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Abstract:

Extant coelacanths (*Latimeria chalumnae*) were first discovered in the western Indian Ocean in 1938; in 1998, a second species of coelacanth, *Latimeria menadoensis*, was discovered off the north coast of Sulawesi, Indonesia, expanding the known distribution of the genus across the Indian Ocean Basin. This study uses ecological niche modeling techniques to estimate dimensions of realized niches of coelacanths and generate hypotheses for additional sites where they might be found. Coelacanth occurrence information was integrated with environmental and oceanographic data using the Genetic Algorithm for Rule-set Production (GARP) and a maximum entropy algorithm (Maxent). Resulting models were visualized as maps of relative suitability of sites for coelacanths throughout the Indian Ocean, as well as scatterplots of ecological variables. Our findings suggest that the range of coelacanths could extend beyond their presently known distribution and suggests alternative mechanisms for currently observed distributions. Further investigation into these hypotheses could aid in forming a more complete picture of the distributions and populations of members of genus *Latimeria*, which in turn could aid in developing conservation strategies, particularly in the case of *L. menadoensis*.

Text of paper:

Predicting suitable environments and potential occurrences for coelacanths (*Latimeria* spp.)

Hannah L. Owens*, Andrew C. Bentley, and A. Townsend Peterson

Department of Ecology and Evolutionary Biology, Natural History Museum & Biodiversity Institute,
University of Kansas
Dyche Hall, 1345 Jayhawk Blvd., University of Kansas, Lawrence, KS 66044-7593

*Corresponding author. E-mail: hannah-o@ku.edu; office: +1-785-864-3369; fax: +1-785-864-5335

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Abbreviations:

- ENM: Ecological Niche Modeling
GARP: Genetic Algorithm for Rule-Set Prediction
GBIF: Global Biodiversity Information Facility
OBIS: Ocean Biogeographic Information System
MESS: Multivariate Environmental Similarity Surface

Introduction:

The order Coelacanthiformes, notable as an apparent link between lungfishes and tetrapods, was originally known only from fossils that were more than 80 million years old (Holder, *et al.*, 1999). In 1938, the first known specimen of an extant species of coelacanth, *Latimeria chalumnae*, was discovered off the east coast of Africa (Smith, 1939). *Latimeria chalumnae* is now known to inhabit a range encompassing the east coast of Africa from Kenya to South Africa, and extending east to Madagascar and the Comoros Islands. In 1997, a second species of coelacanth, *L. menadoensis*, was discovered off the northeast coast of Sulawesi, Indonesia (Erdmann, *et al.*, 1998). *Latimeria menadoensis* cannot be differentiated conclusively from its African sister species on the basis of morphology, but the species diverge substantially enough in their genetics that they are recognized as unique lineages (Holder, *et al.*, 1999). The IUCN currently lists *L. chalumnae* as critically endangered and *L. menadoensis* as vulnerable (IUCN, 2011). Further investigations into the evolutionary relationships, biogeography, life history and appropriate conservation status of this genus are hampered by their rarity in their natural environment and their inaccessibility: coelacanths typically live at depths of 100-300 m in underwater caves on steep, rocky cliffs, emerging only at night to feed (Fricke and Hissmann, 2000).

This study seeks to contribute to the understanding of distributions of *Latimeria* by generating hypotheses for additional sites where the environment might be suitable for coelacanths using ecological niche modeling (ENM). The distribution of a species is limited by the interactions between biotic and abiotic factors, as well as dispersal capability—the realized niche of a species (Soberón, 2007). ENMs ideally arrive at an estimation of the realized niche of a species after being trained in a geographic area limited to habitats that are accessible to the species of interest (Barve, *et al.*, 2011). Biotic factors, which are challenging to model explicitly, may nonetheless be implicitly represented in the model because they strongly correlate with abiotic factors, or disappear because such fine-scale interactions disappear in large-scale analysis (Soberón and Nakamura, 2009). Projections of such models into other geographic areas are primarily an expression of abiotic niche—the combinations of environmental factors that, based on the model's estimations, are most similar to areas where the species is known to occur.

ENM is a technique that has been implemented successfully for prediction and subsequent field verification of additional localities of known endangered species (Siqueira, *et al.*, 2009) and to focus searches for new species (Raxworthy, *et al.*, 2004). Such studies often are subject to very low sample sizes, which pose methodological challenges but are still useful, especially if researchers adopt a conservative interpretation of model results as areas similar to those from which a species is known (Pearson, *et al.*, 2007). While ENM applications to marine ecosystem studies are not new (e.g. Wiley, *et al.*, 2003), this methodology has yet to be applied explicitly to the problem of locating suitable habitat for reclusive marine species. In the present case, to the extent that coelacanth niche characteristics are conservative in their evolution (c.f., Peterson, 2011), such models may help in focusing future searches for new populations — or even additional species — of coelacanths.

Materials and Methods:

Occurrence locality records for *Latimeria chalumnae* were downloaded from the Ocean Biogeographic Information System (OBIS) database via the Global Biodiversity Information Facility (GBIF) biodiversity information portal (<http://www.gbif.org>); data were quality-controlled by removing duplicate records, records sharing cells at the resolution of our data layers, and data points which did not fall within the area covered by these layers (e.g. terrestrial records). This information was supplemented with data from submersible sightings (South African Institute for Aquatic Biodiversity/African Coelacanth Ecosystem Programme/JAGO-Team), which were also reduced to unique localities. Two *L. menadoensis* locality records were taken from Erdmann (1999) and Erdmann *et al.* (1999). All localities used are listed in Table 1.

To limit over-fitting ENMs (Peterson, *et al.*, 2007) the number of environmental variables was restricted to 13. Data on world ocean bathymetry were drawn from Amante and Eakins (2009); slope and aspect were calculated from bathymetry in ArcGIS 9.3 (ESRI, Redlands, CA) to incorporate documented preferences of these fish for steep slopes (Fricke and Hissmann, 2000). Worldwide sediment thickness estimates, used as a proxy for substrate type, were supplied by the National Geophysical Data Center (Divins, 2009). Owing to scarcity of detailed knowledge of definitive ecological preferences of the species, we used datasets with previously demonstrated predictive power for a number of marine fish species (Wiley, *et al.*, 2003) summarizing benthic temperature, salinity, dissolved oxygen, percent oxygen saturation, apparent oxygen utilization, phosphate, silicate, nitrate, and chlorophyll were derived from NOAA's World Oceanic Atlas 1998 (NOAA, 1999). Preliminary ENM runs using parameters as described below were run, jackknifing environmental variables. To investigate the amount of noise introduced by each variable, suitability scores of each jackknifed model were qualitatively compared to the known range of *L. chalumnae* to assess the degree to which individual variables influenced the model's ability to predict the range of the species.

Latimeria chalumnae occurrence data were integrated with environmental data via two common ENM algorithms: a maximum entropy algorithm (Maxent; Phillips, *et al.*, 2006) and a genetic algorithm (GARP; Stockwell and Peters, 1999). Models were trained using a region encompassing the western Indian Ocean from the approximate tip of the Indostanic Peninsula in the northeast to the Cape of Good Hope in the southwest. The GARP algorithm develops a model by choosing a rule iteratively to describe the occurrence-environment relationship, testing the rule's accuracy based on an independent random subset of occurrence points, and consequently evolving, accepting, or rejecting that rule. Desktop GARP (ver. 1.1.6; www.nhm.ku.edu/desktopgarp, Stockwell and Peters, 1999) was used to develop these models, deriving 1000 replicate models with 1250 pseudoabsence points, a 0.01 convergence limit and a maximum of 1000 iterations. Best subsets of model replicates were selected using 50% of the occurrence points for intrinsic model testing, with an omission error tolerance of 0%, producing 20 models for that omission tolerance and a commission error tolerance of 50%, resulting in a sample of 10 models (Anderson, *et al.*, 2003). Maxent estimates the suitability of each grid cell by generating a probability distribution of maximum entropy from environmental variable layers on that map subject to the constraints of observed presences. Maxent (ver. 3.2.19; www.cs.princeton.edu/~schapire/maxent, Phillips, *et al.*, 2006) models were developed using 10,000 background points, a maximum of 1000 iterations, a convergence threshold of 0.00001, and a random 50% of the data points set aside for intrinsic testing. Maxent generates an additional layer for "clamping" the model (i.e., extending the terminal values of suitability beyond the limits of environmental variables represented in the calibration region), incorporating combinations of environmental variables that do not exist in the training region in predictions that tends to lead to over-prediction; no clamping was tolerated in generating Maxent ecological suitability maps—cells with nonzero clamping scores were removed from the final projection. Maxent also calculates a multivariate environmental suitability surface (MESS) map indicating areas where environmental variables occur outside the range of values in the training region; ENM suitability projections in these regions are unreliable (Elith, *et al.*, 2010). ENMs were not developed for *L. menadoensis* owing to paucity of locality information available for this species.

As a consequence of the relatively small number of available locality records for *Latimeria chalumnae*, typical independent model validation approaches involving partitioning the data into training and testing subsets were inappropriate; instead, we used a jackknife approach to validate ENM that is specifically designed for

situations of small sample size (Pearson, *et al.*, 2007). In this method, independent GARP and Maxent models were generated iteratively, excluding one locality in each turn. The lowest suitability score of a presence point, or lowest presence threshold (LPT), for each model was then used to determine areas of predicted presence. The proportion of the training area predicted as present and the failure or success of the model to predict jackknifed points were then used to calculate the probability of the observed degree of coincidence between independent test data and predicted areas of suitability for *L. chalumnae*, as described by Pearson and colleagues (2007).

To provide a basis for comparison between our ENMs and previously collected ecological information, a coarse-resolution exploration of model rule parameters in environmental space for *Latimeria chalumnae* was visualized by taking a random sample of 5000 points from the training region. At each point, the abiotic variable values and the Maxent and GARP suitability scores were extracted, and scatterplot visualizations of the niche of these fish developed. Two scatterplots were generated for each model using environmental variables measured by Fricke and Hissmann (2000) describing the ecology of *L. chalumnae* in Jesser Canyon off the coast of South Africa: ocean depth versus salinity and temperature versus dissolved oxygen concentration. Each point represented a combination of variables that exists in the environment and was classified as unsuitable, suitable, or intermediate. For GARP models, points in which none of the 10 best models predicted potential for coelacanth occurrence were categorized as unsuitable, points in which all of the best models predicted potential for coelacanth occurrence were categorized as suitable, and all other points were categorized as representing intermediate suitability. For the Maxent model, suitability thresholds were chosen to yield the same percentage of each classification as the GARP model—for example, if 95% of the points were unsuitable according to GARP suitability scores, the points with the lowest 95% of Maxent suitability scores were also characterized as unsuitable.

Results:

Qualitative comparison of preliminary ENM runs in which environmental variables were jackknifed with the known range of *L. chalumnae* indicates that none of the variables incorporated introduced a disproportionate amount of noise into model results. Predictions of the potential distribution of *Latimeria chalumnae* in the western Indian Ocean as measured by the Pearson jackknife-based test procedure were significantly better than random expectations ($P > 0.01$) for both GARP and Maxent (Table 1). All 10 best subset GARP models trained using *L. chalumnae* occurrence points predicted habitat suitability for all *L. chalumnae* occurrences, and *L. menadoensis* occurrences were predicted by 3 of the 10 models. Maxent-estimated suitability at occurrence points for *L. chalumnae* ranged from 0.24 to 0.78, while suitability for *L. menadoensis* ranged from 0.63 to 0.64.

When all *Latimeria chalumnae* occurrence points were pooled to generate models identifying areas of suitable habitat across the Indian Ocean and western Pacific Ocean, these models identified potentially suitable sites scattered over the known range of the species where it has not as-yet been recorded (Figures 1a and 1b). These areas include most of the east coast of sub-Saharan Africa, as well as along the Mascarene Plateau, and the coasts of India, Indonesia, the Philippines, and the northern Australia. Worldwide projections of suitable habitat (Figures 2a and 2b) also indicate areas of suitability far from known coelacanth localities, including off the coasts of Argentina and the Lesser Antilles. Environmental differences between the training region and the worldwide projections are expressed in the form of a MESS map (Figure 3).

Ecological suitability maps were similar for both the GARP and Maxent models; however, some differences are notable in the suitability ranges of bathymetry, temperature, dissolved oxygen concentration, and salinity between the two models (Figures 4a-d). Perhaps most notable is the disagreement between Maxent and GARP as to whether low-temperature high-oxygen environments were unsuitable or merely unlikely habitat for *Latimeria chalumnae*. Combinations of field measurements of these variables reported in Fricke and Hissmann's (2000) study of coelacanth ecology were not well-represented in the sample (6 points from bathymetry vs. salinity plots, none from temperature vs. dissolved oxygen).

Discussion:

Species in general occur at sites that satisfy three sets of considerations (Soberón and Peterson, 2005; Pulliam, 2000). First, abiotic conditions must be suitable—these physical characteristics of environments are the focus of the analyses in this paper. Second, the biotic realm must be appropriate (i.e. the correct suite of positive interactor species present, and negative interactor species absent)—in this paper, because detailed information on biotic interactions is lacking, we implicitly assume that biotic dimensions will have abiotic correlates. Finally, a site must be accessible for dispersal to and colonization by the species: sites that are readily accessible will likely be inhabited by populations of the same species, while less accessible sites will either be uninhabited or perhaps inhabited by related species.

Owing to the small sample size of occurrence points used to generate ecological niche models, it would be unreasonable to expect these models to describe the complete realized niche of *L. chalumnae*; however, as they do describe dimensions of ecological space in which the species is known to occur, they are still of some utility. The models generated herein predict areas of suitable habitat well beyond the known localities of the two coelacanth species. Among these areas are several previously postulated as harboring coelacanths (although sightings remain unconfirmed), including localities locations off the northern coast of Madagascar and the islands of Mwali and Maore in the Comoros (Stobbs, 2002). Taking into account projection uncertainty as expressed by the MESS map in Figure 3, additional areas in the western Indian Ocean that show promise as potential coelacanth localities include parts of the Seychelles and the Mascarene archipelago, as well as the Malay Archipelago. Further investigation of these localities, informed by regional geology (i.e. the presence of caves) may provide insight into biotic and accessibility factors that influence the range of the coelacanths. Additional information gleaned by these investigations could contribute to a more complete picture of how best to conserve the rare *Latimeria* species.

There has been a great deal of speculation in the literature as to the nature of the disjunct distribution of the genus *Latimeria* in the Indian Ocean. Springer (1999) hypothesized that the genus had been continuously distributed off the shores of Africa and Eurasia, but that the collision of India with Eurasia had led to a vicariance event when the major rivers of India began depositing large amounts of silt in the Indian Ocean, rendering those areas of habitat unsuitable. Our findings lend support to Springer's hypothesis—suitable coelacanth habitat extends almost continuously along the coasts of the northern rim of the Indian Ocean, broken up by large areas of unsuitable habitat at the mouths of the Ganges and Indus Rivers.

When one compares the performance of GARP and Maxent models in predicting both the training species, *L. chalumnae*, and the second species, *L. menadoensis*, it becomes apparent that these algorithms do not behave entirely similarly. All ten GARP models predicted training points to be within suitable habitat, whereas only three predicted suitable habitat for *L. menadoensis*; in contrast, Maxent gave a wide range of suitability scores at training points (from 0.24 to 0.95), with the *L. menadoensis* points falling squarely into the suitability range (at 0.63 and 0.64). Maxent was able to predict one more jackknife point successfully than GARP, which echoes a pattern from previous studies (Pearson, *et al.*, 2007). Unfortunately, the occurrence sample size for *L. menadoensis* is too small to test niche conservatism conclusively in the group, or the differing abilities of the algorithms to predict sister species.

Conclusions:

Coelacanths are rare and reclusive fish about which little is known, so no definitive idea of the full extent of the range exists for either *L. chalumnae* or *L. menadoensis*. Ecological niche model predictions of suitable areas based on occurrence data for *L. chalumnae* through the oceans of the world, combined with rigorous efforts to ground-truth the models, may prove very useful in searches for new populations of coelacanths.

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Figure Legends:

Figure 1. Maps of areas identified as suitable for the species in model projections for *Latimeria chalumnae* projected across the Indian Ocean Basin, with a detail map of Sulawesi in Indonesia. *Latimeria chalumnae* localities are indicated by a filled dot (●) and *L. menadoensis* localities are indicated by a hollow dot (○). Suitability scores are represented by shades of blue, with darker shades indicating greater suitability. A rectangle of missing data exists in the East China Sea extending northeast from Taiwan up through the Ryuku Islands. (a) GARP (b) Maxent.

Figure 2. Maps of areas identified as suitable for the species in model projections for *Latimeria chalumnae* projected worldwide. (a) GARP (b) Maxent.

Figure 3. MESS map for *Latimeria chalumnae*. Cells shown in red indicate areas for at least one environmental variable value occurs outside the range of values in the training region.

Figure 4. Exploration of model rule parameters in environmental space for *Latimeria chalumnae*. X's represent overall availability of environmental combinations at intermediate levels of predicted suitability; black squares represent variable combinations found unsuitable, and white circles represent variable combinations found highly suitable. Gray lines represent the range of observed ecological variables experienced by *Latimeria chalumnae* in Jesser Canyon off the coast of South Africa (Fricke and Hissmann, 2000). (a,b) Bathymetry (m) versus salinity (ppt). (a) GARP. (b) Maxent. (c,d) Temperature vs. dissolved oxygen concentration. (c) GARP. (d) Maxent.

Table Legends:

Table 1. Occurrence Point Statistics. Occurrence points localities are followed by the source of the locality: submersible sighting—Sub., GBIF records—GBIF, or scientific literature—Lit. Also provided is a summary of model success in predicting the excluded point in question, and the percent of training area predicted as suitable. The last statistic is the suitability score of each point in GARP and Maxent models trained using all *Latimeria chalumnae* occurrence points.

Figure 1.

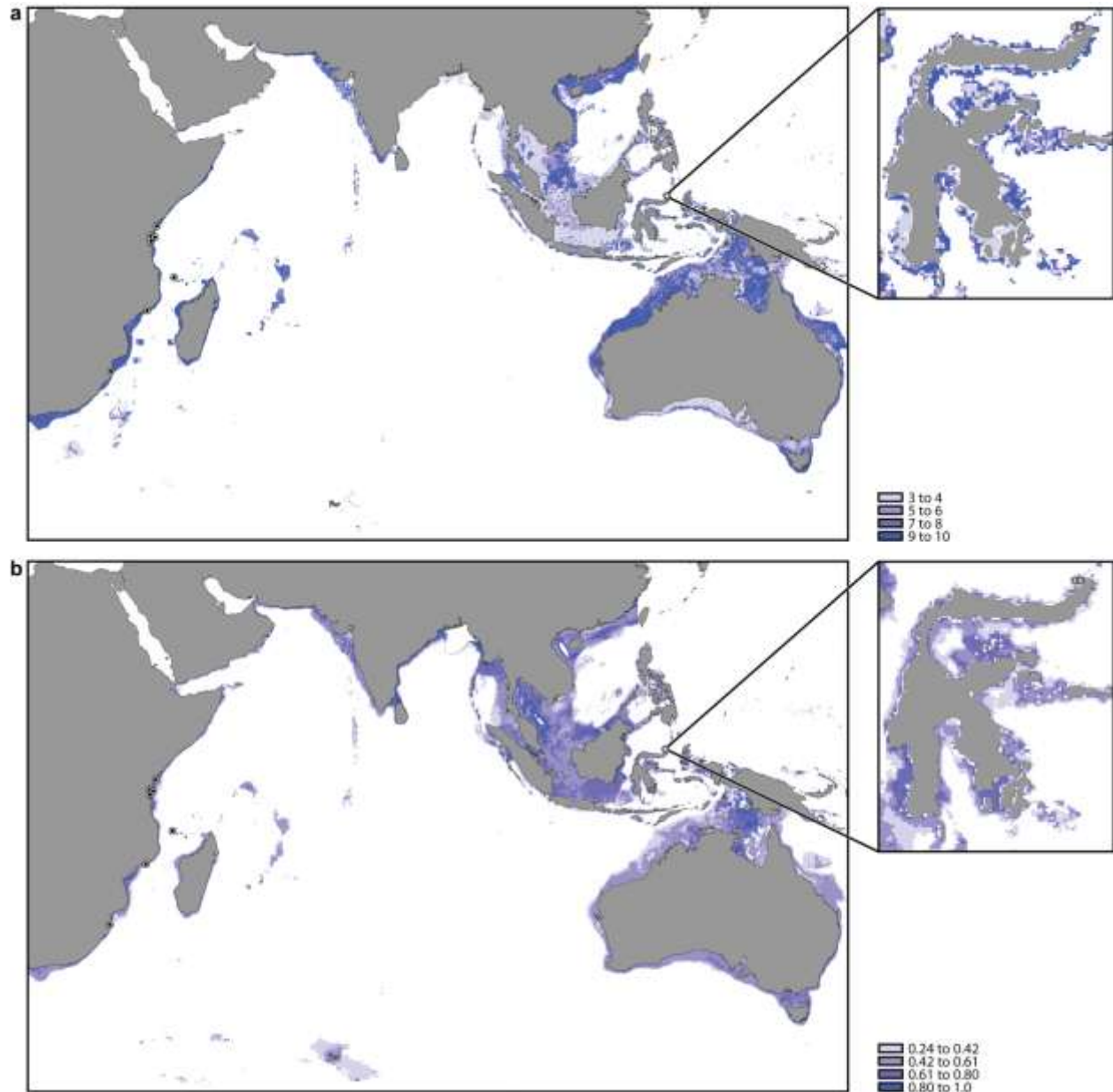


Figure 2.

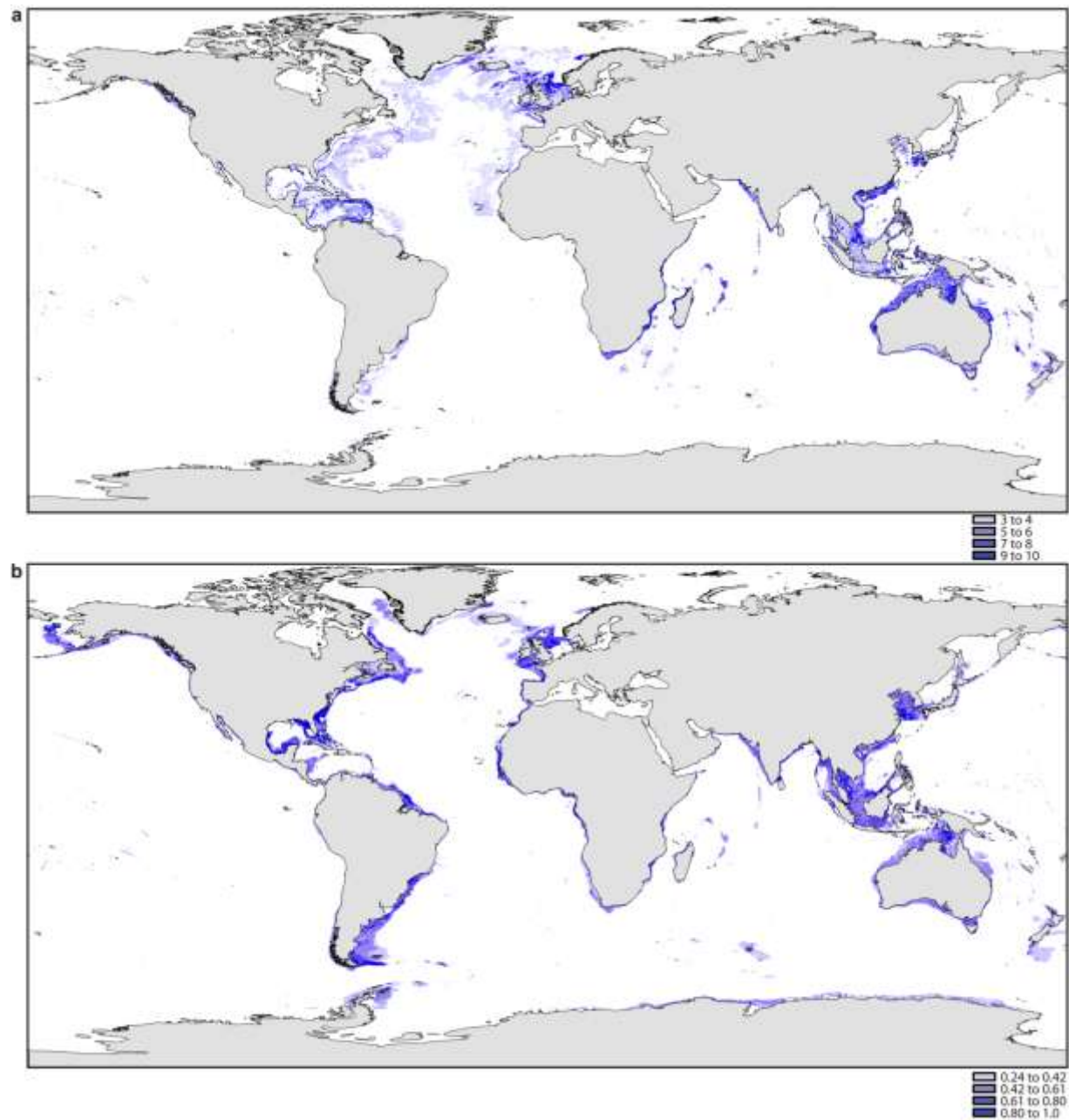


Figure 3.

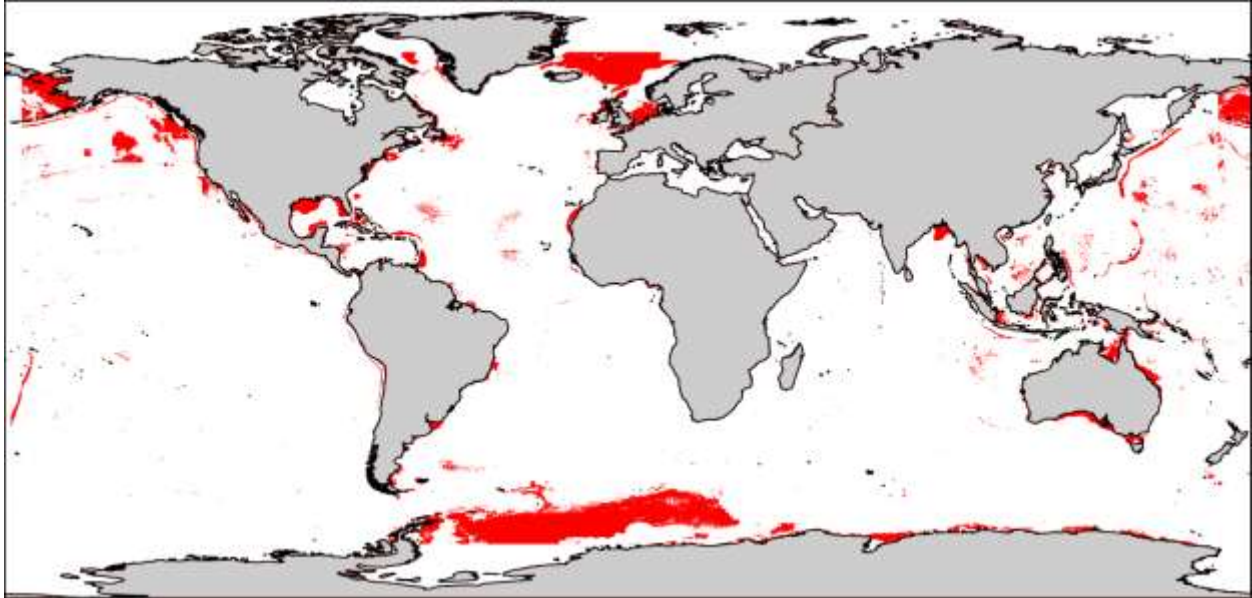


Figure 4.

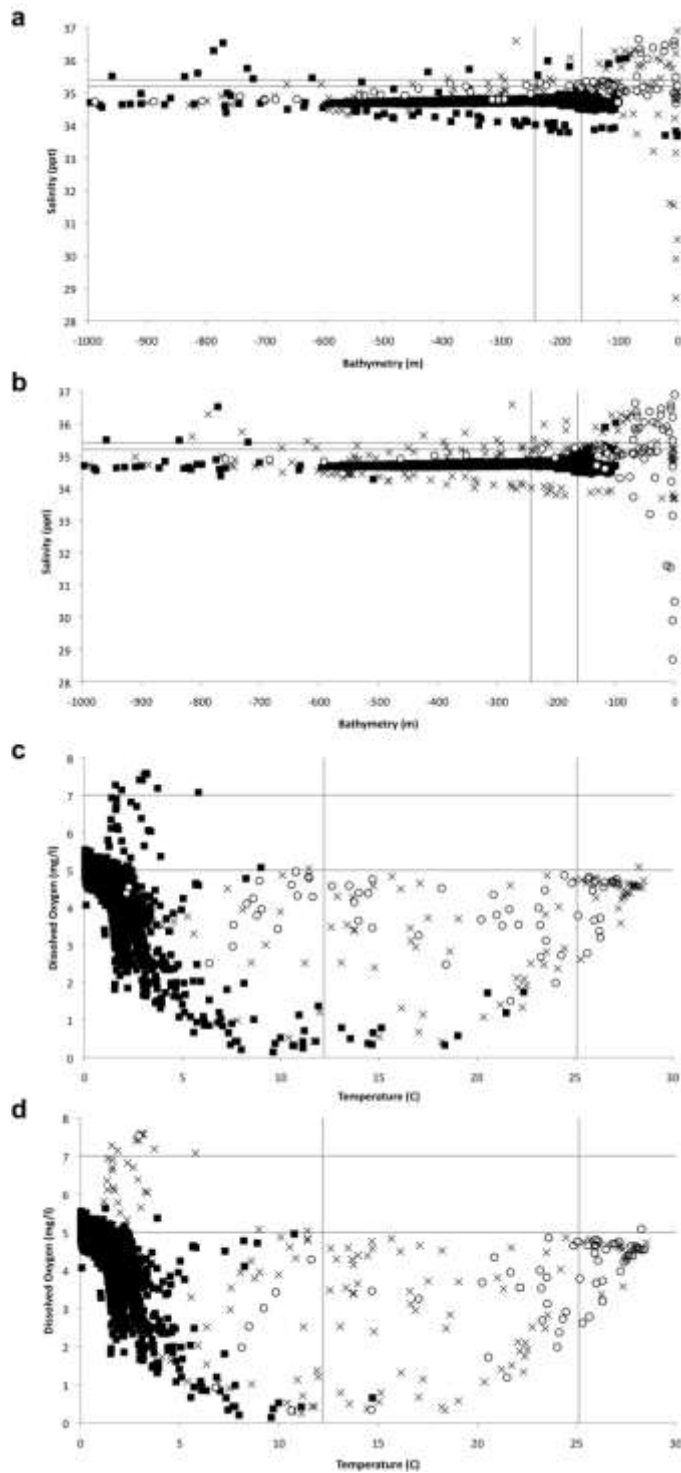


Table 1.

Species	Latitude	Longitude	Source	Jackknife Success		Percent Predicted Area		Full Model Suitability	
				GARP	Maxent	GARP	Maxent	GARP	Maxent
<i>Latimeria chalumnae</i>	-27.53	32.72	Sub.	Y	Y	1.42%	0.73%	10	0.53
<i>Latimeria chalumnae</i>	-27.50	32.72	Sub.	Y	Y	1.38%	0.62%	10	0.95
<i>Latimeria chalumnae</i>	-17.32	38.63	GBIF	N	Y	0.71%	4.57%	10	0.49
<i>Latimeria chalumnae</i>	-11.82	43.02	GBIF	N	N	0.34%	0.82%	10	0.24
<i>Latimeria chalumnae</i>	-5.30	39.13	GBIF	Y	Y	1.01%	4.53%	10	0.77
<i>Latimeria chalumnae</i>	-5.26	39.14	GBIF	Y	Y	1.09%	4.53%	10	0.78
<i>Latimeria chalumnae</i>	-5.15	39.18	GBIF	Y	Y	1.06%	2.82%	10	0.78
<i>Latimeria chalumnae</i>	-3.23	40.23	GBIF	N	N	0.99%	0.63%	10	0.77
<i>Latimeria menadoensis</i>	1.62	124.72	Lit.	N/A	N/A	N/A	N/A	3	0.63
<i>Latimeria menadoensis</i>	1.63	124.63	Lit.	N/A	N/A	N/A	N/A	3	0.64