

**Northward Spread of Marine Nonindigenous Species along Western North America:
Forecasting Risk of Colonization in Alaskan Waters Using Environmental Niche Modeling.**

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ABSTRACT

Marine nonindigenous species (NIS) pose problems to natural resource management and conservation of coastal habitats. They are of particular concern in regions, such as Alaska, that have a wealth of natural resources and have not suffered as greatly as other regions from habitat destruction, pollution, or previous invasions. Because biological invasions are on the rise worldwide and potentially cause economic or ecological harm, it is important to develop tools to predict which areas are susceptible to species introductions. To address this goal, we examined the performance of an environmental niche modeling technique in predicting whether coastal waters of Alaska could be colonized by the northward spread of nonindigenous species present to the south.

We collected global geographically-referenced occurrence records for four species that have invaded regions outside of their native ranges, including western North America. These organisms were selected to encompass a taxonomically diverse group with different life-history and habitat distributions. Our four species were: (a) the barnacle, *Balanus improvisus*; (b) the European green crab, *Carcinus maenas*; (c) the club tunicate, *Styela clava*; and (d) the Atlantic periwinkle, *Littorina saxatilis*. We used species records along with relevant global environmental data in an environmental niche modeling framework, GARP (Genetic Algorithm for Rule-set Prediction). We projected the niche models onto nearshore habitats to visualize the potential geographic ranges of the four species in coastal Alaska and elsewhere. We tested these predictions using known occurrences from successfully established and failed introduced populations of each species. The models had low error rates and multiple runs of the models had high overlap in accurately predicting occurrence records.

Our analyses indicate that Alaskan coastal waters are at risk of invasion by nonindigenous species now present in western North America. Abiotic conditions exist in Alaska and other uncolonized regions that could support populations of all four species examined. More broadly, these results suggest that many nonindigenous species along the west coast may have the capacity for northward spread to Alaska.

Models developed from sampling all the available (global) occurrence records outperformed ones that sampled from the native range data alone, which, in turn, did better than sampling data from a single long-established invaded region. It is noteworthy that the models of *Carcinus maenas* trained with all (global) data predicted a similar but greater potential range in Alaska than results from highly labor-intensive laboratory measures of larval development under different thermal regimes. Thus, environmental niche models can provide quick, valuable, and cost-effective forecasting information as a first critical step in examining potential high risk areas for NIS.

INTRODUCTION

Background

Biological invasions by nonindigenous species (NIS) that become invasive pose problems to natural resource management, including habitat and species conservation. They increase the homogeneity of biological communities world wide, imperil threatened and endangered species, alter the structure and function of critical habitat, and impact valuable fishery and mariculture species. NIS are of particular concern in regions, such as Alaska, that have a wealth of natural resources and have not suffered as greatly as other regions from habitat destruction, pollution, or previous invasions.

Over 500 NIS established in coastal marine waters of the United States, where the observed rates and effects of invasions have increased dramatically (Cohen & Carlton 1995, 1998, Ruiz et al. 2000, Fofonoff et al. 2006). Compared to the eastern U.S., more nonindigenous marine species are reported from the western U.S. For example, over 200 NIS are known from the San Francisco Bay estuary.

A strong latitudinal pattern exists for marine invasions along western North America, with relatively few NIS reported from Alaska compared to the number of species reported from Washington, Oregon, and California (Hines & Ruiz 2000, Ruiz et al. 2000, de Rivera et al. 2005a, Ruiz et al. 2006). Many of these marine NIS were first reported in California then were subsequently reported in Oregon and Washington estuaries, suggesting northward spread along the coast (although new introductions from other sources are possible for some species). An analysis of this spread pattern is the focus of an upcoming report to Prince William Sound Regional Citizens' Advisory Council and U.S. Fish & Wildlife Service (Ruiz et al., in preparation).

We hypothesize that Alaska is susceptible to invasion by many NIS that occur to the south, from California to British Columbia. Despite the relatively low number of marine NIS presently known in Alaska, the documented NIS include a diverse array of taxa that have arrived by multiple transfer mechanisms (vectors). Several of these species have been newly reported in the past 5 years, occurring now in the southeastern part of Alaska (Ruiz et al. 2006). Importantly, considerable opportunity exists for delivery of additional nonindigenous species to Alaska, through human-mediated transfer and (for some species) larval or adult dispersal from existing populations. For example, ships provide several mechanisms for species transport, associated with ballast tanks and hulls (Fofonoff et al. 2003). This vector is especially important given the present level of vessel movement and ballast water delivery to Alaska from the other west coast states (Hines & Ruiz 2000, McGee et al. 2006). Movement of live organisms associated with aquaculture, bait, seafood imports, and aquaria trade create additional transfer mechanisms for NIS. Finally, some species are capable of dispersal and northward spread without human assistance, following an initial invasion, as suggested for the European green crab *Carcinus maenas* (Behrens Yamada & Hunt 2000; de Rivera et al. 2007).

Now that marine NIS are arriving to Alaskan waters by multiple mechanisms, a critical question is the extent to which these species can colonize. The low historical rates of invasion may result from some combination of (a) low supply of organisms (propagules) relative to other regions to

the south, (b) the lack of appropriate environmental (abiotic) conditions, or (c) biological interactions with resident communities that reduce susceptibility to invasion. The recent (1970s) onset of tanker trade into Port Valdez, cruise ships, and aquaculture efforts, however, has no doubt increased NIS propagule supply. In addition, changes in coastal waters of Alaska – from local and regional disturbances (e.g., habitat alteration, chemical discharge, fishing pressure) and global climate change – may increase susceptibility to invasions (Stachowicz et al. 1999, Stachowicz 2001). However, the ability of NIS to exploit these changes (in supply and local conditions) depends upon their physiological tolerance to local environmental conditions.

What proportion of the coastal species arriving from western states can physiologically withstand local environmental conditions? Although it is a key component to assessing the risk of invasion, there are presently several challenges in answering this question. First, we cannot rely on the current rates of invasion to gauge this risk. Many areas of Alaska have not been surveyed, and there exists no such monitoring program to provide repeated measures. Moreover, there is often a lag time, potentially lasting decades, between initial colonization and detection. Such detection lag times occur because new populations tend to have initially low population sizes and limited habitat, local, and regional distributions. Second, direct measures of physiological tolerance for individual species are very labor-intensive, requiring analysis of multiple life stages (e.g., larval, juvenile, and adult) and source populations. Multiplied by the hundreds of non-native species now resident along western North America, this species-by-species approach becomes unwieldy.

Here, we test the capacity of four different NIS to colonize Alaska from lower latitudes of western North America, using environmental niche modeling that relies upon environmental (abiotic) conditions. We assume the organisms are not dispersal-limited and can be delivered to Alaska. We estimate the potential range of these NIS along western North America. Although limited to four species, this research is intended to test the potential application of such cost-effective modeling to a large number of species and to predicted climate change scenarios.

Ecological niche modeling

Ecological niche modeling is designed to characterize the environmental conditions throughout a species' geographic distribution to determine whether this suite of habitat and climate descriptors exists in other geographic regions. This approach has potential utility across a wide range of ecological, evolutionary, and climate change questions (Peterson et al. 2001, Graham et al. 2004, Araújo et al. 2006, Araújo & Rahbek 2006). While many applications are still being evaluated, confidence in using niche modeling for longer-term predictions has been increased through studies that evaluate niche conservatism. For example, Martinez-Meyer et al.'s (2004) study on mammalian climate-based distributions over time concluded ecological niches constructed from one period can be projected onto the climatic scenario of another period to predict the geographic distribution of that time.

Ecological niche modeling can provide a powerful tool to assess the likelihood of nonindigenous species establishing in an area, once it has been transported to a region via anthropogenic or natural dispersal (Peterson & Vieglais 2001, Peterson 2003). Indeed, ecological niche modeling has been used to predict potentially invadable areas by terrestrial and freshwater aquatic species (Peterson & Vieglais 2001, Iguchi et al. 2004, Peterson et al. 2003, Herborg et al. 2007). However, it has not yet been used to predict the potential range expansion of marine species.

Here, we wish to determine whether one ecological niche modeling technique, Genetic Algorithm for Rule-set Prediction (GARP) can be used to forecast regions susceptible to establishment by non-native marine species. GARP uses correlations between known species occurrences and a suite of environmental parameters to develop a series of decision rules that best summarize the niche dimensions of the species in question. It then projects these niche dimensions onto the environmental conditions of selected areas. GARP identifies the niche dimensions through an iterative process of rule selection, testing, and selective incorporation of rules (e.g., logistic regression used to combine a subset of the environmental descriptors) that evolves through a series of small mutations in the rules.

We evaluate whether the GARP models meet two criteria, which together demonstrate predictive value for estimating the potential range of marine NIS. First, given checks with internal and independent data, the models must have low error in leaving out known areas of occurrence (omission) and have low error in falsely including areas that lack known occurrences (commission). Second, we must find high inter-model agreement between 20 iterative runs for each species. In each run, the GARP software program randomly selects half the data for developing a model of environmental descriptors and then uses the remaining half of the data to test how well the model predicts these other known occurrences. Because the training (model development) data are randomly selected and there are infinite ways of selecting the rules to envelope the environmental variables, the iterative runs can vary considerably. Hence, high agreement between different runs suggests areas that are most likely to be habitable by the species should they be introduced.

METHODS

Species

For our analyses, we selected four nonindigenous marine species that have established populations along western North America. These NIS are from different taxonomic groups, life-history types, habitat requirements, and native ranges. These include the barnacle *Balanus improvisus*, crab *Carcinus maenas*, snail *Littorina saxatilis*, and tunicate *Styela clava*. *Carcinus maenas* has been designated as an invasive, aquatic nuisance species in the United States. It is one of the few marine species with this designation and with a National Management Plan. While the other species selected for our analyses have not been designated as such, or evaluated from this perspective, each can achieve relatively high abundance and may cause ecological or economic harm.

Balanus improvisus, the bay barnacle, is native to temperate northwest Atlantic and has been introduced to the NE Pacific, NW Pacific, SW Pacific, and maybe to the NE Atlantic (Fig. 1a). This filter feeder is characteristic of brackish estuarine habitats but occurs across a wide range of salinities (Henry & McLaughlin 1975). The barnacle has planktonic larvae with extended time (18 days @ 15°C, Lang & Marcy 1982) in the plankton that settle on hard substrate.

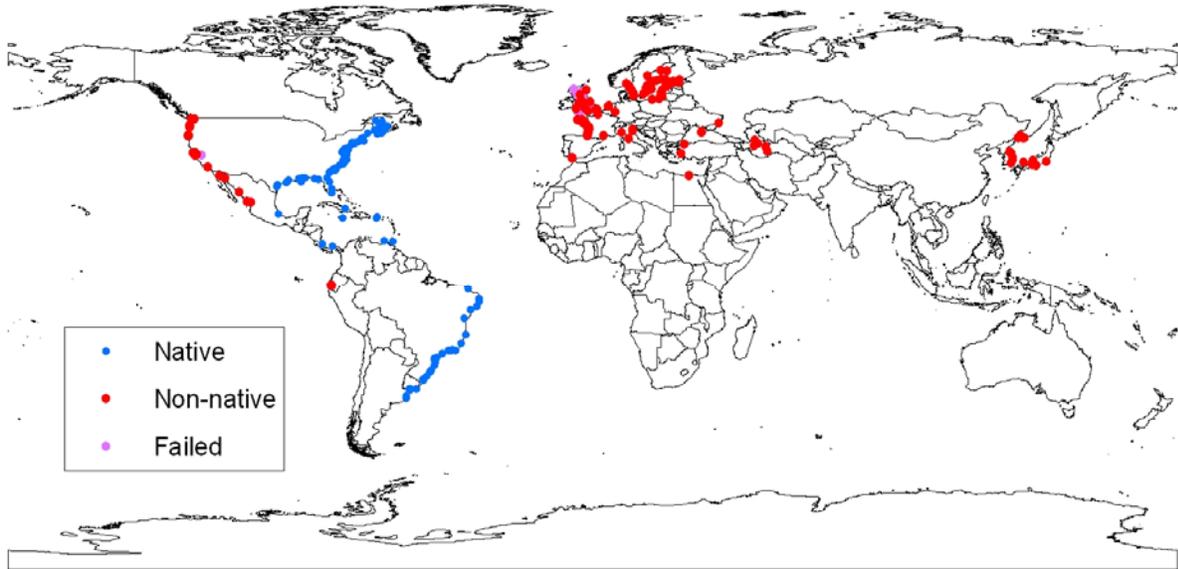
Carcinus maenas, the green crab, is native to the northeast Atlantic (Fig. 1b). It has been introduced to the NE Pacific, NW Pacific, SW Pacific, NW Atlantic, SW Atlantic, and SE

Atlantic. Larvae are planktotrophic, spending one to two months in the water column, depending on water temperature (de Rivera et al. 2007). Green crabs occupy estuarine and marine nearshore waters, and commonly occur in soft-substrate habitats of bays and estuaries. This mobile predator preys on a variety of organisms, including shellfish.

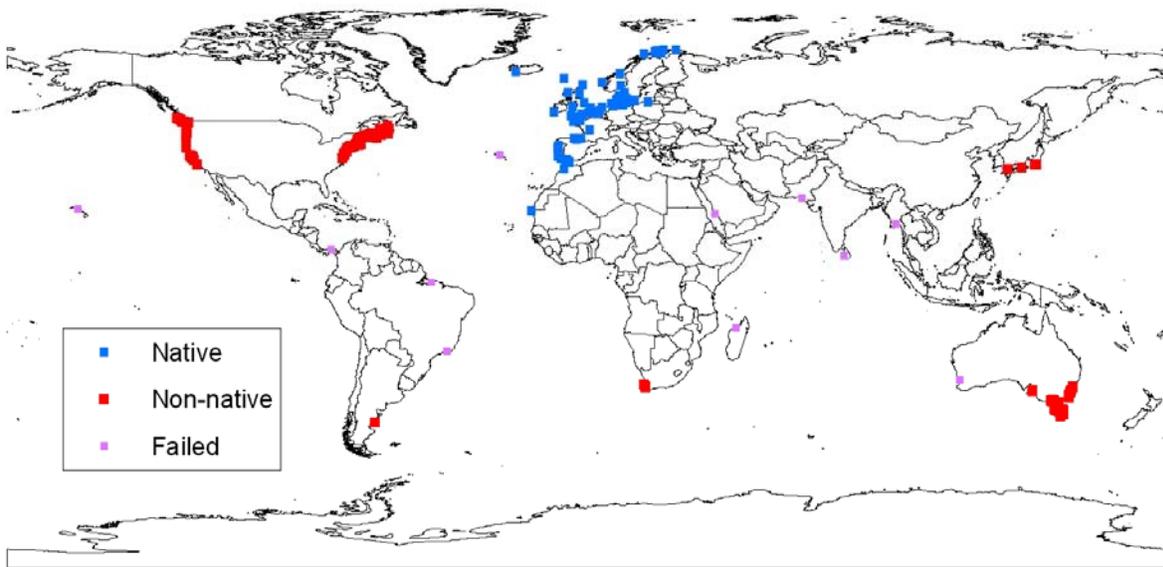
Styela clava, the club tunicate, is native to temperate northwest Pacific (Fig. 1c). It has been introduced to the NE Pacific, SW Pacific, and NE Atlantic. These solitary tunicates have much shorter larval duration (< 2 days) than the two crustaceans. A sessile species and common component of the fouling community, *S. clava* is a filter feeder.

Littorina saxatilis, the rough periwinkle, has a more polar range than the other species: it is native to both sides of the north Atlantic, from the subarctic south to Chesapeake Bay in the west Atlantic and the Strait of Gibraltar in the east (Fig. 1d). Unlike the other three species, which occur in multiple bays along western North America, *L. saxatilis* has only been found at one east Pacific location, San Francisco Bay (Carlton & Cohen 2003). Also unlike the others, this snail is direct developer so does not have planktonic larvae. It lives in the shallow subtidal to high intertidal zones on hard substrate associated with marshes and rocky shores, where it feeds by grazing on biofilms and algae on hard substrates.

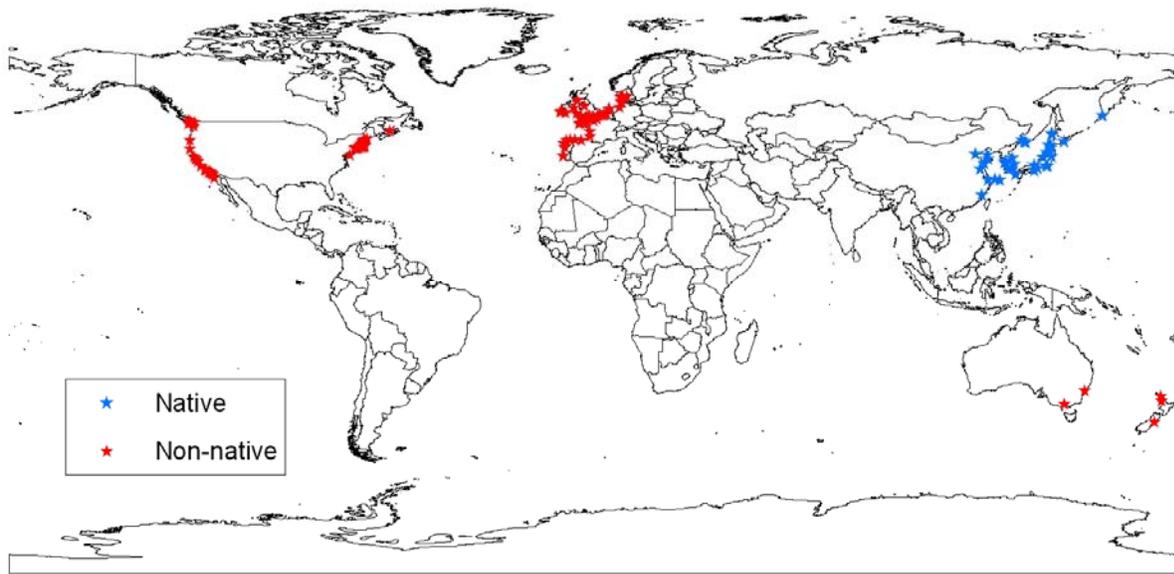
Because *Littorina saxatilis* do not have a planktonic life-stage, they appear less likely to spread intraregionally by natural currents than the other species. However, they may be spread via human-mediated dispersal or rare dispersal events (rafting on current-transported items). Based on comparative research between two littorine species, Johannesson (1988) suggested that if introduced to an area with a suitable environment, species with direct larval development (live brooder) and low adult mobility have a high likelihood of establishing new populations because offspring will hatch within the same area and remain as a dense population until sexually mature. Therefore, though *Littorina saxatilis* is not yet widespread, it is important to examine the potential northern range extension of this species as a model of species with direct larval development.



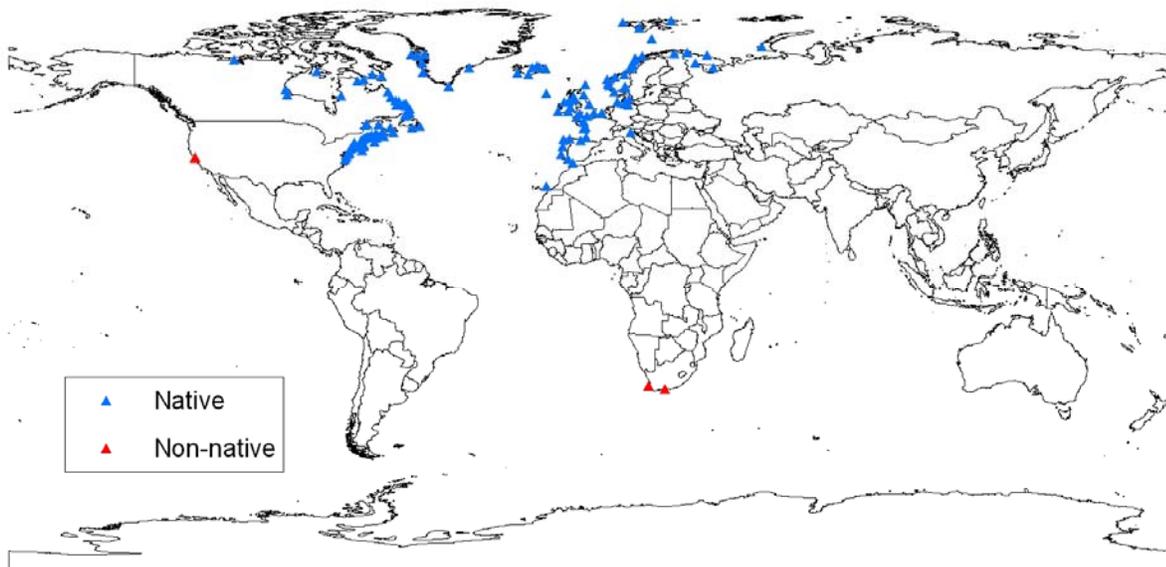
1a) Occurrence records for *Balanus improvisus*



1b) Occurrence records for *Carcinus maenas*



1c) Occurrence records for *Styela clava*



1d) Occurrence records for *Littorina saxatilis*

Figure 1. Occurrence records of the four invasive species used in GARP modeling. Blue indicates the native range, red indicates invaded ranges, and purple indicates areas where the species was introduced but failed to establish.

Data acquisition for species occurrence data

We gathered geographically-referenced global occurrence records from the native and introduced ranges of the four species. We collected this occurrence data from the Smithsonian Environmental Research Center's NEMESIS database (the National Exotic Marine and Estuarine Species Information System), which summarizes information on the invasion ecology of 500

coastal marine NIS, including records from our own collections and from museum collections, gray literature, and primary literature. We then classified the occurrences as Native, Established Non-native, and Failed Non-native based on our NEMESIS database. The geographic coordinates for these locations were all geo-referenced using a gazetteer (<http://biogeomancer.org>). We then culled the occurrence data so that we only included one point for every 0.5 degree latitude grid, as this was the scale of our environmental data. After this culling, we had a total of 207 records for *Balanus improvisus*, 47% of which were from its native range, 255 records for *Carcinus maenas*, 29% of which were from its native range, 148 records for *Littorina saxatilis*, 95% from its native range, and 141 occurrence records for *Styela clava*, 24% from its native range (Table 1).

For the models, we excluded the four occurrence records in our dataset that were classified as cryptogenic (of uncertain native versus non-native status). There were not numerous enough cryptogenic records to include in separate analyses and they could muddle the interpretations of native-only or invaded-only ranges. These included three records for *L. saxatilis*, in Greece, Portugal, and Tunisia, and one record for *C. maenas* in Sweden.

Table 1. Number of occurrence records for each species.

Species	# Native occurrences	# Established non-native occurrences	# Failed non-native occurrences	Total # occurrences used
<i>Balanus improvisus</i>	144	162	1	307
<i>Carcinus maenas</i>	74	170	11	255
<i>Littorina saxatilis</i>	140	8	0	148
<i>Styela clava</i>	34	107	0	141

Data acquisition for environmental data

We selected environmental predictor variables that observation, lab manipulation, and literature review suggested could be limiting for these nearshore, inter-tidal to shallow subtidal organisms: air and sea surface temperatures, salinity, basin runoff, tidal amplitude, bathymetry, and Chlorophyll a as a surrogate of primary productivity.

We obtained all environmental data from the metadata available at the Biogeoinformatics of Hexacorals website, <http://www.kgs.ku.edu/Hexacoral/>, specifically, http://hercules.kgs.ku.edu/hexacoral/envirodata/hex_modfilt_firststep3dev1.cfm. We included seventeen environmental parameters, including atmospheric, basin, geomorphic, and oceanic parameters for all the coastal and oceanic cells. We used the following variables: the 12-month average, the standard deviation of the 12-month average, the average minimum monthly, and the average maximum monthly air temperature (° C, all DEM interpolated); the average monthly basin runoff (m³); the minimum and maximum bathymetry (m, ETOPO2 value); the mean monthly, average maximum monthly, average minimum monthly, and the standard deviation of the average monthly sea surface temperature (° C, all across 18 years); the annual mean, maximum month, and minimum month salinity (PSU); the average of the mean annual pixel values, the average annual value (1997-2000), and the interannual cell standard deviation of Chlorophyll *a* (using color units); and the average of the maximum amplitude tides.

These data downloaded as latitude, longitude, and value (XYZ) coordinates with a 0.5 degree resolution. The XYZ coordinates were mapped and converted to 0.5 degree resolution ASC grid using ArcGIS (9.1). The environmental data grids were for the whole world, Europe, and Eastern North America. We produced maps from these grids in ArcGIS 9.1.

Building the Models

We built ecological niche models with the species occurrence and environmental data using Desktop GARP version 1.1.6. We set the program for 20 runs, each with a convergence limit of 0.01 and a maximum of 1000 iterations to convergence (well over the maximum iterations it took to converge during the runs, 120 iterations). The program used all four rule types with all their combinations to build the model: Atomic, Range (bioclimatic envelope), Negated Range, and Logistic Regression. We used Desktop GARP Dataset Manager to combine layers.

Because of the relatively coarse resolution of the environmental data, many smaller estuaries were obscured by a grid cell representing land. Any species occurrences from those estuaries would have been treated by the model as if they were actually land based. To deal with this phenomenon, which would skew the model, a mask was created to remove these mistakenly land-based occurrences. Models for all four species were based on the same environmental layers and mask.

We built three separate types of models for each species. First we used all the available occurrence data from established populations throughout the world. Second, we restricted the input data to native range occurrences only. Third, we built the model using only data from an established invaded range. We used the invaded European range for *Balanus improvisus*; we used the invaded east coast of North America for *Carcinus maenas*; and we used the west coast of North America for *Styela clava*'s invaded range. There were not enough documented occurrences of *Littorina saxatilis* invasions to build a model from an invaded range for this species.

We entered species occurrence data and two sets of environmental data. Fifty percent of the occurrence data was used for model building (a.k.a. training, learning). In other words, the model randomly selected half of the occurrence data as training and reserved the other half for testing. One set of the environmental data was used for building the model itself, and one was used for re-projection into the Desktop GARP program. For example, for runs of the *Carcinus maenas* native only data, we used the northeast Atlantic occurrence data and the environmental data for the northeast Atlantic (15 to 70° N latitude, -25° W to 30° E longitude) then projected the models using the global environmental data. The error rates for each model run were calculated based on the data input (northeast Atlantic only for this example).

We projected the niche models onto nearshore habitats to visualize the potential geographic ranges of the four species in coastal Alaska and globally. We tested these predictions using known occurrences from successfully established and failed introduced populations of each species.

We also examined how the potential ranges of these four species would change given uniform global warming. Using a midpoint of the predicted range of ocean warming over the next 100 years (IPCC 2007), we added a 2°C increase worldwide to all of the temperature averages (the

12-month average, the average minimum monthly, and the average maximum monthly air temperature and the mean monthly, average maximum monthly, and average minimum monthly sea surface temperatures). We used these higher temperatures along with the other environmental variables (unchanged) and all the available occurrence data from established populations world wide to build predictive models. Because the poles are predicted to warm more than tropical areas and we added 2°C uniformly across latitudes, the effects of warming are likely to be greater in higher latitudes than shown here. Nonetheless, this simplified model identifies how moderate temperature increases may increase the potential range of these temperate species.

Evaluating the Models

The GARP program calculated three error rates: commission, internal omission and external omission. Commission error evaluated over-prediction, the percentage of the predicted area that exceeded the recorded occurrences (not verified to be occupied by the species in question). A model with 100% commission would have predicted every possible pixel. Omission errors fail to predict the occurrence data, the known distribution of each species (instead they were predicted as absent). The internal omission error evaluated how well each model predicted the occurrence data that were used in building that model (the training data). The external omission evaluated how well the model predicted the testing dataset (the 50% of the occurrence records not used in building the model).

The GARP program also calculated a chi square statistic for each model to evaluate whether the occurrence data used to test the model have better than random agreement with the model. It determines the number of correctly predicted data points based on the number of test occurrence records (ones not used in building the model) that fell inside the predicted presence area versus ones that fell outside the predicted presence area. It then calculated the probability that random predictions would have the same number or more correctly predicted records.

We additionally evaluated the forecasts by identifying which areas were predicted to match the environmental requirements of each species in multiple runs of the model building. We conducted 20 runs (built 20 models) for each species then stacked the 20 outputs in ArcGIS 9.1, using the grid calculator. We binned these outputs by percent overlap across models and re-projected the multiple model runs over the globe. This identified how well the series of models predicted occurrences outside the model input scope. The areas for which 19 or all 20 (95-100%) models predicted environmental match are shown in red on the projected maps and indicate high confidence in the forecast due to the high overlap across models. In pink are areas with moderate overlap, 16-18 (80-90%) models predicted environmental match. Gray indicates low overlap, 11-15 (55-75%) models predicting match, while white indicates very low to no overlap, 0-10 (0-50%) models predicting environmental match. Hence, the red shading indicates the greatest confidence in predicted suitable areas, and confidence in the predictions decreases as the hue fades to white.

The second step to this evaluation of multiple models, calculation of a total across-model prediction rate, also enabled direct comparison across species and models. Once multiple runs (models) for a species were stacked and binned by percent overlap, we used GIS to identify the bin (0-50%, 55-75%, 80-90%, or 95-100%) to which each population occurrence record was mapped. We then tabulated the distribution of points among the different bins. The across-model

prediction rate was calculated as the number of occurrence records that fell within the 95-100% model overlap bin divided by the total number of occurrences (excluding those occurrence records that were masked).

For a broader-scale examination, we also tallied the number of ranges that 95-100% of the models missed, partly predicted, or correctly predicted. We marked the north and south range limits of a) the occurrence records of each range and b) each range that was predicted by 19 to 20 of the 20 models. We then calculated the fraction of the range of the occurrence records that each set of models correctly predicted. If the predictions placed the range north or south of the occurrence records, it was considered a missed range prediction. When the model overlapped with the occurrence records, then the overlapped area was used. A 79% to 99% overlap with the occurrence record range was considered to have minor restrictions to the predicted distribution, while a lower percentage (13 to 65%) overlap was considered to have major restrictions to the predicted distribution.

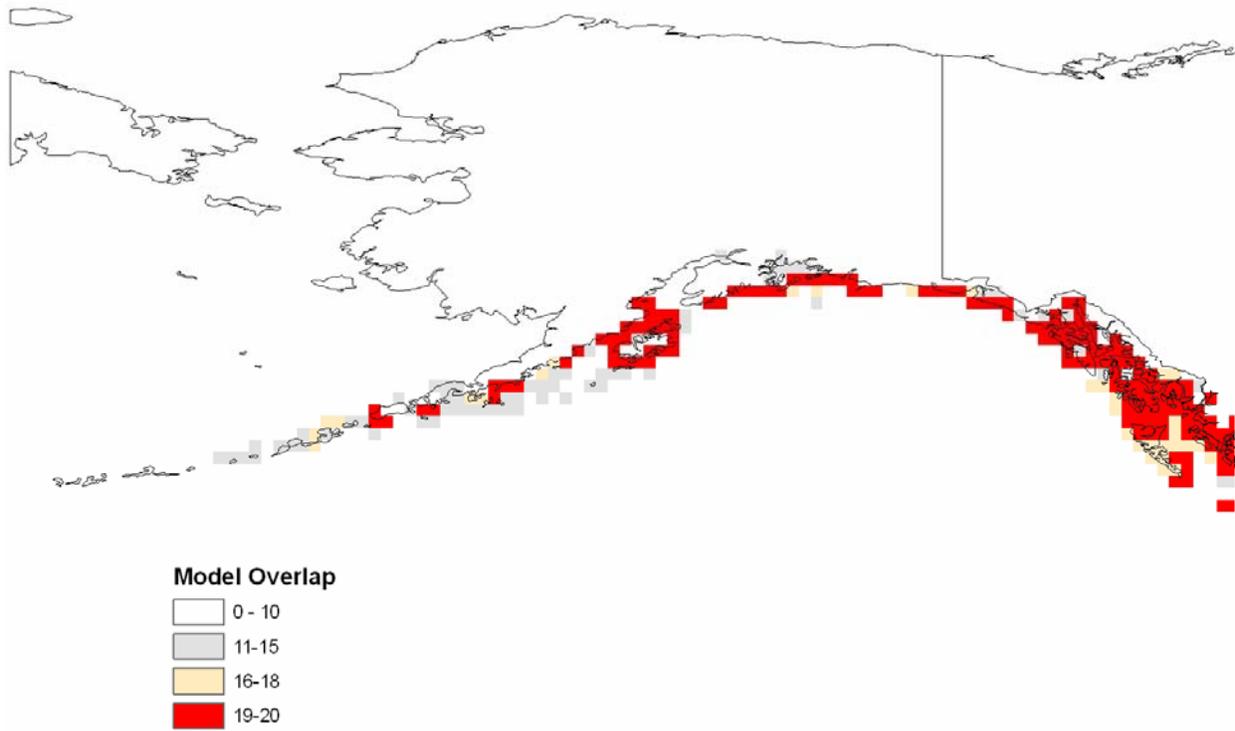
To evaluate whether the stacked models over-predicted suitable environmental space, we also calculated a total model prediction rate of failed introductions. This across-model failure prediction rate was calculated as the number of documented introduced populations that failed to establish but fell within the 55-100% model overlap bins divided by the total number of occurrences (excluding those occurrence records that were masked). We only calculated this across model failure rate for *Balanus improvisus* and *Carcinus maenas* because we lacked documentation of multiple introduced *Littorina saxatilis* and *Styela clava* populations that subsequently failed to establish.

RESULTS

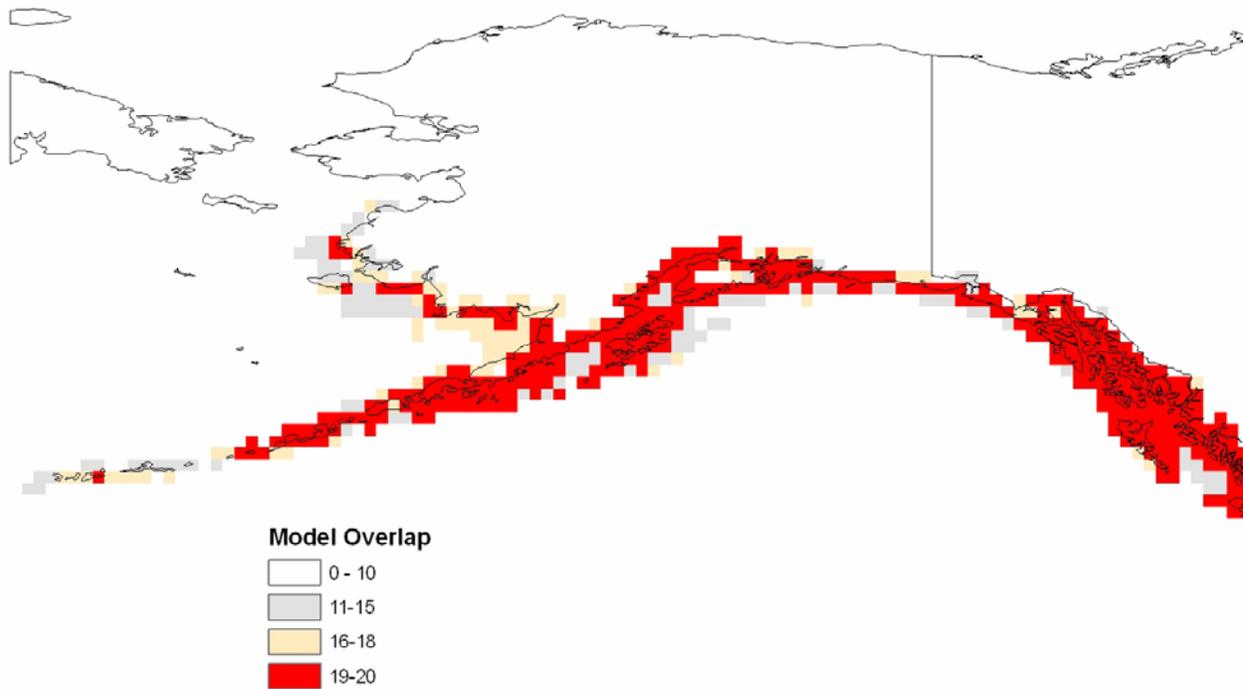
Model predictions

Alaskan predictions

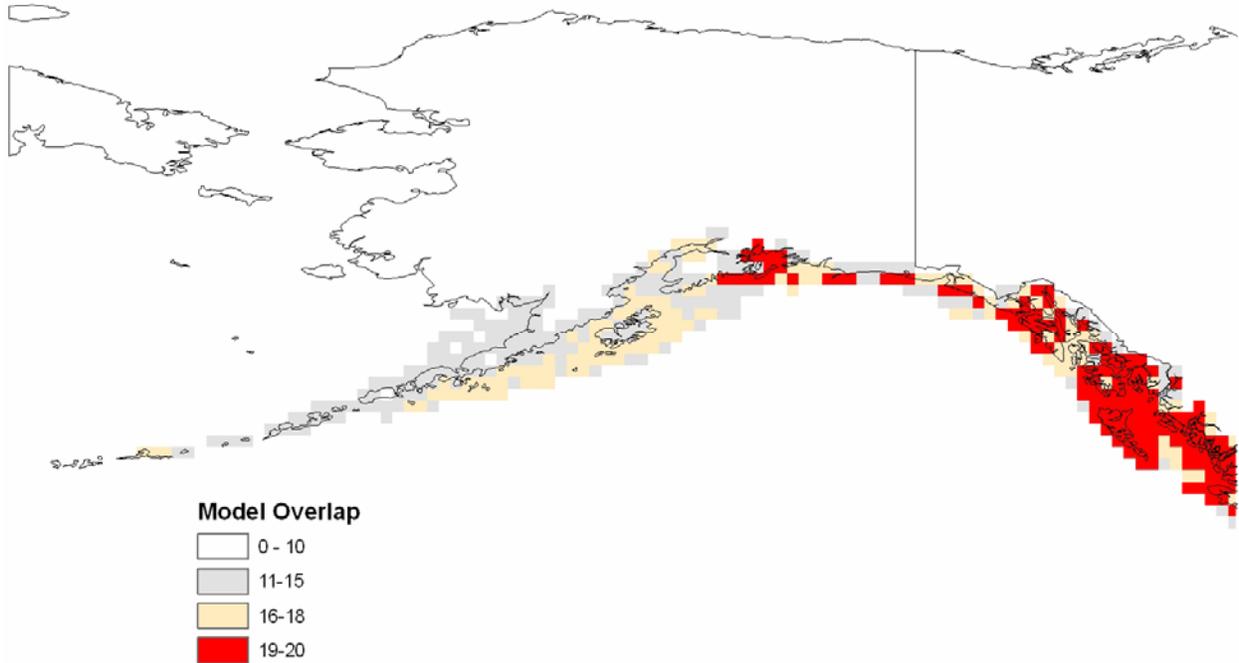
The models developed from sampling all possible occurrence data predicted that all four species would find suitable environmental conditions to establish in Alaskan waters, including Prince William Sound (Fig. 2a-d). *Balanus improvisus* could establish as far west as Unimak Island (Fig. 2a). *Carcinus maenas* could inhabit waters to Adak Island and north to Cape Romanzof (Fig. 2b). *Styela clava*, the most environmentally restricted of the four species in Alaska, could spread west to Seward (Fig. 2c). *Littorina saxatilis* could establish throughout almost all of Alaska, through the Aleutian archipelago and even just north of the Arctic Circle to Cape Lisbourne (Fig. 2d).



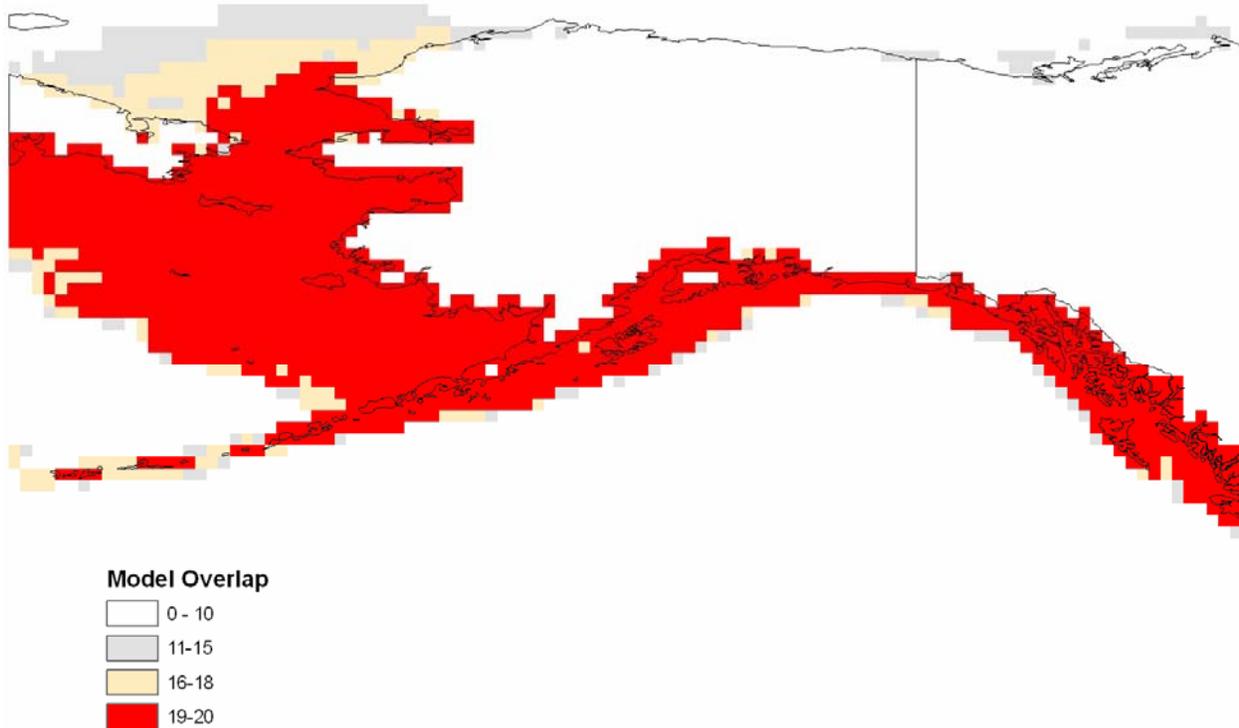
2a) Potential Alaskan distribution for *Balanus improvisus*.



2b) Potential Alaskan distribution for *Carcinus maenas*.



2c) Potential Alaskan distribution for *Styela clava*

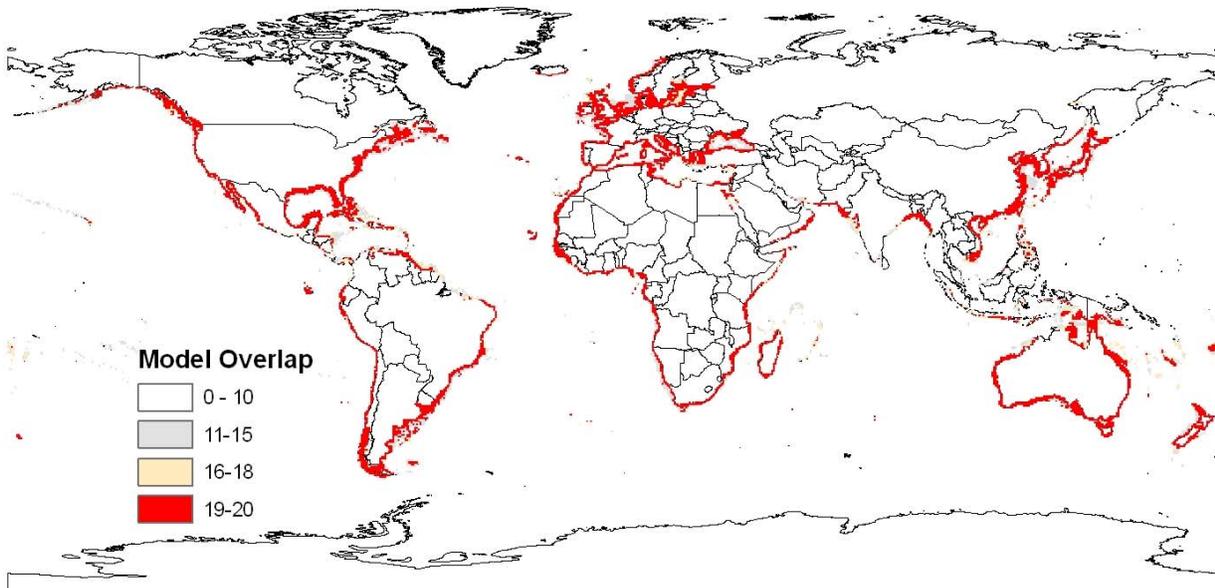


2d) Potential Alaskan distribution for *Littorina saxatilis*.

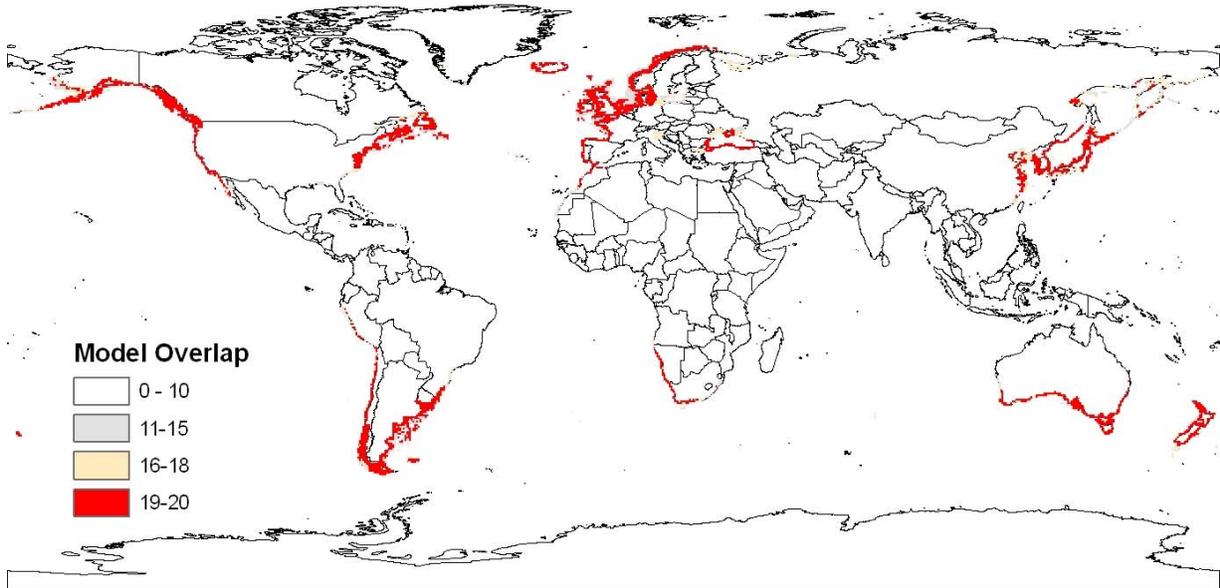
Figure 2. Projected Alaskan potential distributions, based on randomly-selected subsets of all the occurrences in the database for all four species. Refer to Methods: Evaluating the Models for description of color coding.

Global forecasts from all occurrence data

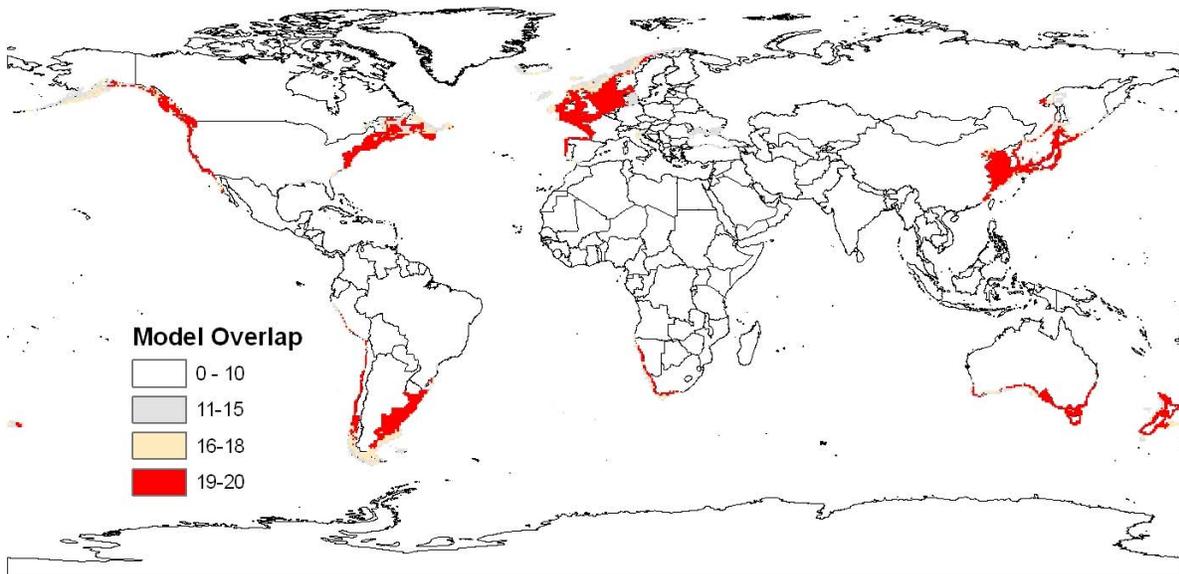
These same global occurrence models also predicted that many regions around the globe provided environmental match for all four species (Fig. 3a-d). They identified environmental match for *Balanus improvisus* throughout most temperate and tropical coasts worldwide, from 55° S to 60° N latitude (Fig. 3a). *Carcinus maenas* would encounter suitable abiotic conditions north and south of its present distributions, and its potential range could include a large part of the world's temperate coasts (Fig. 3b). Pan-temperate distributions are also possible for *Styela clava* and *Littorina saxatilis* (Fig. 3c,d). The potential range of *L. saxatilis* extends north of the Arctic Circle in several areas, even reaching 70° N latitude in Greenland and Europe (Svalbard), and south to the tip of South America. It is more restricted than the other species in temperate to subtropical zones though, with few potential ranges extending equatorial of the 35th parallels (Fig. 3d). Compared with the other three species, *Styela clava* had the most restricted potential range and yet was predicted to find suitable abiotic conditions in eight distinct regions, including its native range and the four regions it has already successfully colonized (Fig. 3c).



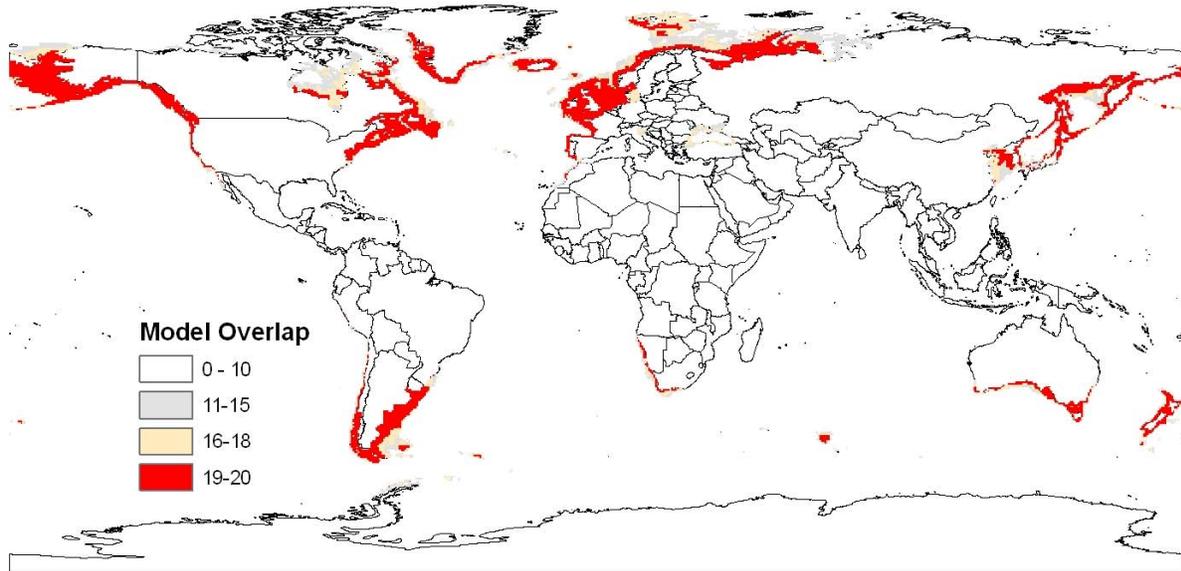
3a) Projected potential global distribution for *Balanus improvisus*



3b) Projected potential global distribution for *Carcinus maenas*



3c) Projected potential global distribution for *Styela clava*

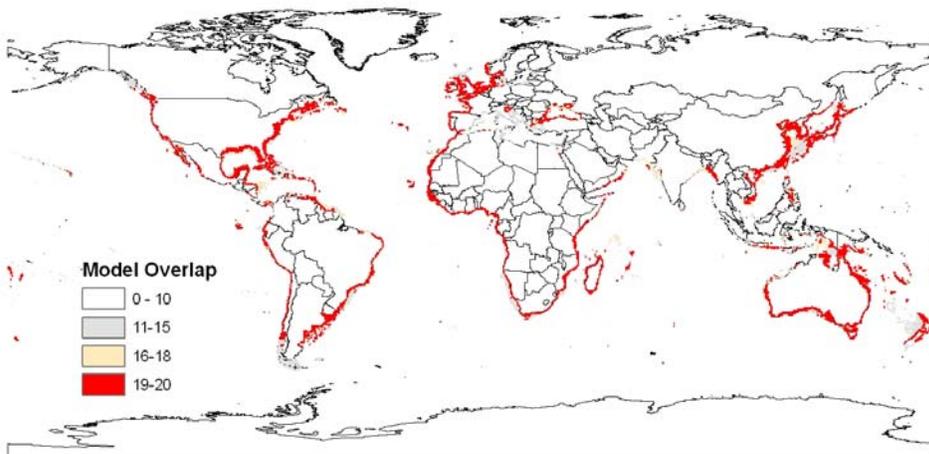


3d) Projected potential global for *Littorina saxatilis*

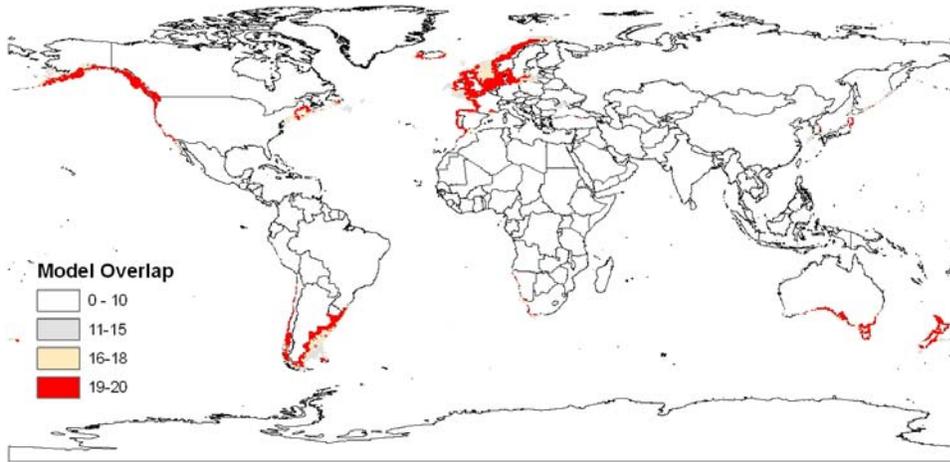
Figure 3. Projected potential global distribution for all four species from models that sampled all the occurrence records in the database. Refer to Methods for description of color coding.

Global forecasts using subsets of occurrence data

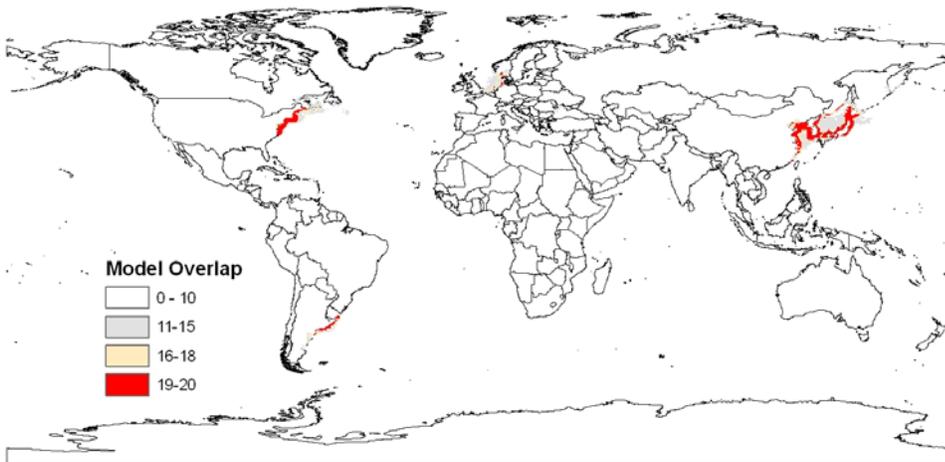
Figures 4 and 5 show the projected global models based on the native range data only and a single, best established invaded range only, respectively. For each species, the models based on the occurrence records from the native range (Fig. 4) each predict a more limited number of suitable regions and often more restricted ranges within each region than the models developed from all the data (Fig. 3). Similarly, all the models based on data from a single invaded range (Fig. 5) predict even fewer areas than the models developed from native-range data (Fig. 4).



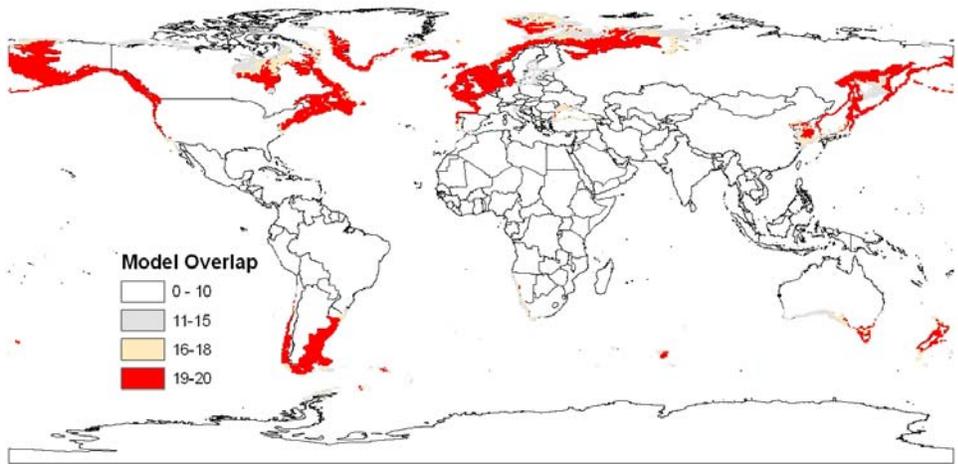
4a. Native range predictions for *Balanus improvisus*



4b. Native range predictions for *Carcinus maenas*

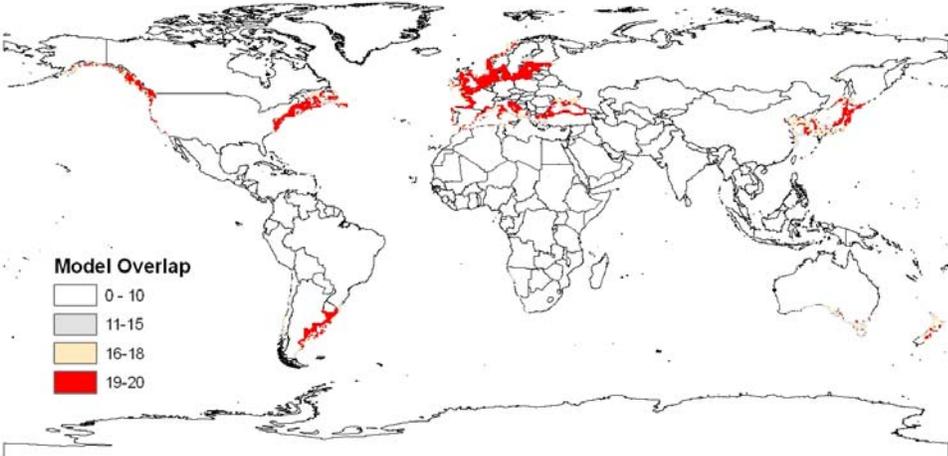


4c. Native range predictions for *Styela clava*

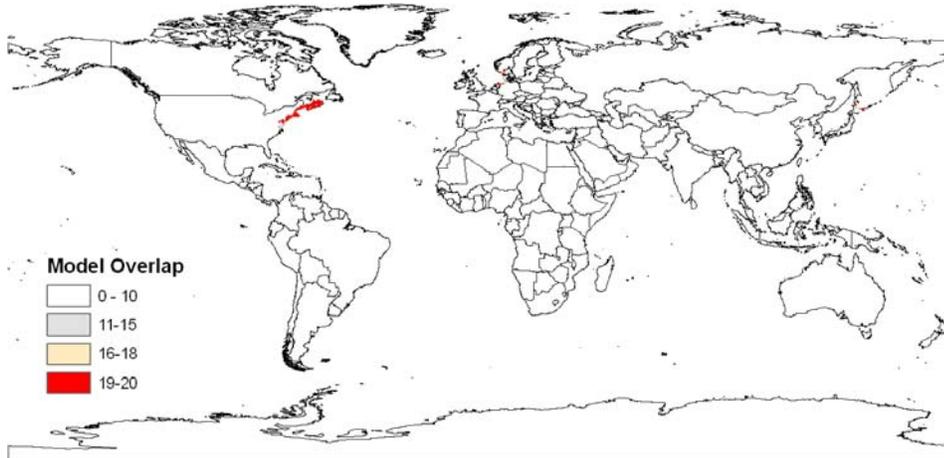


4d. Native range predictions for *Littorina saxatilis*

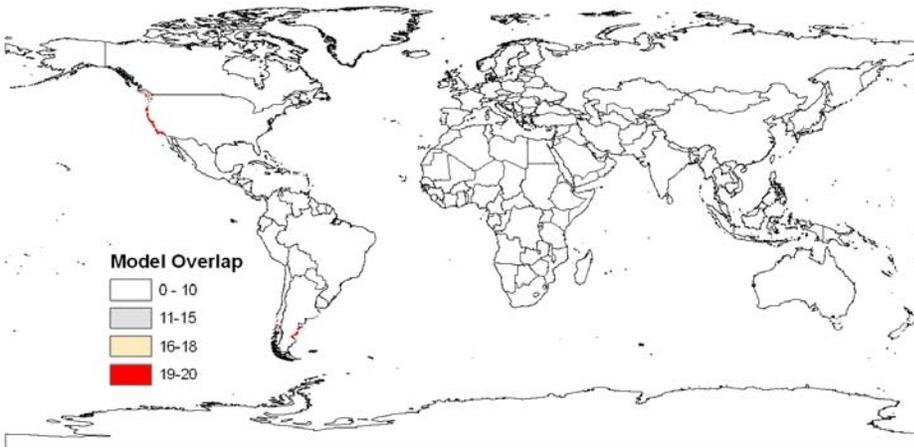
Figure 4. Projected potential global distribution based on native range occurrences only for all four species. Refer to Methods for description of color coding.



5a. Projected potential range for *Balanus improvisus* from their Northeast Atlantic distribution.



5b. Projected potential range for *Carcinus maenas* from their Northwest Atlantic distribution



5c. Projected potential range for *Styela clava* from their Northeast Pacific distribution.

Figure 5. Projected potential global distribution based on the most established invaded range only for a) *Balanus improvisus* from their Northeast Atlantic distribution, b) *Carcinus maenas* from their Northwest Atlantic distribution, and c) *Styela clava* from their Northeast Pacific distribution.

Comparing the projections from these different types of models with the occurrence data revealed that the models trained from samples of all the data outperformed those trained with the native only data, which in turn outperformed those trained with data from one invaded range. This is shown at a coarse scale in Table 2, summarizing figures 2-5. Hence, this comparative measure indicated greatest confidence in the projections from all the occurrence records (Fig. 3).

Table 2. For each type of model, the number of distinct ranges with occurrence records for each species compared to the number of ranges missing, restricted, or displaced from the known ranges. A 13 to 65% overlap with the occurrence record range was considered to have major restrictions to the predicted distribution, while a higher percentage (79% to 99%) overlap was considered to have minor restrictions to the predicted distribution.

Data input	Type of mismatch	<i>Balanus improvisus</i>	<i>Carcinus maenas</i>	<i>Littorina saxatilis</i>	<i>Styela clava</i>
Number of ranges					
<i>Occurrence records</i>		6	7	4	5
Number of mismatched ranges					
<i>All data</i>	Missing	0	0	0	0
	Major restrictions	0	0	0	0
	Minor restrictions	0	1	1	0
<i>Native range data</i>	Missing	0	0	1	2
	Major restrictions	0	2	0	1
	Minor restrictions	1	2	2	2
<i>1 Invaded range</i>	Missing	1	5	n/a	4
	Major restrictions	3	1	n/a	0
	Minor restrictions	1	1	n/a	0

Model evaluation and across-model prediction rates

The predictions of the models based on all global occurrences met our *a priori* requirements for forecasting because of the high overlap between multiple runs, the low error rates, and the statistically significant chi square tests, as described below. Using the global occurrence records, our across-model prediction rates (percent of occurrence records correctly predicted by 95-100% of the models) were high, always over 90%, for all four species (Table 3). Similarly, the across-model failure prediction rates were always low, less than 10% (Table 3).

Comparison of models based on different types of data (all, native, invaded) revealed that the across-model prediction rates declined when using smaller subsets of the occurrence data. The prediction rate ranged from 34-92% when considering the native range data alone, and declined further to a range of 14-53% for the single invaded range occurrence data (Table 3). The models for *Littorina* showed little difference in performance between global and native range data sets, due to the fact that only three occurrence records were available from their non-native distributions.

Overall this comparison, which offers a finer-grained examination than Table 2, indicates models with the most value to forecasting were those that were trained drawing from all potential data, rather than just from a native range or just an invaded range. In addition, the single invaded range predictions performed poorly, missing many known occurrences and even whole ranges (Tables 2, 3).

Table 3. Across-model prediction rates (percent of occurrence records correctly predicted by 95-100% of the 20 models) and failure prediction rates (percent of failed populations predicted by 50-100% of the models) for each species, from models developed with randomly selected occurrence records from: all globally available occurrence records, native range only occurrence records, and one invaded range's occurrence records. The percent predicted rates for the across-model predictions are followed, in parentheses, by the number of records used in training the GARP models (half the number of records available for the region(s)).

Occurrence records used	Prediction rates (sample size) for each species			
	<i>Balanus improvisus</i>	<i>Carcinus maenas</i>	<i>Littorina saxatilis</i>	<i>Styela clava</i>
Global	97.53% (154)	98.75% (128)	90.07% (74)	94.24% (71)
Native range	80.92% (72)	68.33% (37)	92.20% (70)	33.81% (17)
Single invaded range	52.30% (50, in NE Atlantic)	33.75% (43, in NW Atlantic)	n/a	14.39% (12, in NE Pacific)
Failed to establish, using global	0% (154)	9.09% (128)	n/a	n/a
Failed to establish, using native	0% (72)	0% (37)	n/a	n/a

The across-model prediction rates increased with an increasing number of occurrence records used to develop the models (Fig. 6; Logarithmic regression $r^2 = 0.81$, $N = 11$, $F = 38.63$, $P = 0.0002$). Some of the variance in these data was likely due to the fact that some of the prediction rates were based on native-only models while others were based on models built from an invaded range, and these types of occurrences may be inherently different.

We did not have enough species with contrasting native versus invasive range predictions to test whether the native range predictions consistently perform better than the invasive range ones independent of sample size, but visual examination of our limited sample suggested this may be the case (Fig. 6).

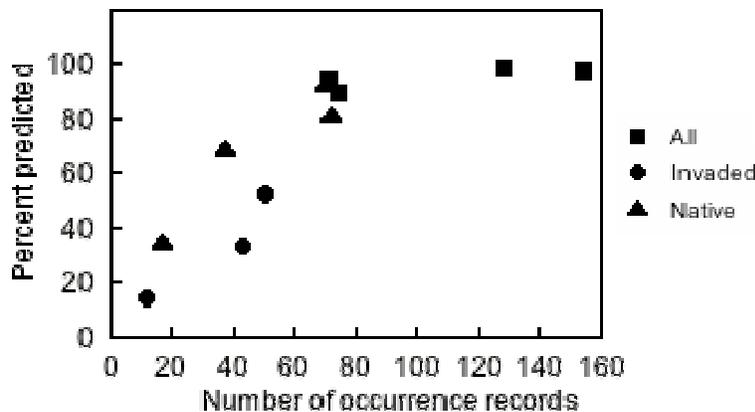


Figure 6. Scatterplot of the percent of occurrence records predicted by at least 95% of the models versus the number of occurrence records used to train the model.

None of our models had any internal omission errors, suggesting they all included the key ecological niche descriptors of each species (Table 4). The median external omission error was also low for most models of most species but approached 1/5 for the *Styela clava* models. This suggests that more sites than predicted might offer a suitable environment for *S. clava*. The commission error was also low for all types of models for all species (Table 4). In other words, the models rarely predicted environmental match in training areas (used for model development) that lacked occurrence records. Together the three types of errors suggest that the models were slightly conservative in their predictions, especially for *Styela clava*.

Table 4. Median (and maximum) commission, internal omission, and external omission errors from the three types of models --using all the data, native range data, and a single invaded range of data-- for the four species.

Occurrence records used	Error rates per species			
	<i>Balanus improvisus</i>	<i>Carcinus maenas</i>	<i>Littorina saxatilis</i>	<i>Styela clava</i>
<i>Global data</i>				
Commission	5.00 (21.47)	2.58 (6.76)	6.99 (10.69)	1.25 (2.32)
Internal omission	0	0	0	0
External omission	2.20 (10.14)	4.13 (22.86)	2.88 (8.57)	19.38 (43.75)
<i>Native range data</i>				
Commission	4.61 (38.55)	2.63 (4.01)	6.71 (8.50)	1.15 (2.65)
Internal omission	0	0	0	0
External omission	2.88 (8.57)	4.25 (22.86)	5.71 (13.24)	18.75 (43.75)
<i>1 Invaded range</i>				
Commission	2.22 (3.28)	0.18 (0.30)	n/a	0.20 (3.93)
Internal omission	0	0	n/a	0
External omission	4.40 (12.50)	2.38 (7.14)	n/a	16.67 (33.33)

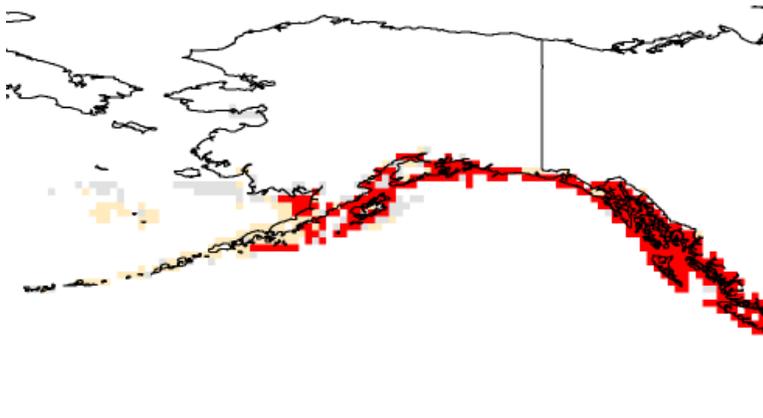
The error rates were similarly low across the different model types, ones based on a subset of all data, native range data, and a single invaded range's data. Therefore, the error rates themselves do not point towards one model type being better or worse than the others. The median commission error was similar or lower for the models using native-range only data compared to those using all the data, and lower again for models that used data from a single invaded range. This does not mean that the models developed from a subset of all the data were the most error prone and therefore worst. Some amount of commission error is useful in these models because it indicates places with suitable habitat that lacked a known, recorded already established population (Anderson et al. 2003, Stockman et al. 2006). Zero commission 'error' means the model is over fitted and only predicts species to occur in and right around the input data, which is not very useful.

The chi square test statistic for internal model evaluation was always high, with a low probability that random test points would have generated as good or better agreement with the model than did the occurrence records used to test the model. The chi square statistic was greater than 246 for predictions from all data ($P < 0.0001$); greater than 99 for native only data ($P < 0.0001$), and greater than 160 for single invaded range data ($P < 0.0001$).

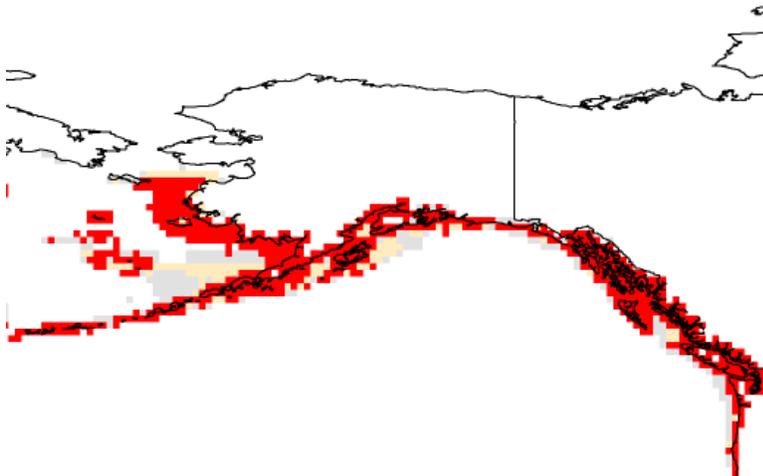
Exploring the effects of climate change

Alaskan forecasts with warming and all occurrence data

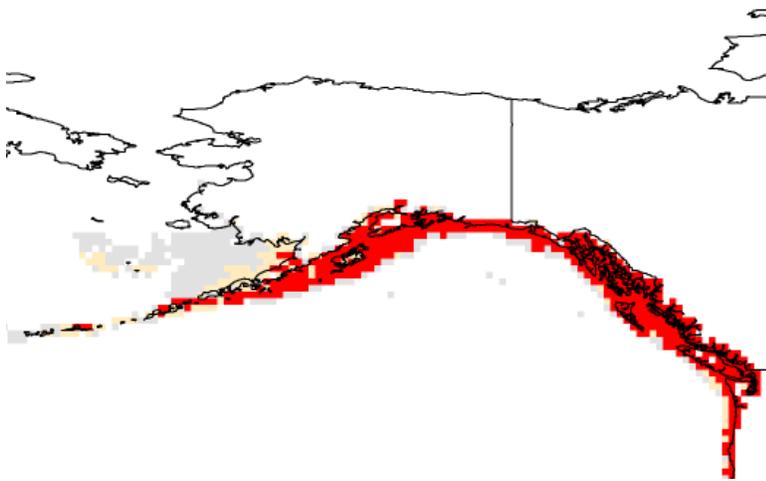
Adding 2°C to the temperature data forecasted that Prince William Sound and much more of the southern Alaskan coastline would be habitable for *Balanus improvisus* (Fig. 7a) and especially *Styela clava* (Fig. 7c) compared to forecasts based on present temperatures. This warming pushed the potential northern boundary further for *Carcinus maenas* (Fig. 7b) than for the other species, yet much less of Alaska's coastline would be affected by this change than the two species discussed above. Most of the Alaskan coast is already suitable for colonization by *Littorina saxatilis* given present environmental conditions, so warming had little effect on the potential range of this species (Fig 7d).



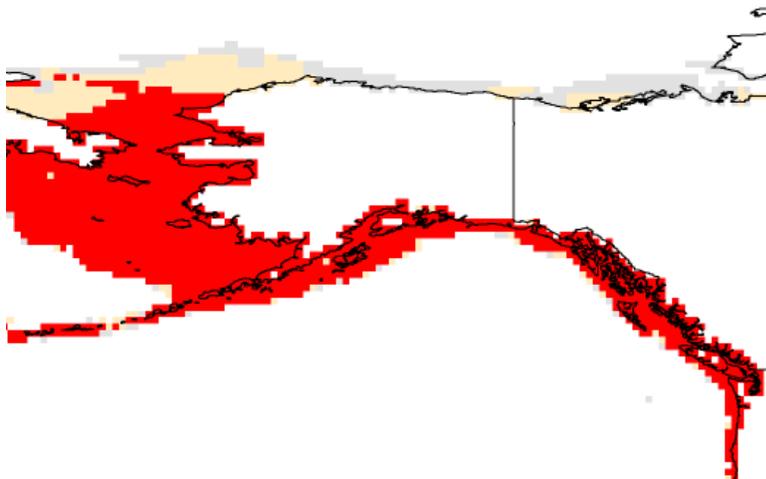
7a) Potential Alaskan distribution for *Balanus improvisus* given 2°C warming.



7b) Potential Alaskan distribution for *Carcinus maenas* given 2°C warming.



7c) Potential Alaskan distribution for *Styela clava* from models given 2°C warming.



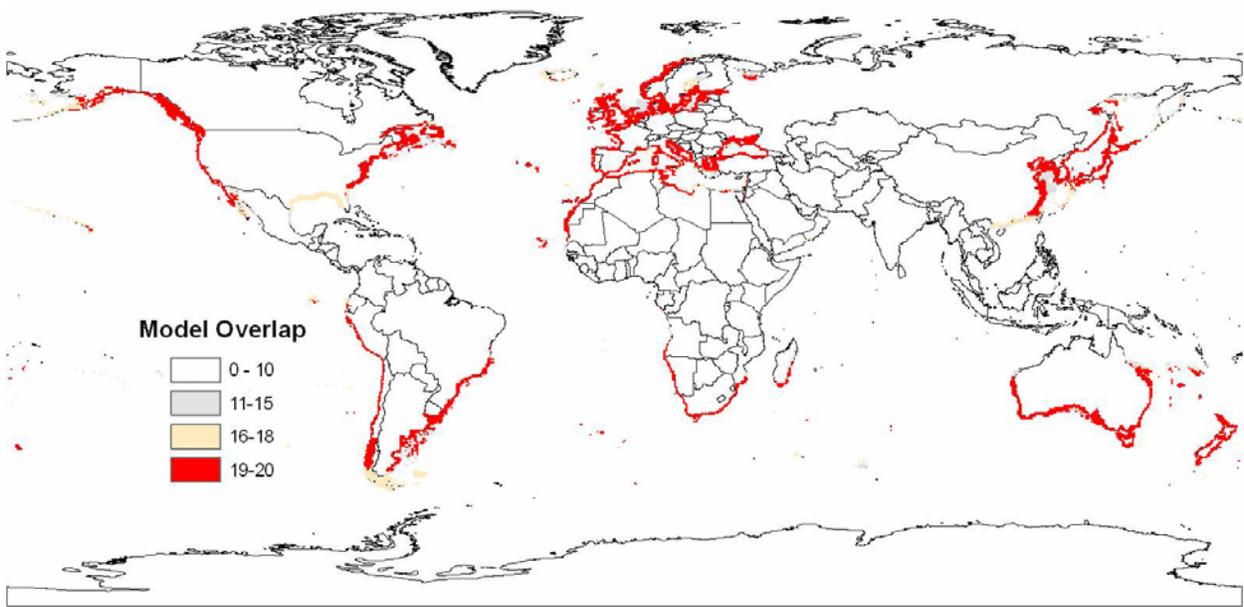
7d) Potential Alaskan distribution for *Littorina saxatilis* given 2°C warming.

Figure 7. Projected Alaskan potential distribution with 2°C added to the temperature averages, based on randomly-selected subsets of all the occurrences in the database for all four species. Refer to Methods: Evaluating the Models for description of color coding.

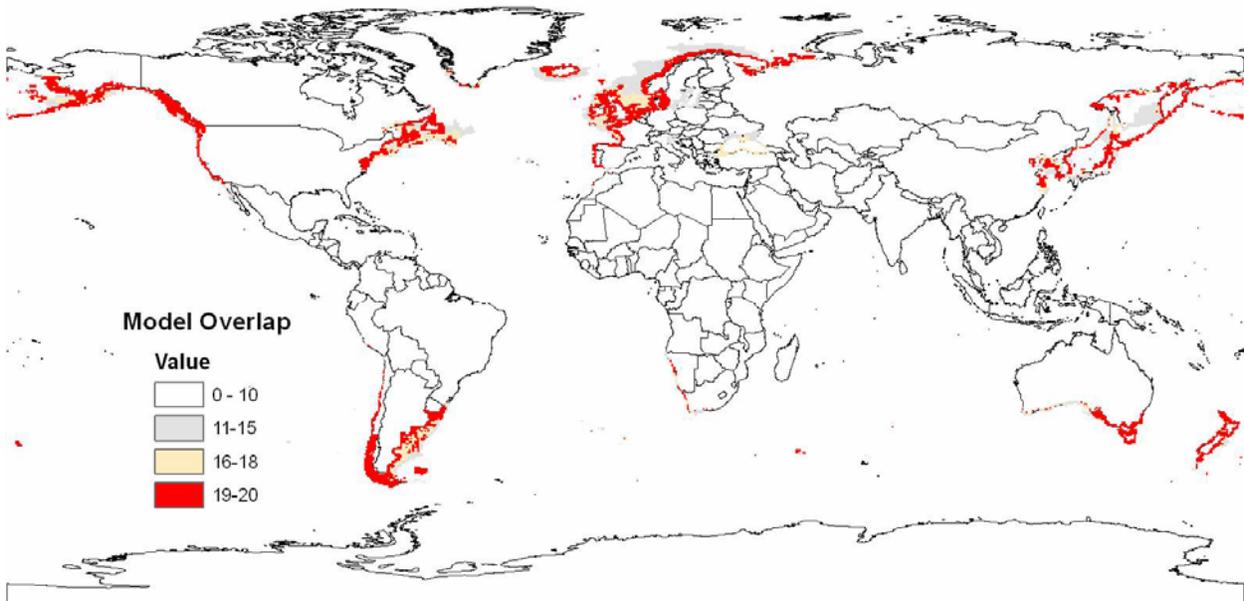
Global forecasts with warming and all occurrence data

Uniform warming of 2°C is predicted to nudge northward some of the northern poleward limits of *Balanus improvisus* but would decrease its tropical coverage and lead to a global decrease in suitable habitat for this species (Fig. 8a). Warming would also decrease suitable habitat for *Carcinus maenas* due to decreases in the subtropics, but the potential northern range of this crab would increase more than for *B. improvisus* and could include new areas such as Greenland (Fig. 8b). For both species, the polar reaches of the southern hemisphere ranges changed little with two degrees added to temperatures. Warming would increase northern habitats for *Styela clava* with less of a decrease in southern habitats for this widespread species (Fig. 8c). *Littorina saxatilis* is already predicted to find suitable habitat through much of the more polar land masses so its potential high latitude range would not be expanded greatly from two degrees of warming

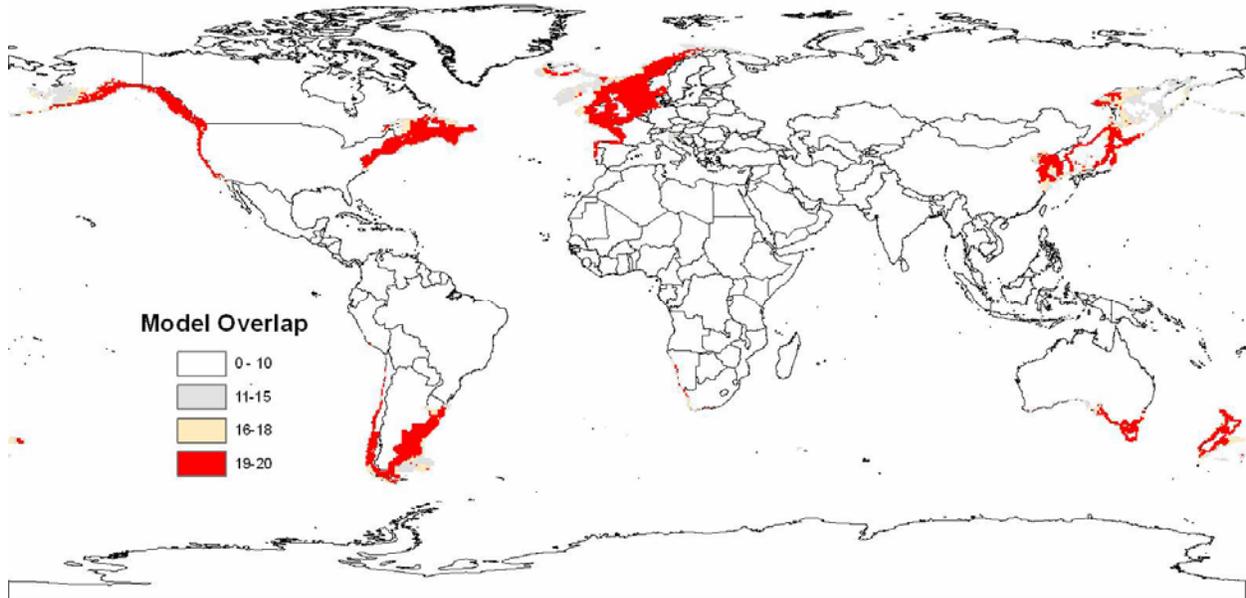
(Fig. 8d). Like the barnacle and crab, it would lose potential habitat in the southern hemisphere given such warming.



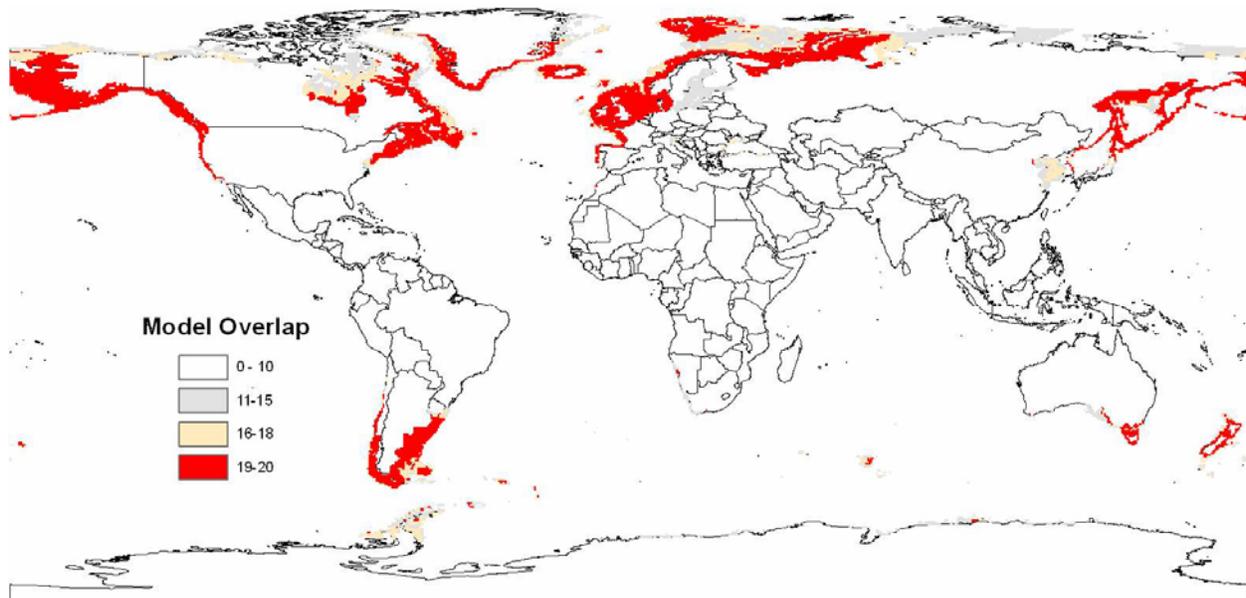
8a) Potential global distribution for *Balanus improvisus* given 2°C warming



8b) Potential global distribution for *Carcinus maenas* given 2°C warming



8c) Potential global distribution for *Styela clava* given 2°C warming



8d) Potential global for *Littorina saxatilis* given 2°C warming

Figure 8. Projected potential global distribution for all four species from models built with 2°C added to each temperature variable. Refer to Methods: Evaluating the Models for description of color coding.

DISCUSSION

GARP predictions of potential northward range extensions for NIS

All four species --*Balanus improvisus*, *Carcinus maenas*, *Littorina saxatilis*, and *Styela clava*-- were predicted to find high environmental match in numerous areas beyond their present ranges

and range limits. Similarly, all models developed from sampling all the available occurrence records found that the abiotic conditions of at least the southeastern coast of Alaska, and often much more, could support all four species. The models showed that *Balanus improvisus* had the broadest potential global distribution, with predicted environmental match in all but polar areas and a few tropical ones. *Littorina saxatilis* had the most extensive possible distribution in Alaska, including the Alaskan coastline south of the Arctic Circle, and even extending slightly north of it. *Styela clava* had the narrowest potential ranges. However, the narrower prediction of areas suitable for *S. clava* relative to the other species (Figs 2-5) may have in part been due to the much higher external omission error for models of this species.

Comparison of established occurrence records (Fig. 1) with these global predictions (Fig. 3) revealed that *Carcinus maenas* has already established in most regions predicted by the model, but that it might spread further in these regions. The other three organisms, on the other hand, have colonized only a fraction of the potential regions that provide suitable environments for them (Figs 1 & 3). Investigations into spread patterns and rates for these and other species (see Ruiz et al. 2007 companion report) and on the potential for native, or even other introduced, predators, parasites, and competitors of these species, combined with vector analysis, will help identify the likelihood that these species arrive to and can establish in these areas with suitable abiotic conditions.

More broadly, the fact that these ecological niche models predicted potential northern, and often southern, geographic range expansion for all four of these temperate species suggests that many species from the U.S., South American, European, central coastal Asian, and Australian coasts could survive in Alaskan waters as well as along many other coasts.

Predictive value of the models for new introductions

All the models had low commission and omission errors and high overlap between multiple runs. In addition, the models developed from sampling all the available data rarely missed predicting environmental match for existing populations, even those not used in model development. Overall, the best models, ones that predicted the most established populations and the fewest failed introductions, were ones based on all the available occurrence data. Across the model types, the greater the extrapolation, the worse each model performed. Therefore, the predictions of the models based on all global occurrences are useful for forecasting potential range of these species, and the method may be suitable for many other marine NIS as well.

We expect that the best models were those developed from sampling all the available data because this combination of data better approximates the fundamental niche (Grinell 1917). Similarly, the native range models may have approximated the fundamental niche better than those developed from a single invaded range. It is likely that a single invaded range either 1) represents a more restricted realized niche (Hutchinson 1957) or 2) has not had time to establish across its full potential distribution.

Ranges are likely influenced by biotic interactions such as predation. For example, the southern range boundary of the invasive northwest Atlantic *Carcinus maenas* population seems to be limited by predation by a native crab, *Callinectes sapidus* (de Rivera et al. 2005b). This may help explain why the predictions developed from occurrence data in this species' invaded range

missed predicting so many other invaded ranges of the world as well as the native range. Typically other biotic constraints are considered to be greatest in native ranges (e.g. Wolfe 2002, Mitchell & Power 2003, Torchin et al. 2003). So native-range only models would be based on a restricted, realized niche rather than, as assumed by ecological niche models, the fundamental niche. The effect of biotic interactions on predictions is more likely to be minimized when many ranges are used, and models based on multiple ranges should best meet the assumptions of ecological niche modeling. Clearly biotic interactions are important to consider when predicting which species can establish where, but these could be considered as a second step after abiotic matching has been projected.

Regardless of biotic interactions, it is quite likely (if not certain) that invaded ranges often have not been colonized long enough for the species to have spread throughout the suitable environmental space and established from the potential northern to southern range limits. This is surely the case for *Carcinus maenas* in Argentina, first documented in 2005 (Hidalgo et al. 2005). Noteworthy, an early 2005 GARP run for *C. maenas* (Steves, unpublished) that preceded this publication identified the same South American range as the models that have been updated to include this newest occurrence record. The other ranges are not as recent and include the Northeast Pacific, with the first established population recorded in 1989 (Cohen et al. 1995, Grosholz and Ruiz 1995), Northwest Pacific in 1984 (Carlton and Cohen 2003), Southeast Atlantic in 1983 (Joska and Branch 1986), Southwest Pacific in 1891 (Ahyong 2005), and Northwest Atlantic 1817 (Carlton and Cohen 2003).

Another potential explanation for why the models sampling all the available data had better fit with occurrence records than the other models is that the sample size we had available from the global occurrence records was much higher for each species than the minimum sample sizes needed to build accurate, predictive species distribution models. Stockwell and Peterson (2002) suggest 10 data points are required to achieve 90% of the maximum accuracy in a predictive model, and 50 data points are required for near maximal accuracy. The multiple runs from the global models, all of which had well over 50 data points used in training the models, had high overlap and predicted over 90% of the occurrence records. In contrast, many (5 of 7) of the native range or a single invaded range models did not have more than 50 occurrence records to train the models and performed poorly (Table 3).

The *Carcinus maenas* models provide an opportunity to evaluate further this question of whether data from a long-established invaded range provides a better prediction of other invaded areas due to new evolutionary pressures or releases in an invaded range. *Carcinus maenas* is especially relevant because the Northeast Pacific range is a secondary introduction from the Northwest Atlantic range. One might expect that models developed based on data from the invaded Northwest Atlantic range would predict the Northeast Pacific range best, because the latter population was a secondary introduction from the Northwest Atlantic (after almost 200 years since its arrival from the European source). Thus, both introduced populations may face similar ecological releases compared with the native populations (see above). However, our model based upon the Northwest Atlantic records failed to predict any occurrences in the Northeast Pacific (Fig. 5b), whereas the predictions based upon the native Northeast Atlantic records predicted environmental match throughout the present Northeast Pacific range as well as to either side of it

(Fig. 4b). Thus, in the case of *C. maenas*, the native range did a better job at predicting an invaded range than another invaded range did, despite secondary introduction.

Guisan and Thuiller (2005) caution that species distribution models for invasive species need to use the area of origin. Our findings support their suggestions and suggest using the combination of native and multiple invaded ranges to develop models, whenever possible.

Comparison of predictions from GARP versus from other methods

Currently, most predictions about the potential distribution of marine NIS are derived from informal comparisons of occurrences and surrounding environmental conditions (especially temperature) rather than a formal, quantitative model. For example, Carlton and Cohen used this informal modeling method for *Littorina saxatilis* and *Carcinus maenas*. Using the Atlantic range of *L. saxatilis*, they suggested its potential western North American distribution could extend from Baja California to western Alaska (Carlton & Cohen 1998). Our GARP model, which is also based primarily on this snail's Atlantic range but incorporates a suite of environmental parameters, predicts a similar potential western North American distribution, including most of the southern and western Alaskan coasts. However, our GARP models do not predict environmental match in Baja California, Mexico, perhaps because more environmental parameters were used in developing the model or perhaps because more (18 years of sea surface temperature) or more recent years of temperature data were used that reflect recent warming.

Global predictions for *Carcinus maenas* based on occurrences combined with known upper temperature limits (Carlton & Cohen 2003 based on review and findings in Cohen et al. 1995) also had high overlap with our GARP-based predictions but forecasted narrower distributions in the North and South American ranges. Such informal, single parameter models not only completely lack internal assessment (only predict where an organism has not yet established) but will be especially limiting for species whose range limits are influenced heavily by multiple environmental conditions and the interactions between these conditions.

We have begun to test the environmental tolerances of *Carcinus maenas* larvae to examine how temperature and changes in temperature and the source of the crabs effect range predictions. We conducted laboratory experiments to measure survival and development rate under temperature and salinity combinations. This approach indicated that *C. maenas* larvae have the physiological capacity to colonize both coasts of Canada as well as Alaska (de Rivera et al. 2007). It had perfect overlap with the GARP predictions for North America, which further supports the GARP predictions. Although this approach provided high-quality data to address questions of range expansion, including more subtle types of questions such as whether larvae from one population could colonize an area as readily as larvae from a different population, it has been highly labor-intensive and not easily accomplished for a large number of species. In addition, it is also limited to one or two environmental variables, rather than the full range of factors that may determine distributions.

Exploring the effects of climate change

We began to explore potential range expansion due to warming by taking a coarse approach -- adding 2°C to all the temperature variables-- to the complex effects and repercussions of global climate change. When warming was approximated by adding 2°C, the potential ranges of the

four species only slightly expanded poleward in the northern hemisphere but, for three of these temperature species, decreased the overall potential range. However, given that warming is predicted to be much greater at high than mid latitudes, scenarios of slight to moderate global warming may not greatly shrink the temperate and tropical ranges of these species while still affording northern gains. *Styela clava* would have the greatest increase in potential range from such a scenario.

Salinity did not have a strong effect on model predictions, so it is unclear how increased river flow would limit the nearshore distributions of these species. The relatively coarse (half degree longitude) resolution of the environmental layers likely obscures the effects of salinity on the nearshore distributions. Therefore, better resolution of environmental data in estuaries, to be included in future models if enough fine-grained environmental data can be collected, will likely show potential increased river flow and glacial melt, predictions of some climate change models, to have a stronger effect. While we also did not explore the changes in bathymetry that would occur from changes in sea level, these and other intertidal species will surely follow the water up into new areas. Modeling potential range shifts due to global climate change is clearly an area that deserves more attention. Future efforts should include the complexity of warming (e.g., greater warming in the polar areas) as well as interactions with the many other environmental features that are predicted to change (e.g. freshwater input, currents...).

Next steps

Although beyond the scope of the current project, we plan two types of related future work. First, we will further explore these models for the four species modeled here. We will examine which predictor factors are most important, compare our results to those of other techniques, conduct finer grained analyses, and incorporate vector analysis and potential biotic resistance. Second, because all our methods of model evaluation suggested these models have strong value to forecasting, we wish to apply these methods to a suite of other species, including ones from different life histories and different regions. This way multiple tropical and polar species and ones native to all hemispheres will also be modeled, creating valuable information on the range of source regions having organisms that could colonize Alaskan waters.

To increase our understanding of the species range predictions and the inherent differences between the predictions based on native versus invaded versus all occurrence data, we plan to determine which environmental factors are key predictors and if these predictors are consistent across regions. The GARP modeling system does not elucidate which parameters influenced each model most. We expect bathymetry, temperature and salinity were the most influential variables but we do not know this nor how their inputs differed across model training scenarios. Therefore, we would like to a) also use other modeling methods that do specify the degree to which each factor influenced the predictions (see below), and b) detect data layers that contribute negatively to model performance by using a jackknife manipulation using various combinations of layers, then calculating correlations between inclusion of each data layer in the model and omission error (as in Peterson et al. 2003). This could help identify why the native range or what about the native range increases the predictive value compared with modeling based on data from an invaded range.

We will also compare our results to those of other quantitative modeling techniques. While ecological niche modeling methods are powerful tools for predicting potential ranges, range shifts, or habitats, their algorithms make limiting assumptions that may cause inconsistencies between the predictions of different modeling tools (Araújo et al. 2005, Pearson et al. 2006, Stockman et al. 2006). Araújo et al. (2005) recommend reducing uncertainty inherent in the predictions of any one model by building consensus projections across multiple modeling methods. We did not set out to compare multiple modeling methods. We did, however, also examine the predictions from MAXENT, another, newer machine modeling procedure. The MAXENT models produced similar projections as GARP (Steves, unpublished), which gives us added confidence in our projections.

While the models reported here are valuable in determining the potential northern and southern limits to each range, resource managers will need to know which habitats to sample to monitor for and control incoming species. Moreover, bays may have quite different conditions than the outer coast, with back bays often warming up considerably more than and having more variable salinities than coastal waters. The data used in our model are primarily derived from remote sensing, which does not represent fine-scale environmental conditions of estuaries. Therefore, we plan to conduct finer grained analyses as well. Guisan and Thuiller (2005) warned that environmental niche model predictions could be misleading when there is a mismatch between the sampling resolution of the species data and that of the environmental predictors. Perhaps more critically, there is likely a mismatch between the resolution of the environmental parameters and habitat features critical for the establishment and local continuation of a species. The half degree grid likely missed the more variable environmental conditions of many of the bays and estuaries, which are important habitat for many of these species. For example, along the west coast of North America, *Carcinus maenas* is restricted to protected (semi-enclosed) bays and estuaries. Many of these bays do not extend to 0.5 degrees latitude by 0.5 degrees longitude and therefore their important microclimates, areas that may be key breeding and larval development grounds in an otherwise harsher surrounding environment, may not be represented. We have started preliminary work, along with EPA and USGS, to follow up on the global scale predictions here with a finer grain analysis to indicate which specific estuaries could support these and other NIS.

Finally, we wish to incorporate vector analysis and potential biotic resistance with the ecological niche modeling projections. The projections from our models identify areas with high environmental match for the species. This is a useful first step in risk evaluation: it can help identify suites of organisms that have the potential to invade specific areas. A logical second step would be to combine these environmental match projections with an evaluation of vector strength (likelihood of introduction) to estimate invasions risk for these areas. For example, in the most pertinent study to date, Herborg et al. (2007) combine environmental niche models with vector analysis to predict ports and bays with the highest risk of invasion by the catadromous Chinese mitten crab, *Eriochier sinensis*. The potential establishment of high risk species, then could be further evaluated by using information on reproductive ecology, such as the degree of self recruitment and connectivity with other populations, and community ecology that includes the effects of biotic interactions (as discussed in Guisan & Thuiller 2005).

CONCLUSIONS

The ecological niche modeling explored here, especially those developed sampling data from all the ranges of each species, produced useful forecasts of the potential future spread of marine nonindigenous species. All the models had low errors based on internal and external checks, and high overlap between multiple runs. They rarely missed predicting environmental match for existing populations, even those not used in model development. The models based on fewer data points, however, especially when drawn from invaded ranges performed the worst, and we recommend using data from all ranges to develop future models. All four species included in these models--*Balanus improvisus*, *Carcinus maenas*, *Littorina saxatilis*, and *Styela clava*--were predicted to find high environmental match in numerous areas beyond their present ranges, including Alaskan coastal waters. The predictions of geographic distributions for *Carcinus maenas* from our environmental niche models were similar to those based on the more labor-intensive models generated from temperature-dependent larval development experimental data and also from more basic, non-quantitative models. We now wish to explore these models further and to apply them to other species.

ACKNOWLEDGEMENTS

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LITERATURE CITED

- Ahyong ST (2005) Range extension of two invasive crab species in eastern Australia: *Carcinus maenas* and *Pyromaia tuberculata*. Mar Pollut Bull 50:460-462
- Anderson RP, Lew D, Peterson AT (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecol Model 162:211-232
- Araújo MB, Rahbek C (2006) How does climate change affect biodiversity? Science 313:1396-1397
- Araújo MB, Whittaker RJ, Ladle RJ, Erhard M (2005) Reducing uncertainty in projections of extinction risk from climate change. Global Ecol Biogeogr 14:529-538
- Araújo MB, Thiller W, Pearson RG (2006) Climate warming and the decline of amphibians and reptiles in Europe. J Biogeogr 33:1712-1728
- Behrens Yamada S, Hunt C (2000) The arrival and spread of the European green crab, *Carcinus maenas* in the Pacific Northwest. Dreissena! 11(2):1-7
- Carlton JT, Cohen AN (1998) Periwinkle's progress: the Atlantic snail *Littorina saxatilis* (Mollusca: Gastropoda) establishes a colony on Pacific shores. Veliger 41(4):333-338
- Carlton JT, Cohen AN (2003) Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *C. aestuarii*. J Biogeog 30: 1809-1820
- Cohen AN, Carlton JT, Fountain MC (1995) Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Mar Biol 122:225-237

- Cohen AN, Carlton JT (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. (link on ANSTF website)
- Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. *Science* 279:555-558
- de Rivera CE, Ruiz GM, Crooks JA, Wasson K, Lonhart SI, Fofonoff P, Steves BP, Rumrill SS, Brancato MS, Pegau WS, Bulthuis DA, Preisler RK, Schoch GC, Bowlby E, DeVogelaere A, Crawford MK, Gittings SR, Hines AH, Takata L, Larson K, Huber T, Leyman AM, Collinetti E, Pasco T, Shull S, Anderson M, Powell S (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 pp
- de Rivera CE, Ruiz GM, Hines AH, Jivoff P (2005b) Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. *Ecology* 86:3364-3376
- de Rivera CE, Ruiz GM, Hitchcock NG, Teck SA, Steves B, Hines AH (2007) Larval development rate predicts range expansion of an introduced crab. *Mar Biol* 150:1275-1288
- Fofonoff PW, Ruiz GM, Steves B, Carlton JT (2003) In ships or on ships? Mechanisms of transfer and invasion for non-native species to the coasts of North America. In: Ruiz GM, Carlton JT (eds) *Invasive Species: Vectors and Management Strategies*, pp. 152-182. Island Press, Washington
- Fofonoff PW, Ruiz GM, Hines AH, Steves BP, Carlton JT (2006) Four centuries of estuarine biological invasions in the Chesapeake Bay region. In: Rilov G, Crooks J (eds) *Marine Bioinvasions: Ecology, Conservation, and Management Perspectives* (In revision)
- Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz C (2004) Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution* 58(8):1781-1793
- Grinnell J (1917) The niche relationship of the California Thrasher. *Auk* 34: 427-433
- Grosholz ED, Ruiz GM (1995) Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. *Mar Biol* 122:239-247
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993-1009
- Henry DP, McLaughlin PA (1975) The barnacles of the *B. amphitrite* complex (Cirripedia, Thoracica). *Zoologische Verhandelingen* 141:1-254
- Herborg LM, Jerde CL, Lodge DM, Ruiz GM, MacIsaac HJ (2007) Predicting invasion risk using measures of introduction effort and environmental niche models. *Ecol Appl* 17(3):663-374
- Hewitt CL, Campbell ML, Thresher RE, Martin RB, Boyd S, Cohen BF, Currie DR, Gomon MF, Keough MJ, Lewis JA, Lockett MM, Mays N, McArthur MA, O'Hara TD, Poore GCB, Ross DJ, Sotrey MJ, Watson JE, Wilson RS (2004) Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. *Mar Biol* 144:183-202
- Hines AH, Ruiz GM (2000) Biological invasions of cold-water coastal ecosystems: Ballast-mediated introductions in Port Valdez/Prince William Sound, Alaska. Final Report. Valdez, AK: Regional Citizens' Advisory Council of Prince William Sound; 2000
- Hutchinson GE (1957) Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415-427; Reprinted in 1991: Classics in Theoretical Biology. *Bull Math Biol* 53:193-213

- Iguchi K, Matsuura K, McNyset KM, Peterson AT, Scachetti-Pereira R, Powers KA, Vieglais DA, Wiley EO, Yodo T (2004) Predicting invasions of North American basses in Japan using native range data and a genetic algorithm. *Transactions of the American Fisheries Society* 133(4):845–854
- 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. littorea*)? *Mar Biol* 99:507-513
- Joska MA, Branch GM (1986) The European shore-crab- another alien invader? *African Wildlife* 40:63-65
- Lang WH, Marcy M (1982) Some effects of early starvation on the survival and development of barnacle nauplii, *Balanus improvisus*. *J Exper Mar Biol Ecol* 60(1):63-70
- Martínez-Meyer E, Peterson AT, Hargrove WW (2004) Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecol Biogeogr* 13:305-314
- McGee S, Piorkowski R, Ruiz G (2006) Analysis of recent vessel arrivals and ballast water discharge in Alaska: Toward assessing ship-mediated invasion risk. *Mar Poll Bull* 52:1634-1645
- Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. *Nature* 421:625-627
- Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, Miles L, Segurado P, Dawson TP, Lees DC (2006) Model-based uncertainty in species range prediction. *J Biogeogr* 33:1704-1711
- Pereira RS (developer), Stockwell D (original GARP algorithm developer), Desktop GARP version 1.1.6, University of Kansas Biodiversity Research Center, <http://www.lifemapper.org/desktopgarp/>
- Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modeling. *Qt Rev Biol* 78(4):419-433
- Peterson AT, Vieglais DA (2001) Predicting species invasions using ecological niche modeling. *Bioscience* 51:363-371
- Peterson AT, Sánchez-Cordero V, Soberón J, Bartley J, Buddemeier RW, Navarro-Sigüenza AG (2001) Effects of global climate change on geographic distributions of Mexican Cracidae. *EcoModel* 144:21-30
- Peterson AT, Papes M, Kluza DA (2003) Predicting the potential invasive distributions of four alien plant species in North America. *Weed Science* 51:863-868
- Reid DG (1996) *Systematics and Evolution of Littorina*. The Ray Society. Intercept, ltd. Andover, Hampshire, England. 463 pp
- Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. *Annu Rev Ecol Syst* 31:481-531
- Ruiz GM, Huber T, Larson K, McCann L, Steves B, Fofonoff P, Hines AH (2006) Biological invasions in Alaska's coastal marine ecosystems: establishing a baseline. Final Report submitted to Prince William Sound Regional Citizens' Advisory Council and U.S. Fish & Wildlife Service. 112p
- Stachowicz JJ (2001) Mutualism, facilitation, and the structure of ecological communities. *Bioscience* 51:235-246

- Stachowicz, JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. *Science* 286:1577-1579
- Stockman AK, Beamer DA, Bond JE (2006) An evaluation of a GARP model as an approach to predicting the spatial distribution of non-vagile invertebrate species. *Diversity Distrib* 12:81-89
- Stockwell DRB, Peterson AT (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling* 148:1-13
- Torchin ME, Lafferty KD, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. *Nature* 421:628-630
- Wolfe LM (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. *American Naturalist* 160:705-711