

# Predicting a range shift and range limits in an introduced tropical marine invertebrate using species distribution models

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Received: 12 March 2015 / Revised: 12 June 2015 / Accepted: 15 June 2015  
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**Abstract** A major goal of invasion biology is to predict range shifts and potential range limits of non-native species. Species distribution models (SDMs) are commonly used to achieve these goals, but the predictive accuracy of these models is rarely tested using natural range shifts. The barnacle *Megabalanus coccopoma* is native to the eastern tropical Pacific and has been introduced to a number of locations globally including the southeastern United States. During the unusually cold winter months of 2010, the range of *M. coccopoma* within the USA SE retracted 825 km. The ability of the SDM MaxEnt to accurately predict the range retraction and *M. coccopoma*'s range within the USA SE was tested using distributional data from before and after the range retraction. Three MaxEnt models were trained using data from the global range, the native range, and the USA SE introduced range.

Only the model trained on data from the USA SE was able to accurately predict the entire extent of the range retraction and most known populations prior to the range retraction. Globally trained models may provide the most conservative estimates of potential distributions; however, niche shifts may limit the ability of these models to accurately predict range shifts.

**Keywords** Range shift · *Megabalanus coccopoma* · MaxEnt · Cold tolerance · Niche shift

## Introduction

All species experience periods of range expansion and contraction, yet there are few direct observational data on the dynamics of natural range fluctuations (Brown & Lomolino, 1998; Parmesan et al., 2005). Range fluctuations have historically occurred over longer time periods, but are now occurring more rapidly due to species introductions and climate change (Grosholz, 1996; Kinlan & Hastings, 2005; Sorte et al., 2010). Extreme climatic events permit range dynamics to be described over even shorter time scales, and the frequency of extreme weather events is predicted to increase with global climate change (Easterling et al., 2000). Species distribution models (SDMs) are commonly used to predict shifts in species' distributions associated with climate change and introduced species (de Rivera et al., 2011), but the predictive accuracy of

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Handling editor: John Havel

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**Electronic supplementary material** The online version of this article (doi:10.1007/s10750-015-2376-0) contains supplementary material, which is available to authorized users.

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these models is not commonly validated using historical range shifts (for exceptions see: Araújo et al., 2005; Lima et al., 2007; Jones et al., 2009; Hilbish et al., 2012).

In most cases, SDMs trained to predict the potential extent of invasive species are trained using presence samples from both the native range and invaded range(s) because these models typically outperform models trained using presence data from only the native or invaded range(s) (Broennimann & Guisan, 2008; de Rivera et al., 2011). SDMs resulting from inclusion of all of the distribution points are thought to perform better because these models may more closely approximate the fundamental niche, although the fundamental niche is rarely fully described (Araújo & Peterson, 2012). Factors such as biotic interactions and dispersal limitation generally play a larger role in limiting the environmental niche within the native range than in the introduced range (Torchin et al., 2003; DeWalt et al., 2004). When species are transported to new habitat types outside of the native range, these barriers may no longer exist and as a result habitat types that were excluded in the native range can now be occupied in the introduced range.

Niche shifts occur when an introduced species occupies environmental conditions outside of those experienced in the native range (Pearman et al., 2008). Niche shifts can result from differences in the range limiting mechanisms among regions, rapid evolution in the introduced range leading to a change in the fundamental niche, or founder effects leading to variation in environmental tolerances in introduced genotypes (Alexander & Edwards, 2010). Niche shifts are most commonly documented through the use of SDMs when inconsistent SDM predictions are found between models trained in the native and introduced ranges (Broennimann et al., 2007; Medley, 2010). Most studies documenting niche shifts suggest that rapid evolution or subsampling of locally adapted populations from the native range are the underlying causes of the niche shift. Rapid evolution is possible (Lee & Bell, 1999), and environmental tolerances can vary among populations (Park et al., 2012). Alternatively, inconsistent predictions between SDMs may result from spatial differences in the range limiting mechanism(s) between the native and introduced ranges (Soberón & Peterson, 2011; Woodin et al., 2013), especially when low levels of genetic

differentiation and similar levels of diversity exist among native and introduced populations. However, it is not possible to determine whether any shift is due to evolutionary changes in the fundamental niche or changes in the range limiting mechanism unless the fundamental niche is definitively described (Peterson, 2003).

The tropical barnacle *Megabalanus coccopoma* (Darwin, 1854) is native to the eastern tropical Pacific and was first documented along the shorelines of Florida, Georgia, South Carolina, and North Carolina in 2006 (Crickenberger & Moran, 2013). Genetic evidence collected to date suggests the barnacle is globally panmictic. Native and introduced populations of *M. coccopoma* are not genetically differentiated from each other, genetic diversity in introduced populations is similar to the genetic diversity of native populations, and there is no evidence of genetic admixture in introduced populations (Yamaguchi et al., 2009; Cohen et al., 2014). The introduction of *M. coccopoma* to the USA SE is relatively recent, but several lines of evidence suggest this barnacle is in equilibrium with its environment in this region. In 2006, *M. coccopoma* colonized the entirety of its current range with its northern limit occurring near Cape Hatteras, NC, a well-established biogeographic break (Spalding et al., 2007; Crickenberger, 2014). Between 2006 and 2009, seasonal populations were known to occur north of Cape Hatteras to Kitty Hawk, NC. These seasonal populations would recruit during the spring, summer or fall and then die-back during the winter (Crickenberger & Moran, 2013). During the exceptionally cold months of the winter of 2010, the range of *M. coccopoma* retracted back to northern Florida, but was re-established north to its previous northern range limit by the summer of 2012. The establishment of the northern range limit for permanently established populations in the same location at two different time points suggests *M. coccopoma* is in climate equilibrium within the USA SE.

The winter months of 2010 were the coldest in more than 30 years in the USA SE (National Climate Data Center, 2010) and resulted in localized extinctions or reductions in abundance of a number of tropical marine invaders (Canning-Clode et al., 2011; Firth et al., 2011; Spinuzzi et al., 2013). The die-offs were most likely associated with an extremely cold 25 day period during January 2010, and possibly the less extreme dips in temperature during February and

March 2010 (Canning-Clode et al., 2011). It is unknown whether the observed mortality in most of these species was a consequence of short-term exposure to the exceptionally cold minimum during the valley of this cold snap or if the mortality was caused by long-term exposure to colder-than-average temperatures during the 25 day cold period.

The purpose of this study was twofold. First, the presence and absence records of *M. coccopoma* collected before and after the range retraction in the USA SE and distributional data from a number of other locations were used to better understand whether acute or long-term exposure to cold temperatures was responsible for the range shift and range limits in this species. Second, these same data were used to test the predictive accuracy of SDMs trained on all known presence points globally, presence data from the native range, and presence data from the invasive range (Atlantic USA SE).

## Materials and methods

### Presence and absence records

*Megabalanus coccopoma* is a large, lower intertidal barnacle native to the eastern tropical Pacific that has successfully established populations worldwide (Henry & McLaughlin, 1986; Crickenberger & Moran, 2013). Established populations of *M. coccopoma* are known from the USA SE (Gilg et al., 2010; Crickenberger, 2014), Brazil (Széchy & Paula, 2000; Young, 2000; Breves-Ramos et al., 2005; Farrapeira et al., 2007; Silveira et al., 2007; Souza et al., 2007), the Atlantic coast of Mexico (Celis et al., 2007), southern Japan, the east coast of Australia (Yamaguchi et al., 2009), and western Africa (Kerckhof et al., 2010). Seasonal populations exist north of Cape Hatteras, NC in the USA SE (Crickenberger & Moran, 2013), in the North Sea off the coasts of Belgium and the Netherlands (Nilsson-Cantell, 1932; Kerckhof & Cattrijsse, 2001; Kerckhof, 2002; Wolff, 2005), and have been reported in southern California following an El Niño year (Newman & McConnaughey, 1987).

The presence and absence records were collected from a variety of sources including primary literature, biogeographic databases, and personal communications; only presence records were used in SDM training. A total of 172 occurrences were documented

prior to the USA SE range retraction in 2010. Occurrences included 46 presence records and three absence records from the native range, 64 presence records and three absence records from the invaded range (USA SE), and 156 presence records and 16 absence records globally, which encompasses the native range, the USA SE invaded range, and other invaded locations. A total of three presence records and 11 absence records from the year of the range retraction (2010) were documented in the USA SE invaded range. All absence records were from sites with known seasonal populations. In some cases, presence locations occurred in estuaries or bays that were excluded due to the resolution of the land mask and environmental data rasters. In these cases, location points were moved to the closest environmental raster cell (Verbruggen, 2012a).

### Environmental data

Environmental data including annual average salinity (1961–2009) and annual averages based on monthly maximum, minimum, mean, and range chlorophyll concentration (2002–2009) were acquired from Bio-ORACLE at a 0.083° resolution (Tyberghein et al., 2012). Reynolds optimally interpolated daily sea surface temperature (SST) data (Reynolds et al., 2007) were downloaded at a 0.25° resolution from 1 January 2006 to 31 December 2010 using MGET, which is a suite of tools for working with marine spatial data in ArcGIS (Roberts et al., 2010). Daily temperature rasters were then used to calculate mean, maximum, minimum, and range daily sea surface temperature (SST) and the number of extremely cold days (the number of days when SSTs were less than 12°C) for each year from before the range retraction (2006–2009) and for the year of range retraction (2010) using ArcGIS 10. Annual averages from before the range retraction (2006–2009) were calculated for SST mean, maximum, minimum, range, and the number of extremely cold days. We used this time period because *M. coccopoma* was first documented along the Atlantic USA SE coast in 2006 (Crickenberger & Moran, 2013), and a number of introduced tropical marine invertebrates in the USA SE also experienced die-offs in 2010 (Firth et al., 2011; Canning-Clode et al., 2011). The threshold used to define the number of extremely cold days (the number of days when SSTs were less than 12°C) was based on

physiological sensitivity of another crustacean, *Petrolisthes armatus* (Gibbes, 1850), that is also introduced to the USA SE, has a native range matching that of *M. coccopoma*, and suffered dramatic decreases in abundance within the USA SE during the cold months of 2010. In laboratory experiments with the crab *P. armatus* exposure to temperatures less than 12°C for 19 days resulted in 100% mortality (Canning-Clode et al., 2011). We chose to use the temperature threshold of 12°C to define the number of extremely cold days because comparable data do not exist for *M. coccopoma*.

Environmental rasters were brought to a uniform cell size (0.083°, ~9 km) and extent (70°N, 180°W, 70°S, 180°E). A uniform landmask was applied to all environmental data, and missing coastal temperature data were bilinearly interpolated (Verbruggen, 2012b). Environmental data were then clipped to within 300 km of the coastline to eliminate background sampling within the MaxEnt models of locations where *M. coccopoma* is unlikely to occur because background sampling can strongly influence model predictions (Merow et al., 2013). MaxEnt compares background environmental data, which includes locations without presence data, to environmental conditions at known presence points to determine the environmental conditions suitable for the presence of a given species. Limiting background sampling to within 300 km of the coastline encompasses both nearshore habitat and offshore oil platforms and buoys where shallow water, intertidal, hard substrates suitable for *M. coccopoma* recruitment are common, but excludes locations further offshore where these types of substrates are very rare or non-existent. Environmental data to train the native range model and the USA SE model were further clipped to smaller extents to limit background sampling using marine biogeographic ecoregions as defined by Spalding et al. (2007). Marine biogeographic ecoregions for the native range model included those of the Eastern Tropical Pacific realm, and the USA SE model included the Floridian, Carolinian, and Virginian ecoregions (Fig. 1).

Temperature data and comparisons to measures of lethality

Poleward range boundaries can be determined by short-term exposure to acute limits to thermal

tolerance or by repeated long-term exposures (Woodin et al., 2013). To determine the distribution of temperatures that could lead to lethality over the short-term, annual average daily minimum SSTs (2006–2009) experienced within the Atlantic USA SE distribution and globally were examined for all known presence and absence locations of *M. coccopoma*. This distribution of daily minimum SSTs was then compared to acute lower thermal limits to lethality (LT<sub>50</sub>) (Crickenberger, 2014). To determine the distribution of temperatures that could lead to mortality over longer time periods, the number of extremely cold days (the number of days when SSTs were less than 12°C; annual average 2006–2009) was examined for all known presence and absence locations within the Atlantic USA SE and globally.

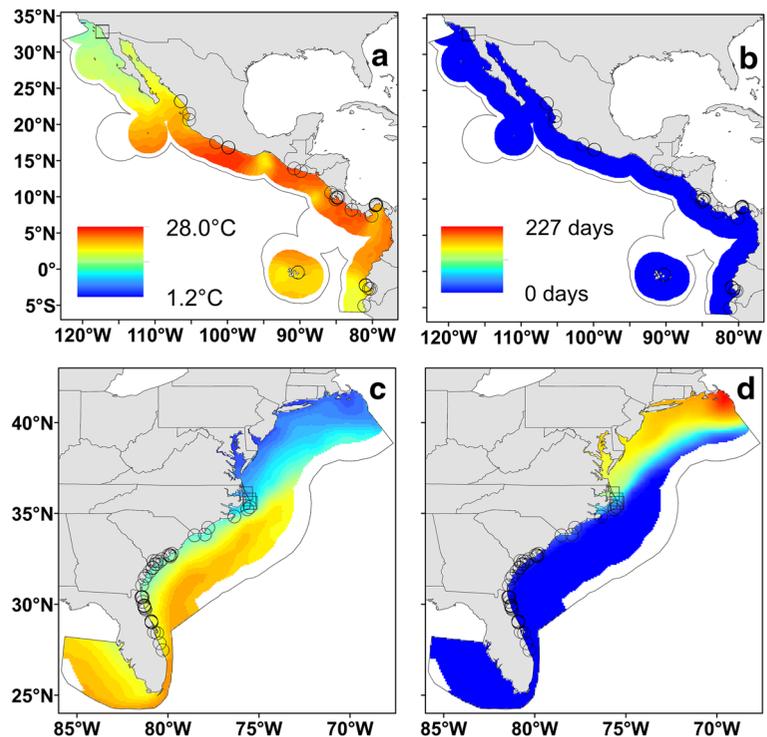
### Species distribution modeling

MaxEnt models were trained on three different datasets to predict the distribution of *M. coccopoma* in the USA SE before and after the range retraction. The first MaxEnt model was trained on all known presence points (dates of records ranging from 1957 to 2009; 71 presence records) and global environmental data. The second MaxEnt model was trained using only presence data from the native range (dates of records ranging from 1957 to 2005; 19 presence records) and environmental data clipped to this region. For the third MaxEnt model, the presence data from the Atlantic USA SE (dates of records ranging from 2006 to 2009; 29 presence records) and environmental data clipped to this region were used.

### MaxEnt

MaxEnt is a machine-learning-based SDM that compares environmental data found at presence locations to background environmental data to predict species' distributions. MaxEnt is a widely used SDM for predicting both range shifts and the potential distributions of introduced species that outperforms other presence-only SDMs (Elith et al., 2011; Merow et al., 2013). MaxEnt version 3.3.3 (Phillips et al., 2006; Phillips & Dudík, 2008) models were trained using presence locations documented prior to 2010 culled to include one presence point per environmental raster cell to avoid spatial bias in model training. All

**Fig. 1** Reynolds optimally interpolated daily sea surface temperature (SST) in the native and USA SE introduced ranges of *Megabalanus coccopoma*. Native range **a** average daily minimum and **b** the number of extremely cold days (SST < 12°C). USA SE range **c** average daily minimum and **d** the number extremely cold days. *Open circles* represent present populations, and *open squares* represent seasonal populations. *Black lines* represent the biogeographic regions used to clip environmental data. All values were calculated as annual averages between 2006 and 2009



environmental variables were used to train the models because MaxEnt is a machine-learning-based approach that, contrary to traditional statistical models, is not strongly affected by correlations (Elith et al., 2011). Using the cross-validate procedure, randomly selected subsets of presence data were used for training (70%) and testing (30%) each model. Five replicate models were run for each scenario and averaged. All other settings were left as default to limit overfitting among models with fewer numbers of presences and to allow linear, quadratic, and hinge features to be used to train all of the models (Phillips et al., 2006, 2009). MaxEnt constrains model predictions using a regularization penalty that is inversely proportional to the sample size to prevent model overfitting on only a few presence records. Average model output was projected onto Atlantic USA SE environmental data from before and/or after the range retraction for each of the three scenarios outlined above. To assess the predictive accuracy of the models, maximizing the sum of sensitivity and specificity logistic threshold (max SSS) was applied to the average model predictions to maximize both the probability of predicting where *M. coccopoma* is

present (sensitivity) and absent (specificity) (Liu et al., 2013). In many cases where the potential distribution of introduced species is predicted, increased sensitivity (proportion of true presences) is preferred to specificity (proportion of true absences) to ensure that all potential introduction sites are monitored. However, the goal of this study was to determine the most accurate predictions of both presences and absences found before and after the range retraction so max SSS was used. Application of the threshold resulted in binary maps of predicted presence and absence for each model from before and after the range retraction. Presences and absences were used to calculate test omission rate (rate), Cohen's  $k$  statistic of similarity ( $\kappa$ ), and the true skill statistic (TSS) as measures of predictive accuracy (Allouche et al., 2006). Extrapolation to environmental conditions outside of the training range of MaxEnt can affect model predictions. Multivariate environmental similarity surfaces (MESS) analysis was used to assess the differences between the environmental conditions used to train the models and the environmental conditions into which the models predictions were projected (Elith et al., 2010).

## Results

### Temperature data and comparisons to measures of lethality

The acute lower lethal limit ( $LT_{50}$ ) of *M. coccopoma* has been estimated to be 2.3°C (Crickenberger, 2014), and no locations where *M. coccopoma* have been documented had temperatures colder than 2.3°C (annual average 2006–2009). Within the USA SE and globally, no locations where established populations of *M. coccopoma* are known to occur experienced more than 32 extremely cold days (the number of days when SSTs were less than 12°C; annual average 2006–2009). All absence locations within the USA SE experienced 48 or more extremely cold days both before and after the range retraction. Globally, all absence locations had 48 or more extremely cold days with the exception of three known seasonal records from San Diego, CA, which is north of the northern range limit in the native range. All three of these locations experienced one extremely cold day (Fig. 2).

### Globally trained model

Prior to the range retraction of 2010, the range of *M. coccopoma* in the Atlantic USA SE extended from Ft. Pierce, FL to Cape Hatteras, NC (34.3°N) with some seasonal populations north to Kitty Hawk, NC (36.1°N) (Fig. 3a). After the coldest months of 2010, the range of *M. coccopoma* in the USA SE retracted equatorward to northern Florida (Fig. 3e). The northern range limit of *M. coccopoma* was overpredicted when global presence and environmental data were used to train the MaxEnt model. Both known presence and absence populations were predicted to have populations present (Fig. 3b; rate =  $0 \pm 0$  SE;  $\kappa = 0.098 \pm 0.098$  SE; TSS =  $0.067 \pm 0.067$  SE). When projected onto the data for 2010, only the seasonal population at Kill Devil Hills, NC (36.0°N) was predicted to be absent (Fig. 3f; rate =  $0 \pm 0$  SE;  $\kappa = 0.034 \pm 0.016$  SE; TSS =  $0.073 \pm 0.034$  SE). Environmental conditions along the east coast of the USA in 2010 were similar to those used to train the model (Fig. 4a, e).

### Native trained model

The MaxEnt model trained on the native range of *M. coccopoma* underpredicted the barnacle's

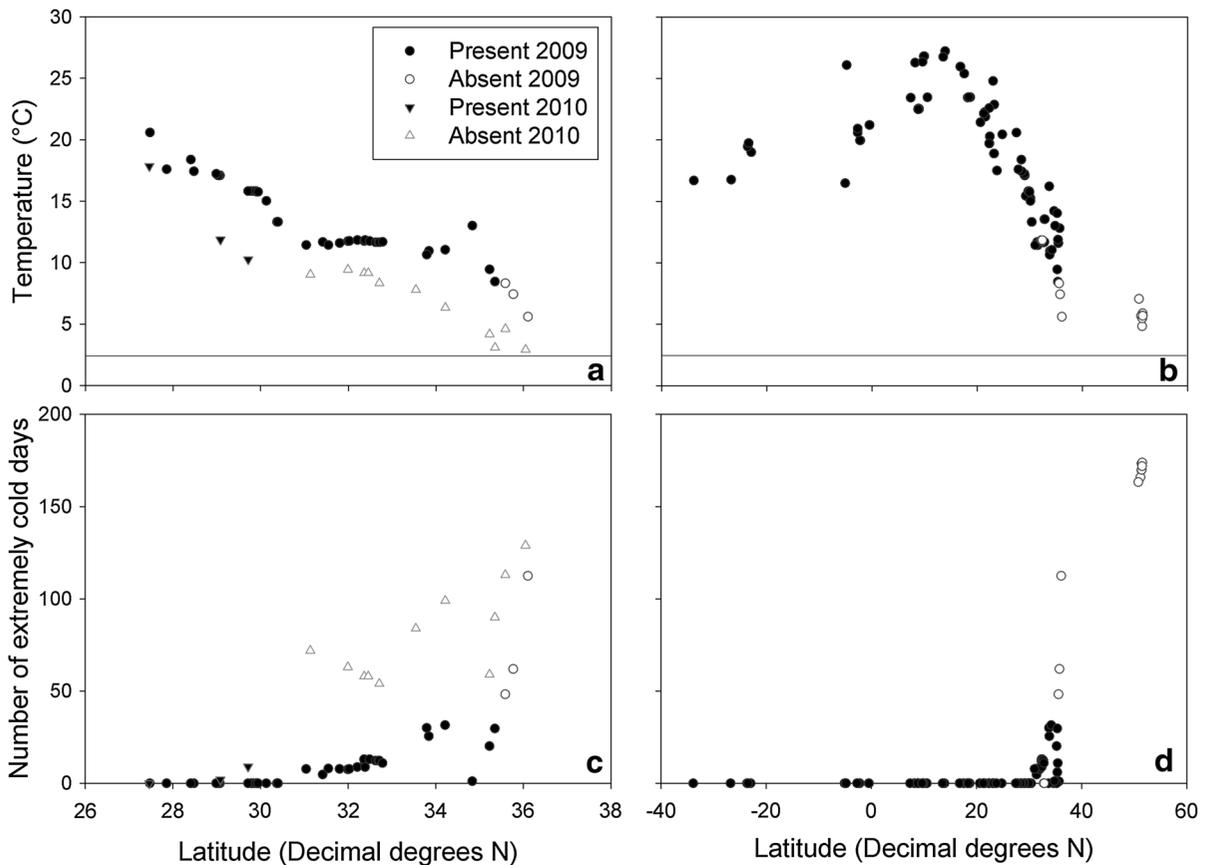
biogeographic distribution in the USA SE. *M. coccopoma* was predicted to be present south of St. Johns, FL (30.1°N) with the exception of the predicted absence at Sebastain, FL (27.9°N). North of St. Johns, FL *M. coccopoma* was predicted to be absent. Out of the 63 presence locations, 19 were accurately predicted as present and all of the absence locations were accurately predicted (Fig. 3c; rate =  $0.79 \pm 0.054$  SE;  $\kappa = 0.011 \pm 0.0044$  SE; TSS =  $0.21 \pm 0.054$  SE). Environmental conditions used to train the models were similar to those within the range of *M. coccopoma* in the USA SE prior to the range retraction, with the exception of a few areas where SST range was higher in the USA SE. Beyond the range limits of *M. coccopoma* in the USA SE, the number of extremely cold days was very different from the number found in the native range (Fig. 4b, f). When projected onto environmental data for 2010, only a single population was predicted to be present at Ft. Pierce, FL (27.5°N) and all other populations were predicted to be absent (Fig. 3g; rate =  $0.80 \pm 0.082$  SE;  $\kappa = 0.26 \pm 0.11$  SE; TSS =  $0.20 \pm 0.082$  SE). In 2010, environmental conditions were different both within and beyond the range of *M. coccopoma* along most of the east coast of the USA. Specifically, the number of extremely cold days and the SST range were unprecedented in the training region (Fig. 4c, g).

### USA SE only trained model

Predictions based on only USA SE presence and environmental data accurately predicted 62 out of 63 presence locations and all of the absence locations (Fig. 3d; rate =  $0.028 \pm 0.010$  SE;  $\kappa = 0.79 \pm 0.071$  SE; TSS =  $0.97 \pm 0.010$  SE). All populations were correctly predicted when the model was projected onto the SST data for 2010 (Fig. 3h; rate =  $0 \pm 0$  SE;  $\kappa = 0.96 \pm 0.038$  SE; TSS =  $0.98 \pm 0.018$  SE). Environmental conditions used to train the model were similar to those in the USA SE in 2010 (Fig. 4a, e).

### Contributions of environmental variables to model performance

MaxEnt calculates both the percent contribution of each environmental variable, which is dependent on the path used to train the model, and the permutation importance of each environmental variable, which is



**Fig. 2** Sea surface temperatures and the number of extremely cold days at known presence (*filled symbols*) and absence (*open symbols*) locations of *Megabalanus coccopoma* within the Atlantic USA SE and globally. Minimum daily sea surface temperatures within the **a** Atlantic USA SE and **b** globally with a

*horizontal line* depicting the lower lethal limit (2.3°C). The number of extremely cold days (number of days when SSTs were less than 12°C) within the **c** Atlantic USA SE and **d** globally

dependent on the final model. A large drop in permutation importance relative to percent contribution suggests the final model is heavily dependent on a particular variable (Phillips et al., 2006; Phillips & Dudík, 2008).

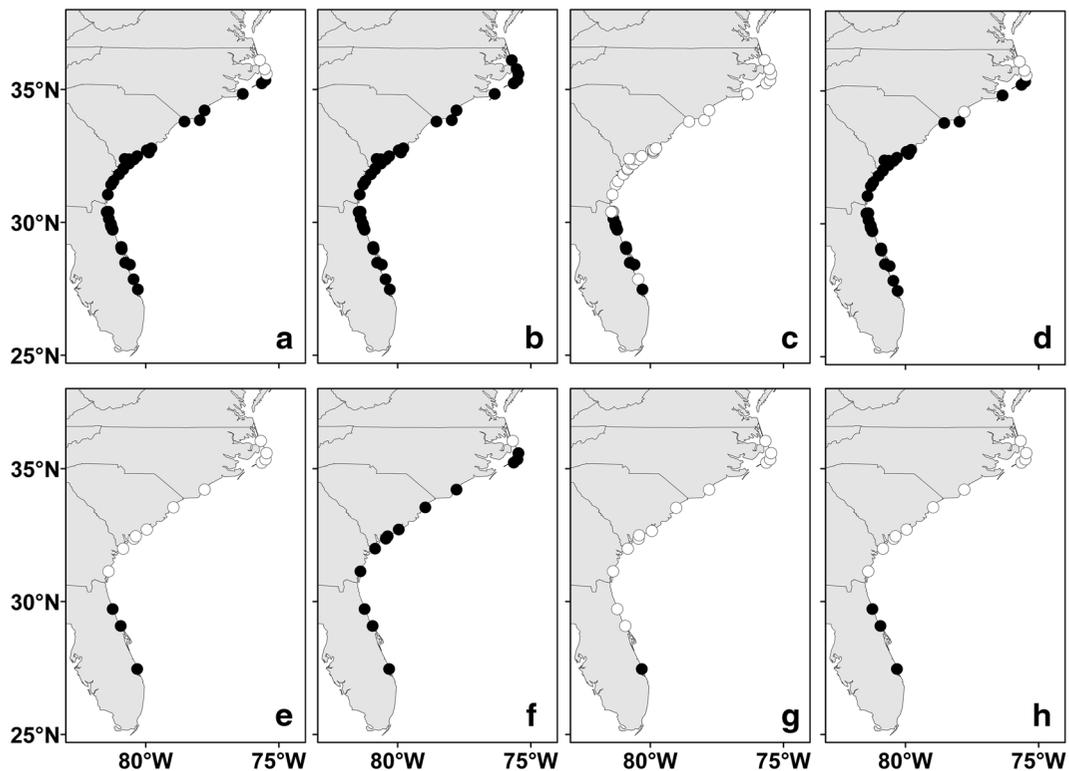
The global-range-trained model had the greatest percent contribution from the number of extremely cold days when compared to the other SST variables. Permutation importance did not decrease for any of the SST variables in this model (Table 1). In the model trained on the native range, SST minimum had the greatest percent contribution when compared to the other SST variables, and the number of extremely cold days had no influence in training the model. SST minimum had the largest drop in permutation performance when compared to the other SST variables

(Table 1). In the model trained on the USA SE range, the number of extremely cold days had the highest percent contribution compared to the other SST variables. Permutation importance values dropped for SST maximum and SST minimum (Table 1).

All models were strongly influenced by mean and maximum chlorophyll concentration (Table 1). Minimum chlorophyll, chlorophyll range, and salinity contributed little to increased performance in all models (Table 1).

## Discussion

Numerous studies have documented an improvement of the ability of SDMs to predict the distribution of

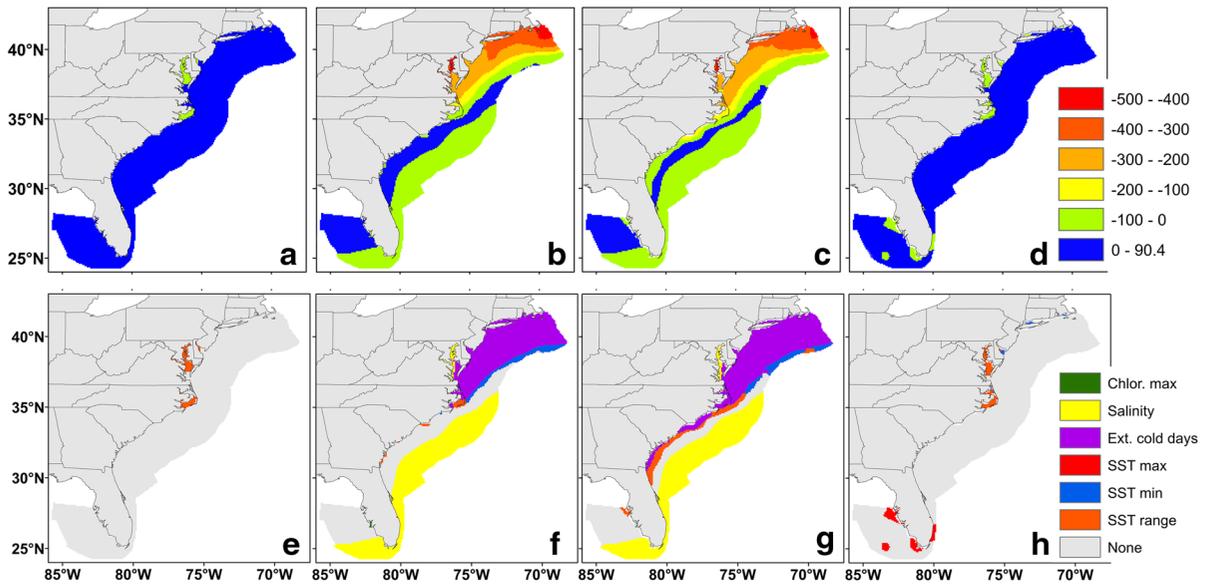


**Fig. 3** The distribution of *Megabalanus coccopoma* along the Atlantic USA SE coast **a** before and **e** after the range retraction displaying populations that were present (*black circles*) and absent or seasonal (*white symbols*) (see Crickenberger & Moran, 2013 for further details). Predictions of the average MaxEnt model based on the global range of *M. coccopoma* **b** prior to the range retraction and **f** after the range retraction. Predictions of

the average MaxEnt model based on the native range of *M. coccopoma* **c** prior to the range retraction and **g** after the range retraction. Predictions of the average MaxEnt model based on the USA SE distribution of *M. coccopoma* **d** prior to the range retraction and **h** after the range retraction. *Black circles* represent predicted presence locations and *white circles* represent predicted absence locations

introduced species in the introduced range when all known presence locations are included in the models to best describe the fundamental niche and, therefore, increase the probability of prediction in different geographic regions (Broennimann & Guisan, 2008; de Rivera et al., 2011). The goal is often to predict the potential distribution for future monitoring and prevention efforts. In these cases, overprediction (error of commission) is preferred to underprediction (error of omission) to ensure that all potential sites are monitored (Araújo & Peterson, 2012). However, if a niche shift has occurred, then predictions will be less accurate, and sometimes dramatically so (Alexander & Edwards, 2010; Medley, 2010). Globally trained models did accurately predict all locations where *M. coccopoma* have been found within the USA SE, whether they were seasonal or not, and predicted the

poleward range limit at Corolla, NC (36.4°N), which is just north of the most northern known seasonal population at Kitty Hawk, NC (36.1°N). However, the globally trained model overpredicted the northern extent of the range and failed to predict the range retraction (Fig. 3b, f). The imprecise predictions of the global model were due to a low dependence on any of the SST variables (no drops in permutation importance), which was likely the result of differences among the temperatures found near the poleward range limits in the native and the introduced ranges (Fig. 1). Sampling all known presence records does seem to be the best approach for predicting the potential ranges of invasive species (Alexander & Edwards, 2010; de Rivera et al., 2011), but niche shifts, such as the one in the USA SE range (supplementary Fig. 1), may lead to inaccurate predictions of



**Fig. 4** Multivariate environmental similarity surface (MESS) values and the most dissimilar variables (MoD) from MESS analyses of the environmental conditions in the training regions and the projected region in the USA SE for the models that were projected into novel environmental space. MESS values (a) and MoD (e) for the globally trained model projected onto the 2010

USA SE environmental data. MESS values (b) and MoD (f) for the native trained model projected onto the 2009 USA SE environmental data and MESS values (c) and MoD (g) for the 2010 USA SE environmental data. MESS values (d) and MoD (h) for the USA SE trained model projected onto the 2010 USA SE environmental data

**Table 1** Percent contribution and permutation importance of each variable for MaxEnt models trained on data from the global range, the native range, and the Atlantic United States southeast range

Variable	Global range		Native range		Atlantic US SE	
	Percent contribution	Permutation importance	Percent contribution	Permutation importance	Percent contribution	Permutation importance
Number of cold days	28.5	34.3	0	0	19	36.2
SST mean (°C)	3.9	28.8	0.3	0.1	0.1	0.5
SST maximum (°C)	6	7.3	0.3	2.9	11.5	9.9
SST minimum (°C)	0.3	0.9	9.9	5	7	1
SST range (°C)	8.2	19.5	3.2	5.9	0.1	0.3
Chlorophyll mean (mg/m <sup>3</sup> )	41.1	7.1	43.2	21.5	31.4	6.7
Chlorophyll max. (mg/m <sup>3</sup> )	9.1	1.8	37.8	63.6	24.1	41.2
Chlorophyll min. (mg/m <sup>3</sup> )	1.8	0	2.8	0.2	0.2	0.1
Chlorophyll range (mg/m <sup>3</sup> )	0.3	0.1	0.6	0.1	6.5	4
Salinity (PSS)	0.7	0.2	1.9	0.6	0	0.1

Number of cold days is the number of days less than 12°C and SST stands for sea surface temperature

range shifts when all known presence records are included in SDM training.

The MaxEnt model trained on native range data was unable to accurately predict the distribution of *M. coccopoma* in the Atlantic USA SE (Fig. 3c, g). For

*M. coccopoma*, the number of extremely cold days was a good predictor of the range limit and range retraction within the USA SE (Fig. 2), and the lack of predictive accuracy in the model trained on the native range was driven by low dependency on the number of

extremely cold days in training the model and the final model (Table 1). Numbers of extremely cold days similar to those found at the northern range limit in the USA SE do not occur in the native range (Fig. 4g, h). In fact, there were zero extremely cold days at any presence locations and only one extremely cold day at absence locations in the native range (Figs. 1, 2). Instead of being dependent on the number of extremely cold days, the training of the model was strongly influenced by SST minimum, and therefore, the distribution of SST minimum temperatures determined model predictions. SST minimum temperatures near the northern range limit of the native range of *M. coccopoma* match minimum temperatures found in northern Florida, and as a result, the model predicted the northern range limit to occur in this region of the USA SE (Figs. 1, 3).

The MaxEnt model trained on only USA SE data accurately predicted the distribution of *M. coccopoma* before and after the retraction (Fig. 3d, h). The number of extremely cold days was a good predictor of both the range limit and the range retraction in the USA SE (Fig. 2), and high predictive accuracy was partially the result of the number of extremely cold days contributing to training the model. Although the exact physiological mechanisms underlying cold-related mortality are unknown in *M. coccopoma*, the patterns described here suggest long term rather than acute thermal limits are responsible for determining the poleward range limit and the range retraction of *M. coccopoma* in the USA SE.

A number of factors other than temperature may set the northern range limit of *M. coccopoma* in its native range and as a result drive the differences found in model predictions. Biotic interactions are typically stronger in native ranges when compared to introduced ranges and can result in a smaller realized niche in the native range (Torchin et al., 2003; DeWalt et al., 2004). Predators of *M. coccopoma* have not been identified in either the native or introduced ranges, making comparisons difficult. Interspecific competition could also be a factor, and *M. coccopoma* would come into contact with a congener, *M. californicus* (Pilsbry, 1916), north of its native range limit. Interactions between these two species have not been examined, but may be important in limiting the range of *M. coccopoma* throughout the Baja Peninsula and Southern California. Oceanographic currents, and possibly extended larval development or the inhibition

of embryonic development at cool temperatures during the spawning season, are some other potential factors that might underlie northern range limits in this region and could work in concert with biotic interactions. The California Current flows southward along the western coast of the USA during much of the year, turns toward shore near Mexico's border, and continues along the length of Baja California until it turns westward into the North Equatorial Current (Fiedler & Talley, 2006). During El Niño years, patterns of oceanographic currents change, and these currents can transport subtropical water to more temperate latitudes and move more offshore water onto the shelf (Simpson, 1984a, b; Shanks & Eckert, 2005). Therefore, larvae may occasionally be transported northward during El Niño years, recruit, develop into adults, and then fail to successfully establish due to Allee effects, which are known to be particularly strong in barnacles because they are sessile animals with internal fertilization (Crisp, 1958; Kent et al., 2003). This pattern of widely spaced recruits that fail to form established populations is in agreement with a study by Newman & McConnaughey (1987), reporting a temporary range expansion that consisted of three widely spaced individuals of *M. coccopoma* in southern California following an El Niño event. One of the three barnacles was able to overwinter, but *M. coccopoma* did not establish permanent populations.

Based on thermal tolerances of larvae of *M. coccopoma* from the USA SE, temperatures should allow complete larval development and metamorphosis north to Point Conception in California (Stark et al., 2007; Crickenberger, 2014). However, development at colder temperatures in these more northern latitudes will increase the length of development and could lead to transport away from suitable habitat (Jackson & Strathmann, 1981). Shanks & Eckert (2005) found that nearshore species in the California Current System had short planktonic larval durations, released their pelagic larvae during times of weaker or fluctuating oceanographic currents, and had larvae that were found nearshore or near the sea floor; all of these factors would tend to reduce southern transport away from adult habitat. Species that are not native to the California Current System may lack these traits, suggesting adaptation of behavior and physiology at the larval stage may play an important role in setting the northern range limit of *M. coccopoma* in its native range.

Climate change and species introductions have resulted in dramatic shifts in species' distributions (Hickling et al., 2006; Sorte et al., 2010). As tropical species make their way into temperate climates, these range expansions may be punctuated by range retractions, which could affect estimates of rates of range expansion out of the tropics (Canning-Clode et al., 2011; Crickenberger & Moran, 2013). SDMs are useful tools for understanding the location and extent of range shifts; however, spatial variation in the mechanisms responsible for determining range limits in both historical and novel environments needs to be carefully considered to enable accurate predictions.

**Acknowledgments** The author would like to thank the staffs at GTMNERR, Sapleo NERR, ACE Basin NERR, and J. Crickenberger for assistance with sampling. Comments from Amy Moran and two anonymous reviewers significantly improved this manuscript. This research was conducted under an award from the Estuarine Reserves Division, Office of Ocean and Coastal Resource Management, National Ocean Service, National Oceanic and Atmospheric Administration to SC.

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