 300 years from now.

The range expansion simulation was generally reliable, because standard deviation (SD) of the invasion probability in bootstrapping was less than 30% (Fig. 6). The reliability of prediction became smaller at the front

of range expansion, Pacific coasts in 2030, and northern areas in 2205. However, green crabs finally spread all shores in our all trials. SD in 3005 was nearly zero in all shores meaning complete invasion.

To assess the effectiveness of domestic quarantine within Japan, the immigration pathway by domestic coastal shipping was excluded from the simulation model (Fig. 7). The effect was quite significant especially in the northern area of Japan, on the Hokkaido Island and on the Japan Sea side of the northern Honsyu Island. The crab spread gradually

Fig. 7 Prediction of range expansion of *Carcinus aeatuarii* by natural range expansion using a model excluding the effect of human-mediated shipping. Only the distance-dependent natural range expansion was considered. The average incidence in 100 iterated simulations is shown
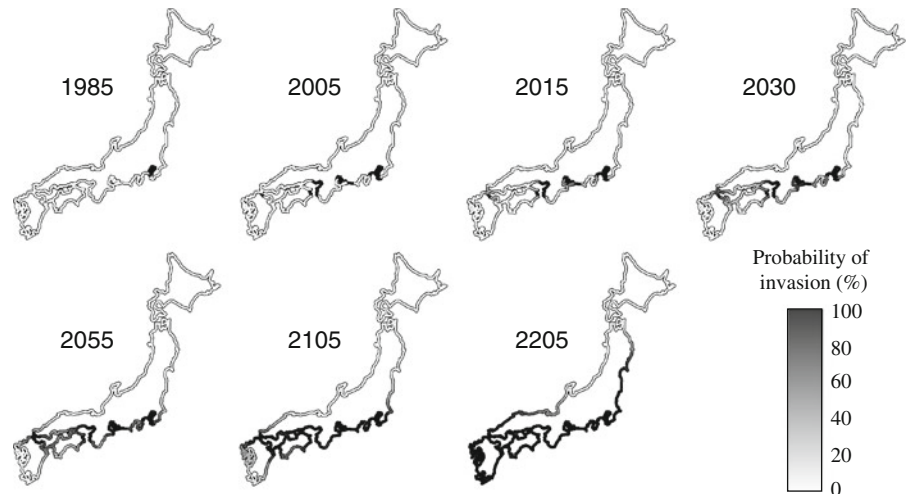
only from the current distribution range, and more than one-third (69/185) of the number of segments will not be infested even after 300 years. All coasts will be invaded about 1000 years from now (Fig. 8).

Discussion

Pathways, rate and pattern of range expansion

Natural range expansion was the first surest pathway for the expansion of the green crab (Table 1). Domestic coastal shipping was the second surest factor, although it can cause longer-distance range expansion than natural dispersal (Figs. 7, 8). No ocean-going shipping from the native range was detected using the model (Table 1), although it can cause the longest-distance range expansion beyond ocean. Our results suggest that the primary introduction of the Mediterranean green crab (*C. aestuarii* phenotypically) from its native range in the Mediterranean Sea may be a rare event (Table 1), and it occurred only at once from a site at the border of *C. maenas* and *C. aestuarii* native ranges (Darling et al. 2008). The world distribution of invaded green crabs supports this hypothesis; all Japanese isolated populations have unique genetic composition having major parts of genes from *C. aestuarii* with a smaller fraction from *C. maenas* (Darling et al. 2008), whereas those in regions other than Japan (e.g., Pacific and Atlantic North America, Australia, and Africa) are *C. maenas* (Carlton and Cohen 2003; Darling et al. 2008).
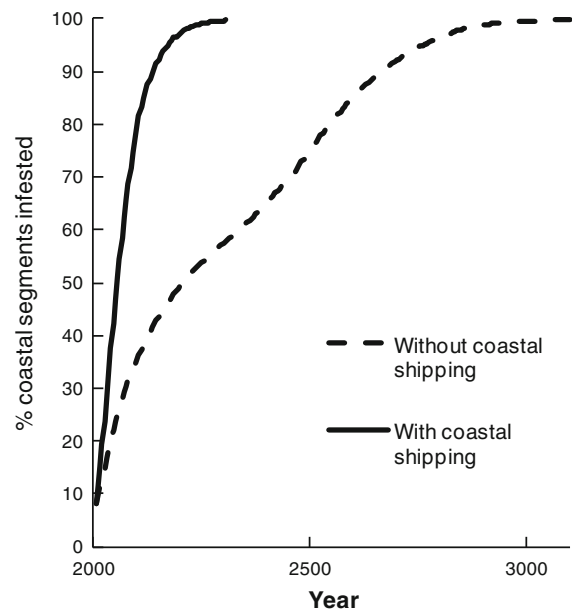

Fig. 8 Length of invaded coasts (in percentage) of Japan in two simulations of range expansion with (Fig. 5) and without (Fig. 7) human-mediated shipping pathway

The difference between international ocean-going shipping and domestic coastal shipping may be in absolute distance (about 17,500 km from the Mediterranean Sea to Tokyo, and 1,000 km from Tokyo to Kyusyu; World Port Distance http://www.distances.com), and the difficulty in voyage through high-temperature tropical oceans where the crab cannot maintain its population (Carlton and Cohen 2003).

The average range expansion rates of the green crab by natural dispersal are quite slow: 1.7 km year^{-1} in Australia (Thresher et al. 2003) and 1.55 km year^{-1} in our simulation of natural range expansion in a hypothetical linear coast. Although the planktonic duration of the green crab is about 50 days at maximum (Roff et al. 1986; Lindley 1987; Queiroga 1996), planktonic larvae might not contribute significantly to long-distance dispersal beyond ocean.

Effectiveness of quarantine

Reducing propagule pressure by coastal shipping was quite effective in delaying range expansion (Figs. 7, 8). An ecosystem without green crabs can be maintained for more than 700 years, if propagules on ships can be removed completely. However, already infested areas include economically important harbors, and simple shipping ban may not be agreed.

Development of harmless anti-fouling systems (surface treatment, non-toxic coating, copper-based paints and other devices removing sessile organisms mechanically and chemically), and also the actual application to coastal ships will be effective to reduce the propagule pressure because post-larval crabs can inhabit among fouling organisms and be transferred to a distance (Coutts and Taylor 2004). Some authors assumed that ballast water is also a possible pathway (Carlton and Cohen 2003). If this is the case, we will be able to prevent green crab transfer by many methods under development such as offshore exchange and mechanical, chemical and/or heat treatments for ballast water (Rolim 2008).

Simulation and forecast in future

The multiplicative immigration model, which explicitly deals with various pathways, was significantly better than the conventional logistic model (Table 1). The multiplicative immigration model in this research describes actual process of invasion through multiple pathways, i.e. invasion at least one pathway among many pathways can causes invasion (Eq. 3). However in logistic regression, linear link of multiple pathways (Eq. 1) does not represent such real process. The multiplicative immigration model for multiple pathways will be used in forecasting the range expansion of various nonindigenous organisms.

In the simulation, we assumed shipping data as of 2005, however; shipping will change depending on economical activities in the world in the future. The immigration of crabs is a stochastic process, and a stochastic establishment in habitats far from the source population will change the range expansion pattern. Sudden range expansion sometimes occurs depending on unusual ocean conditions (Thresher et al. 2003; Yamada et al. 2005). In this research, we predicted average range expansion based on current knowledge, but we need to update the forecast based on the latest information.

The nearest population of another green crab species (*C. maenas*) is on the west coast of North America, about 7,000 km from Japan. The world range expansion model, which does not distinguish between ocean-going shipping and coastal shipping, will clarify the risk of range expansion of these populations to Asia.

Predicting the future range expansion of nonindigenous organisms will enable the development of pre-arrival countermeasures, as well as raise concerns among the general public, which is necessary for the consensus development of countermeasures. Biological invasions sometimes cause very long-timescale hazards as in the case of green crabs, whereas policy makers are usually interested in very short time horizons. Visualization of our range-expansion simulation can cause concerns for very long-timescale hazards caused by biological invasions. We provide a range expansion forecast of nonindigenous organisms at http://vege1.kan.ynu.ac.jp/forecast/, and we plan to provide an updated forecast of the green crab.

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