



Potential for high-latitude marine invasions along western North America

Catherine E. de Rivera^{1,2*}, Brian P. Steves^{1,2}, Paul W. Fofonoff¹,
Anson H. Hines¹ and Gregory M. Ruiz^{1,2}

¹Smithsonian Environmental Research Center,
PO Box 28, Edgewater, MD 21037, USA,

²Aquatic Bioinvasion Research and Policy
Institute, Environmental Science and
Management, Portland State University, PO
Box 751 (ESM), Portland, OR 97207-0751,
USA

ABSTRACT

Aim High-latitude regions host many fewer non-native species than temperate ones. The low invasion loads of these colder regions may change with increases in human-mediated propagule supply. We test the hypothesis that colonization by non-native species that have already invaded temperate shorelines would be precluded by environmental conditions if they were introduced to Alaska and other high-latitude regions by shipping or other vectors.

Location Pacific coast of North America as well as coastal oceans world-wide.

Methods Using 16 habitat descriptors in ecological niche models, we characterized the conditions throughout the native and introduced distributions of four marine species (*Amphibalanus improvisus*, *Carcinus maenas*, *Littorina saxatilis* and *Styela clava*) that have invaded multiple global regions to test the extent to which suitable conditions for these species exist in Alaska and other high-latitude regions under current and predicted future climate scenarios.

Results Models projected environmental match for all four species in many areas beyond their present range limits, suggesting that Alaska and other high-latitude shorelines are currently vulnerable to invasion by non-native species that occur in lower latitudes.

Main conclusions Given current and possibly increasing human-mediated species transfers and suitable environmental conditions that exist now and with projected warming, policy and management efforts are urgently needed to minimize invasion opportunities at high latitudes.

Keywords

Abiotic resistance, *Amphibalanus improvisus*, biological invasions, *Carcinus maenas*, environmental niche model, *Littorina saxatilis*, *Styela clava*.

*Correspondence: Catherine E de Rivera,
Smithsonian Environmental Research Center,
PO Box 28, Edgewater, MD 21037, USA.
E-mail: derivera@pdx.edu

INTRODUCTION

Biological invasions by non-native species are an important force of change in coastal marine ecosystems (Carlton, 2001; Grosholz, 2002; Teck *et al.*, 2010). The reported number of non-native marine species has been increasing in many global regions, driven largely by human-mediated spread through trade (Cohen & Carlton, 1998; Kerckhof *et al.*, 2007; Meyerson & Mooney, 2007). Although increasing in most places, non-native species are not distributed uniformly across the globe. A key question is whether habitats or locations with a low invasion load (considered here low non-native species richness) have a high resistance to invasion. Low abiotic resistance and magnitude of propagule pressure both affect the likelihood of establishment or invasion success (Lonsdale, 1999; Rouget & Richardson, 2003; Lockwood *et al.*, 2005). For marine and estuarine systems, this

largely translates to (1) the presence of critical temperature, salinity, depth and perhaps substrata to meet the physiological requirements of a species and (2) opportunities for species transfer especially via vessel movements, mariculture or other vectors (Ruiz *et al.*, 2000; Herborg *et al.*, 2007).

To date, relatively few non-native species are reported from high-latitude (polar and subpolar) marine systems (Barnes *et al.*, 2006; Aronson *et al.*, 2007; Ruiz & Hewitt, 2009). This pattern is illustrated along western North America, where there is a steep decline in the documented number of non-native species with increasing latitude from California to Alaska (Ruiz *et al.*, 2011). Over 250 non-native species of invertebrates and algae are considered established in marine and estuarine waters in California. Within western North America, most of these species were first recorded in California, and many have spread northward (Cohen & Carlton, 1995; Ruiz *et al.*, 2011). In sharp

contrast, < 15 non-native species are known from marine waters in Alaska, most of which were only reported within the past decade (Ashton *et al.*, 2008; Lambert *et al.*, 2010; Ruiz *et al.*, 2011; S. Cohen, personal communication). While this overall spatial pattern of invasion could result partly from bias in the existing literature, standardized field surveys of sessile invertebrate communities found that non-native species richness decreased strongly with latitude across this range in western North America (de Rivera *et al.*, 2005a; G. Ruiz unpublished data).

The paucity of high-latitude invasions may result from any combination of (1) a low supply of non-native organisms (propagules) relative to temperate regions; (2) a lack of environmental conditions required physiologically for survival, reproduction and growth; (3) lack of retention in advective environments (e.g., Byers & Pringle, 2006); or (4) biological interactions with resident communities that limit establishment. The historical level of human activities in the coastal zone at high latitudes has been minimal, suggesting that opportunities for human-mediated species transfers have been relatively low (Barnes *et al.*, 2006; Ruiz & Hewitt, 2009). While extreme temperatures likely create a significant barrier to colonization in polar regions (Aronson *et al.*, 2007), it is not clear the extent to which this exists for invasion of subpolar coastal waters, such as those in Alaska below the Arctic Circle.

In this study, we use projections from ecological niche models to test whether abiotic conditions limit potential northward range expansion and invasion of Alaska by non-native species already established in western North America. We are interested broadly in whether species that have invaded temperate waters have the capacity to establish at high latitudes. We focused on Alaska as a model to examine the potential for such high-latitude invasions, especially given the large pool (number) of non-native species already present in adjacent southern regions (California–British Columbia). Our analyses examine the potential range of four species, which are established in western North America, and were selected to include three distinct Phyla (four Orders) and represent a wide spectrum of species traits (see Methods). We also evaluate the effect on geographic distribution of a moderate increase in seawater temperature, as may be expected from climate change. Suitable environmental ‘match’ in high latitudes for the species examined here would indicate that Alaska and other regions are at risk to invasion, given sufficient propagule supply, and suggest that management efforts to reduce human-mediated dispersal to high latitudes deserve serious consideration. If environmental mismatch, abiotic resistance, would prevent the establishment, even under increased thermal regime, management efforts may be more efficiently focused elsewhere.

METHODS

Study organisms

For our analyses, we selected four non-native marine species that represent distinct taxonomic groups, are established in

coastal habitats in western North America and also differ in their life history characteristics, habitat requirements and native ranges. These species include the barnacle *Amphibalanus improvisus* (Darwin, 1854), the crab *Carcinus maenas* (Linnaeus, 1758), the snail *Littorina saxatilis* (Olivi, 1792) and the tunicate *Styela clava* (Herdman, 1881). Importantly, each species is morphologically distinctive and readily recognized, providing confidence in the taxonomic identity of existing records. Furthermore, these particular species also had enough geographically referenced occurrence data, across many global regions, for building credible models. The occurrence data used in the models is given in Appendix S1.

Amphibalanus improvisus, the bay barnacle, is a filter feeder that occurs across a wide range of salinities. It reproduces from 10–20°C and 2–40 PSU (Bousfield, 1955; Furman & Yule, 1991) and has planktonic larvae that, after around 18 days (Lang & Marcy, 1982), settle on hard substrate, often in high abundance. Its settlement on hard substrate has economic impact as it fouls boat hulls and power plants (e.g., Gren *et al.*, 2009). It competes with native organisms in the recipient ranges and has been implicated in a trophic cascade in the Baltic (Kotta *et al.*, 2006). Native to the western Atlantic, from Argentina through Canada, *A. improvisus* has invaded the north-east Atlantic, south-east Pacific, north-east Pacific and north-west Pacific (Appendix S1). Its first established population in western North America (north-east Pacific) was in San Francisco Bay, California, in 1853. The species was detected subsequently in Willapa Bay, Washington, and southern Vancouver Island, British Columbia, in 1955, 102 years after it established in California. The northernmost record in 2005 was Port Alberni, Vancouver Island, British Columbia (49.2369° N latitude).

Carcinus maenas, the European green crab, has planktonic larvae that spend one to 2 months in the water column. Adult green crabs occupy nearshore waters and commonly occur in bays. It reproduces from 3–17 °C and 13–54 PSU (Broekhuysen, 1936). Native to the eastern Atlantic from Mauritania to Norway, it has invaded six other regions: north-west Atlantic, south-west Atlantic, south-east Atlantic, south-west Pacific, north-west Pacific and north-east Pacific. In many regions, it has a narrow latitudinal range (e.g., Argentina and South Africa, Australia, and Japan; Appendix S1). *Carcinus maenas* can achieve high abundances and have strong effects as a predator on benthic invertebrates (Grosholz *et al.*, 2000; de Rivera *et al.*, 2011) and has been designated as an aquatic nuisance species in the United States (Grosholz & Ruiz, 2002).

In contrast to the *A. improvisus* invasion, the expansion of *C. maenas* in the north-east Pacific has been rapid so far. First reported to be established in San Francisco Bay, California, in 1990, the crab reached nearby Bodega and Tomales Bays to the north, and Monterey Bay to the south, by 1993. It was reported on Vancouver Island, British Columbia (increase of 11.65° latitude), by 1999. Its north-east Pacific range extended all the way north to Kyuquot Sound, British Columbia (to 50.03333° N latitude), by 2002 (Behrens Yamada & Gillespie,

2008), representing the known northern range limit along the Pacific coast.

Littorina saxatilis, the rough periwinkle, produces crawl-away young without a planktonic larval stage. It lives throughout the littoral zone on hard substrate associated with marshes and rocky shores, where it grazes biofilms and algae from hard substrates. It occupies intertidal areas with salinities from 5 to 35 and temperatures -2 to 35 °C (Reid, 1996; Sokolova & Pörtner, 2003). While *L. saxatilis* has not had reported impacts in its recipient range, grazing by congeners along the Atlantic coast has been shown to greatly alter habitat (Carlton, 1999). Native to both sides of the north Atlantic, from Spain to Norway (to 80° N) and Chesapeake Bay, Virginia to Canada (to 68.5° N), it has a more extensive poleward range than the other species (Fig. S1:4). This snail has been reported as introduced in a very narrow range in each of the north-east Pacific and south-east Atlantic (Carlton & Cohen, 1998).

In the north-east Pacific, *Littorina saxatilis* was first detected in San Francisco Bay, California, in 1993 (Cohen & Carlton, 1998). Although it has increased its local distribution and abundance in this bay (G. Ruiz, personal observation), it has not yet been reported elsewhere along the coast. Although *Littorina saxatilis* does not have a planktonic life stage, it may spread by human-mediated dispersal or rare dispersal events (e.g., rafting on current-transported items). Johannesson (1988) suggested that such direct larval development (brooding) and low adult mobility may enhance the likelihood of establishing new populations.

Styela clava, the solitary club tunicate, has short larval duration (<2 days). This sessile, filter feeder is a common component of the sessile invertebrate (fouling) community in the temperate areas it inhabits, colonizing ship hulls, pilings, rock, and other hard substrata. It withstands temperatures of -2 to 27° C and salinities 18–35 PSU (Lutzen, 1999; Davis & Davis, 2008). Native to the north-west Pacific from China through Russia, *S. clava* has spread to both coasts of North America, Europe, Australia and New Zealand. It competes with other sessile filter feeders in the recipient regions and can have significant impacts on commercial shellfish (Lutzen, 1999; LeBlanc *et al.*, 2003). The species was first reported for the north-east Pacific in 1933 in Newport Bay, California. It invaded San Francisco Bay, California, by 1949. In 1993, *S. clava* was detected in Coos Bay, Oregon, as well as further north in the Strait of Georgia, British Columbia (49.35° N latitude, an increase of 15.74° from Newport Bay).

Niche modelling

We used ecological (or environmental) niche modelling to project the fundamental niche space for these organisms. Environmental niche modelling is now a commonly used modelling approach for determining the potential geographic range of non-native species (e.g., Peterson *et al.*, 2003; Roura-Pascual *et al.*, 2004; Therriault & Herborg, 2008; Herborg *et al.*, 2009; Ba *et al.*, 2010), predicting changes in distribution

owing to climate change (Peterson *et al.*, 2001), and estimating distribution for conservation assessment (Anderson & Martinez-Meyer, 2004). We built ecological niche models using MaxEnt version 3.3.3a (Phillips *et al.*, 2006; <http://www.cs.princeton.edu/~schapire/maxent/>). Recent comparisons of techniques for predicting species distributions suggest that MaxEnt is a useful modelling tool that performs better than similar modelling techniques and generates projections that are well supported by subsequent field validation (Lawler *et al.*, 2006; Elith & Leathwick, 2009). It requires data on the presence of an organism as well as information about the environmental conditions where the organism is found. The statistics, components, mechanics and outputs of MaxEnt are explained for ecological data in Elith *et al.* (2011). Briefly, MaxEnt finds the probability distribution that is closest to uniform (maximum entropy) for the geo-referenced environmental parameters associated with the species occurrence records. It then uses this distribution to identify the likelihood of environmental suitability (degree of habitat and climate match) of pixels within the occurrence regions and outside (see Phillips *et al.*, 2006 and Elith *et al.*, 2011 for further explanation).

We gathered geographically referenced global occurrence records from the native and introduced ranges of the four species from a synthesis of literature, collections and museum-based records (NEMESIS 2008). We only included one presence point for every 0.5° latitude grid, as this was the spatial resolution of our environmental data (See Appendix S1 in Supporting Information, Fig. S1:1–4). We selected environmental predictor variables that could be limiting for these organisms, including 16 atmospheric, basin, geomorphic and oceanic parameters (Table 1) obtained from coastal grids in the Hexacoral Biogeoinformatics website (<http://www.kgs.ku.edu/Hexacoral/>; Fautin & Buddemeier, 2008). Projections of Maxent are not strongly affected by correlation between the covariates (predictor variables) (Elith *et al.*, 2011). These data, primarily derived from satellite readings, were compiled by NASA and NOAA and covered oceans from latitudes 59 – 75° S to 73 – 77° N (all areas except where there was ice cover that prevented chlorophyll readings). The software uses the minimum common set of pixels across all of the environmental layers, and tidal range and run-off were available for coastal grids only; therefore, the model automatically constrained the predictions to the coastal grids. We set the convergence threshold to 0.00001 and 500 iterations and used a random seed for selecting training points. In each run, the Maxent program randomly selected 50% of the presence data for developing a model of environmental descriptors and then used the remaining 50% of the data to test how well the model predicted the other known occurrences. In addition to the presence data (see Fig. S1:1–4), the models each used 7025 points (background plus presence), including over 6873 randomly selected background points (as there were no true absence data), to determine the distribution for training. We used 152 occurrences of *A. improvisus*, 135 of *C. maenas*, 91 of *L. saxatilis* and 98 occurrences of *S. clava* to model the

Table 1 Environmental parameters used for niche modelling.

Data type	Units*
12-month average air temperature	°C DEM interpolated
Standard deviation of 12-month average air temperature	°C DEM interpolated
Average min. monthly air temperature	°C DEM interpolated
Average max. monthly air temperature	°C DEM interpolated
Average monthly basin run-off	m ³
Max. bathymetry	m, ETOPO2 value
Mean monthly sea surface temperature	°C over 18 years
Average min. monthly sea surface temperature	°C over 18 years
Average max. monthly sea surface temperature	°C over 18 years
σ average monthly sea surface temperature	°C over 18 years
Annual mean salinity	PSU
Max. monthly salinity	PSU
Min. monthly salinity	PSU
Average annual value of chlorophyll α (1997–2000)	Colour value
Interannual cell σ of chlorophyll α	Colour value
Average max. amplitude of the tides	m

*Explanation of units: ‘°C DEM interpolated’ = temperature, interpolated using a digital elevation model; ‘m, ETOPO2’ = metres relative to mean sea level, derived from satellite global relief data (2-min grid of this global DEM); PSU = practical salinity units (derived from conductivity and equivalent to parts per thousand); colour value = chlorophyll concentration estimated from the colour of the ocean.

distribution; for each species, half of these presence data were used for training and the remaining half for testing.

We built models from sampling all the occurrence data (global presence data). These models met the 50-occurrence record cut-off recommended for near-maximal accuracy in species distribution models (Stockwell & Peterson, 2002). These models consistently yielded better performance indicators than exploratory models built from sampling occurrences only from the native range or only from one established invaded range. Because biotic constraints are typically considered to be greatest in native ranges (e.g., Keane & Crawley, 2002; Torchin *et al.*, 2003), native-range-only models could be based on a restricted, realized niche rather than, as assumed by ecological niche models, the fundamental niche. The effects on predictions of biotic interactions or of lack of dispersal to an area with different environmental conditions are more likely to be minimized by using multiple and complete ranges (Phillips *et al.*, 2006; Alexander & Edwards, 2010). Such models should best meet the assumptions of ecological niche modelling and so improve predictions of the geographic potential of invaders.

Maxent estimates which parameters contribute most to model results by jackknife tests on each of a series of models built with parameters singly and by excluding each parameter sequentially. In assessing the contributions of the models, test gain and area under the receiver operating characteristic curve (AUC) better inform extrapolation than does training gain, while training gain informs which parameters are most important in predicting the training data.

We also examined how the geographic potential of the four species would change given global warming, again using MaxEnt. To align the input data with expected increases in temperature, we used the program R to add the projected zonal temperature increase for 2080–2099 relative to 1980–1999 determined by Intergovernmental Panel on Climate Change (IPCC) models on the zonal means over the ocean for annual mean surface warming under the A2 scenario (Meehl *et al.*, 2007). For every 10° latitude mark, we took the value from the IPCC plot and added it to the current values for that latitude $\pm 5^\circ$ latitude. We added these latitudinally adjusted temperature increases to the mean, maximum and minimum sea surface and air temperature values. We did not change the standard deviation of the temperatures. We used these elevated temperatures along with the other environmental variables (unchanged) and all available occurrence data. This simplified model of global climate change identifies how average projected temperature increases may affect the potential range of these temperate species in high latitudes and elsewhere.

A priori, we decided only to use models that had low error in leaving out known areas of occurrence (omission) and in falsely including areas that lack known occurrences (commission). In addition, a binomial test of omission for each model evaluated whether the occurrence data used to test the model provided significantly better-than-random agreement with the model by comparing the number of test occurrence records inside the predicted presence area – given a selected threshold – and ones outside the predicted presence area to the occurrence distribution from random predictions.

We used the ‘minimum training presence’ or ‘lowest presence threshold’ as our threshold for this binomial test and to explore projections of potential range. We used this as our threshold because it is a conservative prediction, providing the minimum predicted area with no omission of the known training occurrence points (Pearson *et al.*, 2007). We examine minimum training presence as well as two additional thresholds to account for different levels of omission that are useful for different applications in the Supplementary material (see Appendix S2), where we also present the cumulative logarithmic output of predicted probability world-wide.

RESULTS

Forecasted ranges and capacity for northward spread

All models projected environmental match in Alaska for each of the four species, indicating that current environmental conditions do not prevent colonization there (Figs 1–4). For *A. impropisus*, our analysis indicated that suitable conditions occur through to Prince William Sound and a few points north of the Aleutian Islands (to 61.0–61.5° N). The potential ranges of *Carcinus maenas* (to 61.0–61.5° N) and *Littorina saxatilis* (to 64.5–65.0° N) extended further north and also include the Aleutian Islands. The capacity for northward spread was greatest for the periwinkle *L. saxatilis*, as it presently has the

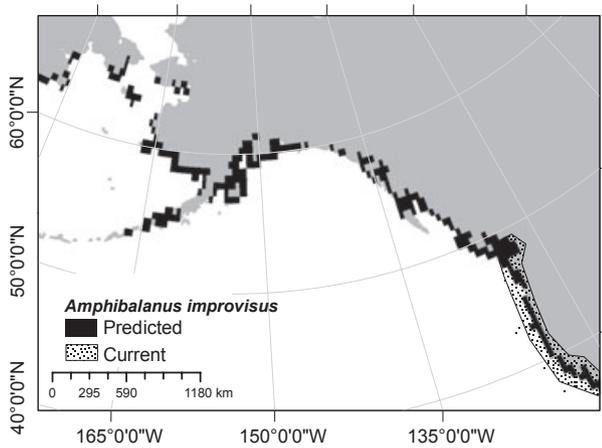


Figure 1 Map of the geographic potential of *Amphibalanus improvisus* for the west coast of northern North America projected onto NAD1983 Alaska Albers Equal Area Projection (false easting: 0.000000, false northing: 0.000000, central meridian: -154.000000, standard parallel 1: 55.000000, standard parallel 2: 65.000000, latitude of origin: 50.000000). The current non-native distribution along the coast is indicated by a broad, stippled polygon, while the potential distribution of the species predicted by the Maxent model, using a threshold that minimized the training presence, is plotted in black.

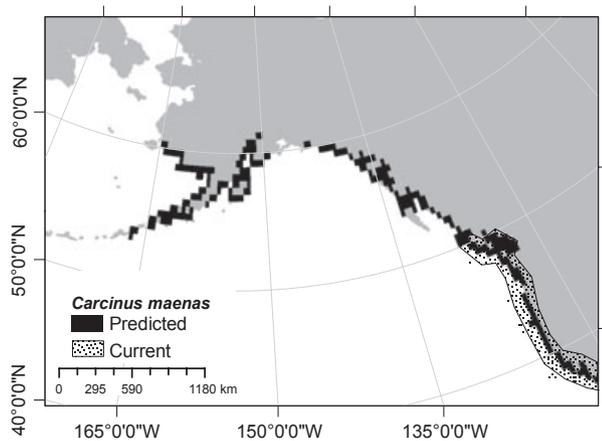


Figure 2 The geographic potential of *Carcinus maenas* projected onto NAD1983 Alaska Albers Equal Area Projection. See Fig. 1 caption for explanation of the shading.

most restricted distribution on the eastern Pacific coast (occurring only in San Francisco Bay, as shown in Appendix S1) and our models projected high environmental match in most temperate areas up to 65° latitude (Fig. 3, Appendix S2 Fig. S2.3). Potential distribution further north was most restricted for the tunicate *Styela clava* (to 58.5–59.0° N) as suitable environmental conditions only extended to north-western Canada and a few areas of south-eastern Alaska; however, conditions were suitable for it at higher latitudes in other parts of the world (see Appendix S2 Fig. S2.4 for map).

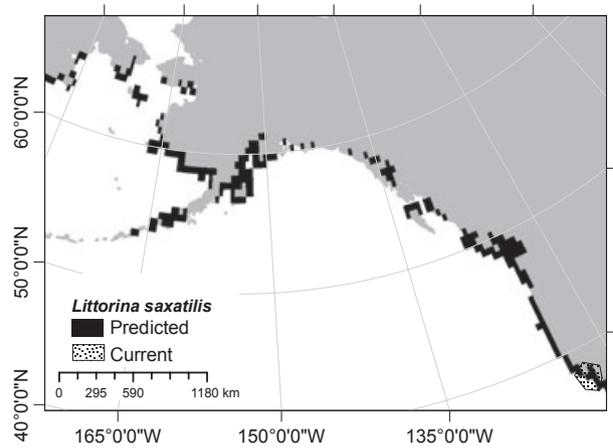


Figure 3 The geographic potential of *Littorina saxatilis* projected onto NAD1983 Alaska Albers Equal Area Projection. See Fig. 1 caption for explanation of the shading.

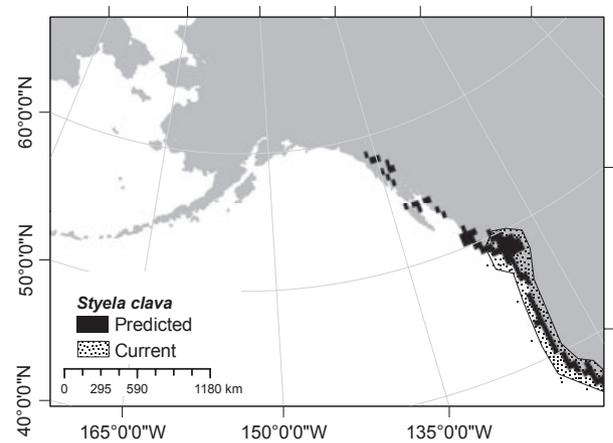


Figure 4 The geographic potential of *Styela clava* projected onto NAD1983 Alaska Albers Equal Area Projection. See Fig. 1 caption for explanation of the shading.

On a global scale, the suitability of Alaskan waters is not unique, as other high-latitude areas also offer environmental match for these species (see Appendix S2, Figs S2.1–S2.4). Moreover, our analyses projected that the potential ranges for all four species include new global regions (coastlines) as well as expanded regional distributions. Environmental match was projected for *A. improvisus* world-wide from 55° S to 60° N latitude and even includes the 69.5–70° N cell in Norway. Suitable abiotic conditions occur north and south of the present distributions of *C. maenas*. The potential range of *L. saxatilis* extends north of the Arctic Circle in several areas, reaching 70° N latitude in Greenland and Europe (Svalbard) and 72.5–73° N in Russia, and south to the tip of South America. Compared with the other three species, *S. clava* had the most restricted potential range yet would find suitable abiotic conditions in eight distinct coastlines, three not yet invaded by it, and could reach 65.5° N in Norway.

Potential effects of climate change

Warming across latitudes is forecasted to nudge poleward the limits for these species, with large potential range shifts for all four species (Figs 5–8). Our models predicted that the largest northward shifts in Alaska, given warming, would occur for *A. improvisus* (to the 68.5–69.0° N cell) and *L. saxatilis* (to 70.0–70.5° N on the west coast of North America). Geographic potential would also expand for *C. maenas* (to 64.5–65.0° N cell) and *S. clava* (to the 61.0–61.5° N cell) on the west coast of North America. Given warming, the potential global range was projected beyond the Arctic Circle for all four species (see

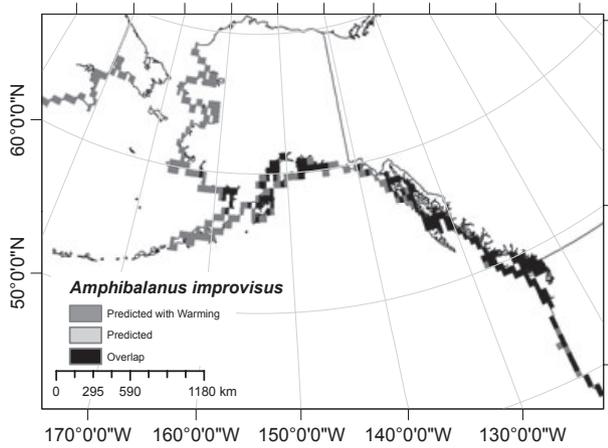


Figure 5 The geographic potential of *Amphibalanus improvisus* given the annual mean surface warming predicted by the Intergovernmental Panel on Climate Change A2 scenario projected onto NAD1983 Alaska Albers Equal Area Projection. Pixels predicted to be suitable for the species given present conditions are shaded light grey, pixels predicted to be suitable given warming are shaded dark grey, and pixels predicted to be suitable under either scenario are shaded black.

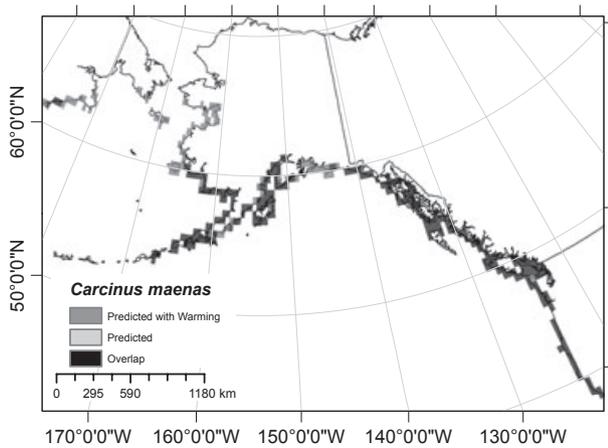


Figure 6 The geographic potential of *Carcinus maenas* given Intergovernmental Panel on Climate Change-predicted warming (A2 scenario) projected onto NAD1983 Alaska Albers Equal Area Projection. See Fig. 5 caption for explanation of the shading.

Appendix S2, Figs S2.5–S2.8): *A. improvisus* (to 71–71.5° N in Norway), *C. maenas* (to 71–71.5° N in Norway), *L. saxatilis* (to 76–76.5° N in Novaya Zemlya, Russia) and *S. clava* (to 71.0–71.5° N in Norway). None of the species projections showed large poleward increases in the Southern Hemisphere given warming.

Evaluation of models and parameters

The predictions of the models met our *a priori* requirements for forecasting because of their low error rates, as indicated by low omission and high AUC (here the receiver operating characteristic curve is based on presence versus random rather than presence versus absence, Phillips *et al.*, 2006). Using the binomial test of omission for all potential thresholds of

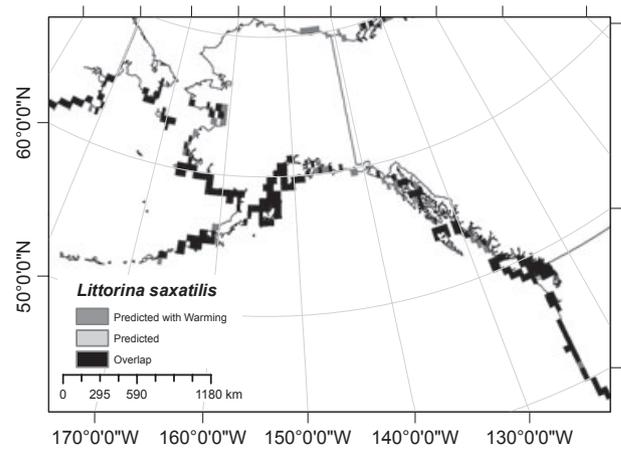


Figure 7 The geographic potential of *Littorina saxatilis* given Intergovernmental Panel on Climate Change-predicted warming (A2 scenario) projected onto NAD1983 Alaska Albers Equal Area Projection. See Fig. 5 caption for explanation of the shading.

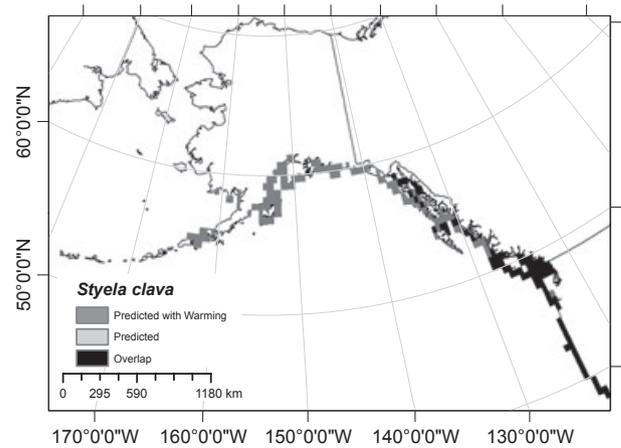


Figure 8 The geographic potential of *Styela clava* given Intergovernmental Panel on Climate Change-predicted warming (A2 scenario) projected onto NAD1983 Alaska Albers Equal Area Projection. See Fig. 5 caption for explanation of the shading.

predicting presence, the models fared very well (P always < 0.001). With our selected threshold, training omission rates were 0 and test omission rates were very low for all species (from 0.015 to 0.082, $P < 0.001$ for all). All the models had high average AUC values for the test data (*A. improvisus*: 0.879 ± 0.018 , *C. maenas*: 0.931 ± 0.009 , *L. saxatilis*: 0.904 ± 0.016 , *S. clava*: 0.943 ± 0.008) despite being based on relatively large ranges in the available space. Therefore, these Maxent models had strong predictive power, providing high confidence that they were suitable for estimating the potential range of these marine non-native species.

For all species, inclusion of mean, maximum, or minimum monthly sea surface temperature, and for some species and stage of models, mean or maximum air temperature, contributed more than the other parameters to the training gain, test gain and the AUC of the models (see Appendix S2, Table S2.1). For each model, no single variable contained a substantial amount of useful information not already contained in the other variables, but most gain was lost from the exclusion of mean run-off (*A. improvisus* and *L. saxatilis* for training models), tidal range (*C. maenas* training model) and mean chlorophyll (*A. improvisus* test model; Appendix Table S2.1).

DISCUSSION

These ecological niche model projections indicate that the current environmental conditions along the coastline of Alaska and many other high-latitude areas would not prevent successful invasion by non-native marine species with distributions now restricted to lower latitudes. Three of the four species examined – *Amphibalanus improvisus*, *Carcinus maenas* and *Littorina saxatilis* – had high potential to colonize much of the south-eastern coast of Alaska and often much more northern habitat. *Littorina saxatilis* had the most extensive potential northern distribution, reaching 62° N in Alaska as well as 65° on the west side of the Bering Sea. Moreover, all species except *C. maenas* have thus far only colonized a fraction of the potential continental margins (e.g., eastern versus western N. America) that have suitable environmental conditions for them. These projections identify potential distribution given adequate propagule pressure, retention of planktonic larvae and low biotic resistance.

While the known northern range on this coast of three of these four species is along Vancouver Island, two main factors argue against a conclusion that they cannot disperse further north. First, arrival of all three species to their current northern range limit is recent. Two of the species were first found in their northernmost locations this decade, with *A. improvisus* taking over 100 years to disperse up-coast (recorded at its current limit in 2005) and *C. maenas* being detected there in 2002. The third species, *S. clava*, has only been in its northernmost point since 1993, taking 60 years to reach this location. Second, further northward spread may go undetected for some time. While there can often be a lag-time in detecting new invasions, this is likely dependent to some extent on

search effort. Given the extensive areas and apparent low search effort north of Vancouver Island (including south-east Alaska), detections of range expansions in this region may be especially prone to long lag-time.

This study focused on testing the hypothesis that the environment excludes colonization by a subset of temperate species that have invaded the north-east Pacific. While the results from the environmental niche models strongly suggest that environmental factors are not limiting for these species, we did not evaluate other factors that also affect the risk of invasion. It appears that many non-native species are spreading northward along western North America, after their initial detection in California (Sorte *et al.*, 2010a; Ruiz *et al.*, 2011). However, the likelihood that these and other non-native marine species spread to high-latitude waters depends partly on the frequency and intensity of species transport.

Considerable opportunity exists presently for delivery of non-native species northward, including to Alaska, through human-mediated transfer. A variety of human activities result in the unintended dispersal of coastal organisms, increasing the number of invasions to recipient regions (Cohen & Carlton, 1995; Carlton, 1999; Ruiz *et al.*, 2000). Among these, shipping remains an important vector, moving large numbers of organisms in ballast tanks and on underwater surfaces (Fofonoff *et al.*, 2003). Although vessel movement and associated ballast water delivery to Alaska was historically low relative to other global regions, this is no longer the case, with over 7000 vessel arrivals in 2004 and > 4 million metric tons of ballast water discharged into Alaska in 2004–2005 (McGee *et al.*, 2006; Miller *et al.*, 2007; Ruiz & Hewitt, 2009). Both vessel arrivals and ballast water discharge are strongly dominated by coastwise traffic, arriving further south from California through Washington, a source for many non-native species already present in North America. Moreover, the level of shipping and other human activities associated with invasions is expected to increase further, especially as polar waters warm (Ruiz & Hewitt, 2009). A next step to evaluate the likelihood of invasion by a given species involves integrating models based on environmental parameters with information on the strength of vectors operating from potential source regions, as has been done for some other non-native species (e.g., Herborg *et al.*, 2009) and habitats (Keller *et al.*, 2010). Robinson *et al.* (2011), however, argue that it is more important for models of marine invasions to incorporate biotic interactions than anthropogenic transport because dispersal may not be as limiting in marine systems as terrestrial ones.

The probability of northern dispersal likely varies across the four species examined here. The barnacle and the crab, *B. improvisus* and *C. maenas*, could each be transferred to Alaskan ports via ballast water and also could spread by currents because of their relatively long-lived planktonic larvae. Prince William Sound, for example, has a high volume of ballast water from vessels arriving from areas that have been invaded by *A. improvisus* and *C. maenas* as well as many other non-native species with planktonic larvae, San Francisco Bay,

Puget Sound and Los Angeles area ports (Ruiz & Hewitt, 2009). Hull fouling of commercial and recreational vessels is a more likely vector for the tunicate *S. clava*, which otherwise has fairly restricted movement because of its short larval duration. This also provides a transfer mechanism for *A. improvisus*, as barnacles are a common constituent of biofouling assemblages. Although less well documented, aquaculture and live trade may also offer opportunities for transport of some of these species. Because it is a direct developer, the snail *L. saxatilis* likely has low propagule pressure to uncolonized regions but could disperse by rafting on algae and may have a higher per capita chance of establishment than a congener with planktonic larvae (Johannesson, 1988).

Opportunity for northward spread and establishment may also be enhanced as the potential suitable range expands with warming high-latitude waters (Ruiz & Hewitt, 2009; Walther *et al.*, 2009; Sorte *et al.*, 2010b). Our analysis has begun to explore how warming could affect forecasts of these marine species, using a coarse approach to the complex effects and repercussions of global climate change. When 1.5–7.0 °C was added to the temperature variables, with the larger increases at higher latitudes following the IPCC mapped predictions (Meehl *et al.*, 2007), the potential ranges expanded poleward in both hemispheres, although especially in the Northern Hemisphere. In addition, while models based on present conditions projected suitable conditions adjacent to and beyond already colonized areas, environmental match increased in these areas following temperature change. As warming occurs, abiotic resistance is likely to decrease in areas presently at the edge of thermal tolerances for these species, reducing the propagule pressure needed for the successful establishment of invading species (Lockwood *et al.*, 2005). Thus, probability of invasion is likely to increase with warming even without an increase in delivery of propagules. Modelling potential range shifts owing to global climate change is clearly an area that deserves more attention. Mean temperature (air and sea surface (SST)) and mean chlorophyll were important parameters to include for extrapolated projections of *A. improvisus* (areas not yet colonized or temporal changes such as global warming scenarios). For *C. maenas*, maximum monthly SST was most important to include. Mean and minimum monthly SST were most important for projecting suitability for *L. saxatilis* and mean monthly SST for *S. clava*. Additional factors are also likely important in determining distribution, but these can be undervalued in the models because of the lack of global, and typically even coastwide, data at a fine enough scale to be useful for projecting potential occurrence. Including all 16 parameters in the models allows (1) larger-scale trends from individual as well as interacting parameters to be incorporated into the projections and (2) multiple measures that may each be biologically relevant (e.g., maximum and minimum as well as mean temperature). In addition, the correlation between the predictor variables, while not decreasing sensitivity, does decrease the ability for clear interpretation about the relative contribution of each. Therefore, while temperature is likely limiting, as indicated by these models,

we discourage interpretation that other factors are not important.

In this study, the coarse (0.5°) scale of the environmental data allows the estimation of environmentally caused potential future range limits but does not consider other potential influences on distribution. This coarse scale fails to incorporate microhabitats of high ecological relevance that may serve as refugia in an otherwise inhospitable climate such as warm or algal-rich shallow water reaches of bays and estuaries that experience radiant heating over shallow flats. Because of the inability to address refugia habitats at a half degree scale, the projections are likely conservative, underestimating the potential ranges and suitable colonization sites of the modelled organisms. The projections are useful despite this limitation because they inform us that the organisms, even without use/consideration of important microhabitats, could expand their ranges much further towards the poles. Managers responsible for likely refugia beyond the projected limits should keep this caveat in mind and monitor such warmer or high retention habitats.

Our analysis does not address any biotic resistance to invasion or variability in the quality and availability of food resources, as that will require a much finer-grain analysis that also can incorporate the effects of predation or competition on habitat use. Clearly, biotic interactions are important to consider when predicting distribution (de Rivera *et al.*, 2005b). We follow Guisan & Thuiller (2005) and Mackey & Lindenmayer (2001) in recommending creation of a hierarchy of models that together capture processes that function at different spatial scales. These can, most simply, progress from coarse-scale prediction of latitudinal range limits to estuaries or parts of coastlines and finally to distribution within estuaries or coastal areas. Considering biotic factors is also an important and possible subsequent step, one modelled at a finer resolution, once abiotic match has been projected at a coarse resolution. In contrast to our findings, Compton *et al.*, 2010 suggested that *Carcinus maenas* individuals genetically similar to the southern European subpopulation are unlikely to invade northern areas. They base this suggestion on environmental match with the southern European population, which lives in warmer waters than its northern European counterpart. Four potential arguments suggest that northward colonization may not be as limited, however, as Compton *et al.* proposed. First, niche modelling projections of the west coast distribution of *C. maenas* built from the entire native range (east Atlantic) greatly outperform those built from the source of the east Pacific invasion, the north-west Atlantic invaded range (de Rivera *et al.*, 2007a). Second, there is good evidence from plants that introduced populations commonly evolve quickly to conditions similar to ones experienced somewhere in the native range of the species as a whole rather than just the source subpopulation (Alexander & Edwards, 2010). Third, from plants to vertebrates, climatic niche space has been demonstrated to shift upon colonization of a distinct region (Broennimann *et al.*, 2007; Rodder & Lotters, 2009; da Mata *et al.*, 2010; Medley, 2010). Similarly, fourth, experimental

evidence on temperature tolerances of *C. maenas* from central California, USA, versus Vancouver Island, BC, Canada, subpopulations of the north-eastern Pacific invasion suggest local thermal adaptation to the colder water in the north (Kelley *et al.* in review).

Ecological niche models provide an efficient technique for formally assessing the possibility of invasion to coastlines. The models explored here produced useful forecasts of potential future spread. They had low errors based on internal and external checks. They rarely missed predicting environmental match for existing populations. More generally, niche models offer three main advantages over other methods. They are relatively quick to execute and they often yield similar results to more labour-intensive approaches. For example, models from the temperature-dependent survival and development of *C. maenas* larvae produced identical projections but were highly labour-intensive to develop (de Rivera *et al.*, 2007b). Second, niche models provide internal assessment of the output, which boosts confidence in forecasts over informal comparisons between occurrences and surrounding environmental conditions. Unlike niche models, informal comparisons do not evaluate model performance in projecting present occurrence as well as potential occurrence. Third, ecological niche models incorporate information from multiple variables and integrate data over time, whereas other approaches are often univariate. For example, projections based only on temperature in established ranges forecasted narrower distributions for *C. maenas* in North and South American ranges than we observed (Carlton & Cohen, 2003). While there was good general concordance in regional predictions, our forecasts likely differed because more environmental parameters were used, including more (17) variables such as temperature maximum, minimum, averages and standard deviation.

This paper highlights the high potential for range expansion and invasion of Alaskan and other high-latitude coastal waters by non-native species established in more temperate areas, suggesting also that management strategies to reduce human-mediated propagule supply may prevent future invasions and deserve serious attention. Given the large pool of non-native species along western North America, any effective management strategy must address the risk of coastwise transport, which appears to be increasing (McGee *et al.*, 2006; Ruiz & Hewitt, 2009). Shipping and live trade (including aquaculture, live bait and live seafood) historically have been the dominant vectors for human transfers (Ruiz *et al.*, 2000), and both should be evaluated for potential efforts to reduce unintentional transfers to Alaskan waters. Similarly, areas with potentially high propagule pressure from these vectors should be prioritized for monitoring (e.g., commercial ports, marinas for leisure craft, aquaculture facilities), and the vectors themselves should be evaluated to minimize unintentional transfers. An obvious area for consideration is management of ships' ballast water, focused especially on coastwise traffic as a major source that has not been addressed in Alaska (McGee *et al.*, 2006; however, see recent restrictions by U.S. Environmental Protection Agency). Future models could include this

layer to predict the probability of invasion. More broadly, an opportunity now exists to prevent the extent of invasions and associated impacts seen in many other coastal regions around the globe. A comprehensive plan is urgently needed to minimize propagule supply and to implement strategies to detect and respond to invasions that pose significant risk of high impacts to the unique nearshore marine and estuarine communities of Alaska and other high-latitude coastlines.

ACKNOWLEDGEMENTS

We thank Lisa Ka'ahue, Denny Lassuy, Bob Piorkowski and Linda Shaw for comments. We also benefited from discussions with Chad Hewitt and Whitman Miller. This project was funded by a grant to GMR, AHH and CED from the Prince William Sound Regional Citizen's Advisory Council and by U.S. Fish and Wildlife Service.

REFERENCES

- Alexander, J.M. & Edwards, P.J. (2010) Limits to the niche and range margins of alien species. *Oikos*, **119**, 1377–1386.
- Anderson, R.P. & Martinez-Meyer, E. (2004) Modeling species' geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador. *Biological Conservation*, **116**, 167–179.
- Aronson, R.B., Thatje, S., Clarke, A., Peck, L.S., Blake, D.B., Wilga, C.D. & Seibel, B.A. (2007) Climate change and invasibility of the Antarctic benthos. *Annual Review of Ecology Evolution and Systematics*, **38**, 129–154.
- Ashton, G.V., Riedlecker, E.I. & Ruiz, G.M. (2008) First non-native crustacean established in coastal waters of Alaska. *Aquatic Biology*, **3**, 133–137.
- Ba, J., Hou, Z., Platvoet, D., Zhu, L. & Li, S. (2010) Is *Gammarus tigrinus* (Crustacea, Amphipoda) becoming cosmopolitan through shipping? Predicting its potential invasive range using ecological niche modeling. *Hydrobiologia*, **649**, 183–194.
- Barnes, D.K.A., Hodgson, D.A., Convey, P., Allen, C.S. & Clarke, A. (2006) Incursion and excursion of Antarctic biota: past, present, and future. *Global Ecology and Biogeography*, **15**, 121–142.
- Behrens Yamada, S. & Gillespie, G.E. (2008) Will the European green crab (*Carcinus maenas*) persist in the Pacific Northwest? *ICES Journal of Marine Science*, **65**, 725–729.
- Bousfield, E.L. (1955) Ecological control of the occurrence of barnacles in the Miramichi estuary. *Bulletin of the National Museum of Canada*, **137**, 1–69.
- Broekhuysen, G.J. Jr (1936) On development, growth and distribution of *Carcinides maenas* (L.). *Archives Néerlandaises de Zoologie*, **2**, 257–399.
- Broennimann, O., Treier, U.A., Muller-Scharer, H., Thuiller, W., Peterson, A.T. & Guisan, A. (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**, 701–709.

- Byers, J.E. & Pringle, J.M. (2006) Going against the flow: retention, range limits and invasions in advective environments. *Marine Ecology Progress Series*, **313**, 27–41.
- Carlton, J.T. (1999) Molluscan invasions in marine and estuarine communities. *Malacologia*, **41**, 439–454.
- Carlton, J.T. (2001) *Introduced species in US coastal waters: environmental impacts and management priorities*. In Pew Ocean Commissions, Arlington, Virginia, 36 pp.
- Carlton, J.T. & Cohen, A.N. (1998) Periwinkle's progress: the Atlantic snail *Littorina saxatilis* (Mollusca: Gastropoda) establishes a colony on Pacific shores. *Veliger*, **41**, 333–338.
- Carlton, J.T. & Cohen, A.N. (2003) Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *C. aestuarii*. *Journal of Biogeography*, **30**, 1809–1820.
- Cohen, A.N. & Carlton, J.T. (1995) Nonindigenous species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. Final Report to U.S. Fish and Wildlife Service and National Sea Grant Program.
- Cohen, A.N. & Carlton, J.T. (1998) Accelerating invasion rate in a highly invaded estuary. *Science*, **279**, 555–558.
- Compton, T.J., Leathwick, J.R. & Inglis, G.J. (2010) Thermogeography predicts the potential global range of the invasive European green crab (*Carcinus maenas*). *Diversity and Distributions*, **16**, 243–255.
- Davis, M.H. & Davis, M.E. (2008) First record of *Styela clava* (Tunicata, Ascidiacea) in the Mediterranean region. *Aquatic Invasions*, **3**, 125–132.
- Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology Evolution and Systematics*, **40**, 677–697.
- Elith, J., Phillips, S.J., Hastie, T., Dudik, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17**, 43–57.
- Fautin, D.G. & Buddemeier, R.W. (2008) Biogeoinformatics of the Hexacorals: <http://www.kgs.ku.edu/Hexacoral/>. Available at: http://hercules.kgs.ku.edu/hexacoral/envirodata/hex_modfilt_firststep3dev1.cfm (accessed July 2008).
- Fofonoff, P.W., Ruiz, G.M., Steves, B.P. & Carlton, J.T. (2003) In Ships or On Ships? Mechanisms of transfer and invasion for non-native species to the coasts of North America. *Invasive species: vectors and management strategies* (ed. by G.M. Ruiz and J.T. Carlton), pp. 152–182, Island Press, Washington.
- Furman, E.R. & Yule, A.B. (1991) *Balanus improvisus* (Darwin) in British estuaries: gene-flow and recolonisation. *Estuaries and coasts: spatial and temporal intercomparisons* (ed. by M. Elliott and J.P.E. Ducrotot), pp. 273–276, Olsen and Olsen, Fredensborg, Denmark.
- Gren, I.-M., Isacs, L. & Carlsson, M. (2009) Costs of alien invasive species in Sweden. *Ambio*, **38**, 135–140.
- Grosholz, E.D. (2002) Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology and Evolution*, **17**, 22–27.
- Grosholz, E.D. & Ruiz, G.M. (2002) Management Plan for the European Green Crab Submitted to the Aquatic Nuisance Species Task Force November 13, 2002.
- Grosholz, E.D., Ruiz, G.M., Dean, C.A., Shirley, K.A., Maron, J.L. & Connors, P.G. (2000) The impacts of a nonindigenous marine predator in a California bay. *Ecology*, **81**, 1206–1224.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Herborg, L.M., Jerde, C.L., Lodge, D.M., Ruiz, G.M. & MacIsaac, H.J. (2007) Predicting invasion risk using measures of introduction effort and environmental niche models. *Ecological Applications*, **17**, 663–674.
- Herborg, L.M., O'Hara, P. & Therriault, T.W. (2009) Forecasting the potential distribution of the invasive tunicate *Didemnum vexillum*. *Journal of Applied Ecology*, **46**, 64–72.
- Johannesson, K. (1988) The paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. litorea*)? *Marine Biology*, **99**, 507–513.
- Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **16**, 199–204.
- Keller, R.P., Drake, J.M., Drew, M.B. & Lodge, D.M. (2010) Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. *Diversity and Distributions*, **17**, 93–102.
- Kerckhof, F., Haelters, J. & Gollasch, S. (2007) Alien species in the marine and brackish ecosystem: the situation in Belgian waters. *Aquatic Invasions*, **2**, 243–257.
- Kotta, J., Kotta, I., Simm, M., Lankov, A., Lauringson, V., Põllumäe, A. & Ojaveer, H. (2006) Ecological consequences of biological invasions: three invertebrate case studies in the north-eastern Baltic Sea. *Helgoland Journal of Marine Research*, **60**, 106–112.
- Lambert, G., Shenkar, N. & Swalla, B.J. (2010) First Pacific record of the north Atlantic ascidian *Molgula citrina* – bio-invasion or circumpolar distribution? *Aquatic Invasions*, **5**, 369–378.
- Lang, W.H. & Marcy, M. (1982) Some effects of early starvation on the survival and development of barnacle nauplii, *Balanus improvisus*. *Journal of Experimental Marine Biology and Ecology*, **60**, 63–70.
- Lawler, J.J., White, D., Neilson, R.P. & Balustein, A.R. (2006) Predicting climate-induced range shifts: model differences and model reliability. *Global Change Biology*, **12**, 1568–1584.
- LeBlanc, A.R., Landry, T. & Miron, G. (2003) Identification of fouling organisms covering mussel lines and impact of a common defouling method on the abundance of foulers in Tracadie Bay, Prince Edward Island. Can. Tech. Rep. Fish. Aquat. Sci. 2477.
- Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.

- Lutzen, J. (1999) *Styela clava* (Herdman) (Urochordata, Ascidiacea), a successful immigrant to North West Europe: ecology, propagation and chronology of spread. *Helgolander Meeresuntersuchungen*, **52**, 383–391.
- Mackey, B.G. & Lindenmayer, D.B. (2001) Towards a hierarchical framework for modelling the spatial distribution of animals. *Journal of Biogeography*, **28**, 1147–1166.
- da Mata, R.A., Tidon, R., Cortes, L.G., De Marco, P. Jr & Felizola Diniz-Filho, J.A. (2010) Invasive and flexible: niche shift in the drosophilid *Zaprionus indianus* (Insecta, Diptera). *Biological Invasions*, **12**, 1231–1241.
- McGee, S., Piorkowski, R. & Ruiz, G.M. (2006) Analysis of recent vessel arrivals and ballast water discharge in Alaska: toward assessing ship-mediated invasion risk. *Marine Pollution Bulletin*, **52**, 1634–1645.
- Medley, K.A. (2010) Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. *Global Ecology and Biogeography*, **19**, 122–133.
- Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J. & Zhao, Z.C. (2007) Global Climate Projections. *Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change* (ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller), pp. 749–845. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Meyerson, L.A. & Mooney, H.A. (2007) Invasive alien species in an era of globalization. *Frontiers in Ecology and the Environment*, **5**, 199–208.
- Miller, A.W., Lion, K., Minton, M.S. & Ruiz, G.M. (2007) *Status and trends of ballast water management in the United States*. Third Biennial Report of the National Ballast Information Clearinghouse. U.S. Coast Guard, Washington, DC.
- NEMESIS (2008) National exotic marine and estuarine species information system. <http://invasions.si.edu/nemesis/>. Available at: <http://invasions.si.edu/nemesis/> (accessed July 2008).
- Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, **34**, 102–117.
- Peterson, A.T., Sanchez-Cordera, V., Soberon, J., Bartley, J., Buddemeier, R. & Navarro-Siguenza, A. (2001) Effects of global climate change on geographic distributions of Mexican Cracidae. *Ecological Modelling*, **144**, 21–30.
- Peterson, A.T., Papes, M. & Kluza, D.A. (2003) Predicting the potential invasive distributions of four alien plant species in North America. *Weed Science*, **51**, 863–868.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Reid, D.G. (1996) *Systematics and evolution of Littorina*. Ray Society, London.
- de Rivera, C.E., Ruiz, G.M., Crooks, J.A. *et al.* (2005a) Broad-scale nonindigenous species monitoring along the west coast in National Marine Sanctuaries and National Estuarine Research Reserves. Report to the National Fish and Wildlife Foundation. 126 p.
- de Rivera, C.E., Ruiz, G.M., Hines, A.H. & Jivoff, P. (2005b) Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. *Ecology*, **86**, 3364–3376.
- de Rivera, C.E., Steves, B.P., Ruiz, G.M., Fofonoff, P. & Hines, A.H. (2007a) Northward spread of marine NIS along western North America: Forecasting risk of colonization in Alaska waters using environmental niche modeling. Report to Prince William Sound RCAC, 64 p.
- de Rivera, C.E., Ruiz, G.M., Hitchcock, N.G., Teck, S.A., Steves, B. & Hines, A.H. (2007b) Larval development rate predicts range expansion of an introduced crab. *Marine Biology*, **150**, 1275–1288.
- de Rivera, C.E., Grosholz, E.D. & Ruiz, G.M. (2011) Multiple and long-term effects of an introduced predatory crab. *Marine Ecology Progress Series*, **429**, 145–155.
- Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P. & Richardson, A.J. (2011) Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Global Ecology and Biogeography*, **20**.
- Rodder, D. & Lotters, S. (2009) Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Global Ecology and Biogeography*, **18**, 674–687.
- Rouget, M. & Richardson, D.M. (2003) Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. *The American Naturalist*, **162**, 713–724.
- Roura-Pascual, N., Suarez, A.V., Gomez, C., Pons, P., Touyama, Y., Wild, A.L. & Peterson, A.T. (2004) Geographical potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change. *Proceedings of the Royal Society of London B, Biological Sciences*, **271**, 2527–2535.
- Ruiz, G.M. & Hewitt, C.L. (2009) Latitudinal patterns of biological invasions in marine ecosystems: a polar perspective. *Smithsonian contributions: smithsonian at the poles: contributions to international polar year science* (ed. by I. Krupnik, M.A. Lang and S.E. Miller), pp. 347–358. Smithsonian Institution Scholarly Press, Washington, D.C.
- Ruiz, G.M., Fofonoff, P.W., Carlton, J.T., Wonham, M.J. & Hines, A.H. (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics*, **31**, 481–531.
- Ruiz, G.M., Fofonoff, P.W., Steves, B., Foss, S.F. & Shiba, S.N. (2011) Marine invasion history and vector analysis of California: a hotspot for western North America. *Diversity and Distributions*, **17**, 362–373.
- Sokolova, I.M. & Pörtner, H.O. (2003) Metabolic plasticity and critical temperatures for aerobic scope in a eurythermal marine invertebrate (*Littorina saxatilis*, Gastropoda:

- Littorinidae) from different latitudes. *Journal of Experimental Biology*, **206**, 195–207.
- Sorte, C.J.B., Williams, S.L. & Carlton, J.T. (2010a) Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography*, **19**, 303–316.
- Sorte, C.J.B., Williams, S.L. & Zerebecki, R.A. (2010b) Ocean warming increases threat of invasive species in a marine fouling community. *Ecology (Washington, DC)*, **91**, 2198–2204.
- Stockwell, D.R.B. & Peterson, A. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, **148**, 1–13.
- Teck, S.J., Halpern, B.S., Kappel, C.V., Micheli, F., Selkoe, K.A., Crain, C.M., Martone, R., Shearer, C., Arvai, J., Fischhoff, B., Murray, G., Neslo, R. & Cooke, R. (2010) Using expert judgment to estimate marine ecosystem vulnerability in the California Current. *Ecological Applications*, **20**, 1402–1416.
- Therriault, T.W. & Herborg, L.M. (2008) Predicting the potential distribution of the vase tunicate *Ciona intestinalis* in Canadian waters: informing a risk assessment. *ICES Journal of Marine Science*, **65**, 788–794.
- Torchin, M.E., Lafferty, K., McKenzie, V. & Kuris, A. (2003) Introduced species and their missing parasites. *Nature*, **421**, 628–630.
- Walther, G.-R., Roques, A., Hulme, P.E. *et al.* (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology and Evolution*, **24**, 686–693.

SUPPORTING INFORMATION

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

Appendix S1 Maps of distribution of occurrence points used for constructing the models.

Figure S1.1 Occurrence records of *Amphibalanus improvisus* that were used in the ecological niche models.

Figure S1.2 Occurrence records of *Carcinus maenas* used in the ecological niche models.

Figure S1.3 Occurrence records of *Littorina saxatilis* used in the ecological niche models.

Figure S1.4 Occurrence records of *Styela clava* used in the ecological niche models.

Appendix S2 Table of the relative influence of the parameters on the models and global maps of the Maxent output for the

potential distribution of the four invasive species given current conditions or predicted future warming.

Appendix Table S2.1 Relative influence of the parameters on the models for the training gain, test gain, and the AUC of the models.

Appendix Figure S2.1 Global projected potential distribution from the cumulative output of Maxent for *Amphibalanus improvisus*.

Appendix Figure S2.2 Global projected potential distribution of *Carcinus maenas*.

Appendix Figure S2.3 Global projected potential distribution of *Littorina saxatilis*.

Appendix Figure S2.4 Global projected potential distribution of *Styela clava*.

Appendix Figure S2.5 Global projected potential distribution for *Amphibalanus improvisus* given the annual mean surface warming predicted by the IPCC A2 scenario.

Appendix Figure S2.6 Global projected potential distribution for *Carcinus maenas* given predicted warming.

Appendix Figure S2.7 Global projected potential distribution for *Littorina saxatilis* given predicted warming.

Appendix Figure S2.8 Global projected potential distribution for *Styela clava* given predicted warming.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCHES

The authors have interests in determining factors that drive patterns in marine and invasion ecology.

Author contributions: G.M.R., C.E.D. and A.H.H. conceived the ideas; P.W.F. gathered the source information; B.P.S. created the models along with C.E.D.; C.E.D. led the writing; and G.M.R. was involved in the writing and revising of the manuscript.

Editor: Reuben Keller