

Global climate changes over time shape the environmental niche distribution of *Octopus insularis* in the Atlantic Ocean

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ABSTRACT: In the Atlantic Ocean, Octopus insularis (Cephalopoda: Octopodidae) Leite and Haimovici, 2008 inhabits warm and shallow habitats, where it is one of the main targets of cephalopod fisheries. Considering the current trend of increasing seawater temperature, warm-water species are expected to expand their geographic distribution ranges. Ecological niche modeling (ENM) is an important tool to help describe likely changes in geographic distribution patterns of a species in different climatic scenarios. To evaluate changes in the distribution of Octopus insularis over time, the maximum entropy approach was used, which estimated a suitable climatic niche for Octopus under 5 scenarios of global climate change. Four environmental variables were chosen to model the suitable climatic niche of O. insularis in the present, past, and future scenarios. The ENM in different climatic scenarios showed good validation and pointed out an increase of the suitable niche for O. insularis settlement, from the Last Glacial Maximum (21 kya) up to future scenarios. In the future projections, suitable niche space will potentially increase in the tropical Atlantic compared to the current distribution. Modeling pointed out the possibility of expansion from the current range of the species to the temperate northern Atlantic, temperate South America, and temperate South Africa. This may cause potential threats, such as possible extinction of endemic species, habitat displacement of native octopuses, and reorganizations in the trophic chain.

KEY WORDS: $Octopus\ insularis\cdot Maximum\ entropy\cdot Environmental\ variables\cdot Climatic\ niche\cdot Global\ warming$

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1. INTRODUCTION

The rapid increase in global temperature due to anthropogenic emissions of CO_2 has been causing important changes in biological communities, which threaten marine ecosystems worldwide (Heneghan et al. 2019). According to Intergovernmental Panel

on Climate Change (IPCC) projections, isotherms will probably shift up to 600 km northwards, global mean sea surface temperature (SST) may increase by 4.5°C, and the sea level will rise between 0.7 and 2 m by 2100 (Hoegh-Guldberg & Bruno 2010, Horton et al. 2014). Several studies have stated that marine organisms, especially warm-water species, may shift

their latitudinal and depth ranges as a consequence of ocean warming, potentially resulting in local or global extinction, species invasions, and changes at marine trophic levels (Lenoir et al. 2011, Chen et al. 2011, Pecl et al. 2017).

Ecological niche modeling (ENM) has been used to examine patterns of species distribution under global climate change in the past, present, and future (Cordellier & Pfenninger 2009, Dambach & Rödder 2011). Modeling these different scenarios allows us to understand evolutionary and ecological processes and how global warming and cooling events have influenced the dynamics of population distribution expansion and retraction over time (Nogués-Bravo 2009). Additionally, these models may facilitate predictions of how species will respond to future climate change, assisting in developing effective management measures (Schwartz et al. 2006).

Maximum entropy modeling, using presence-only records, has been successfully applied in predictions of suitable niches for marine and terrestrial species (Phillips et al. 2006, Elith et al. 2011, Saeedi et al. 2017). Comparative studies of modeling methods based on presence data carried out by Elith & Graham (2009), Tittensor et al. (2009), Reiss et al. (2011), and González-Irusta et al. (2015) have indicated a good performance of the maximum entropy approach.

Cephalopods, in general, are animals characterized by fast growth, short life cycles, and adaptive plasticity, allowing them to swiftly respond to climate changes and environmental perturbations (Liscovitch-Brauer et al. 2017, Alabia et al. 2020). Additionally, there is a general trend of cephalopod proliferation due to the global depletion of fish stocks, which could potentially release them from predation and competition pressures (Doubleday et al. 2016). The unique life traits and ability to adapt to environmental changes, combined with fish overexploitation, could benefit cephalopod populations and make them drivers of ecosystem change and potential climate change indicators (Rosa et al. 2019).

Like most marine invertebrates, *Octopus insularis* (Cephalopoda: Octopodidae) Leite and Haimovici, 2008 undergoes planktonic development during the early stages of its life cycle, dispersing mainly through oceanic currents (Leite et al. 2008, Lima et al. 2014b). The species, previously misidentified as *O. vulgaris* Cuvier, 1797 (Type II), was described initially for the Brazilian northeast and oceanic islands (Leite et al. 2008). Molecular studies conducted by Amor et al. (2017) extended the distribution of *O. insularis* to the mid-Atlantic islands of Ascension and Saint Helena.

Lima et al. (2017) registered the presence of the species in the Caribbean Sea, and González-Gómez et al. (2018) found it in a reef system inside the Gulf of Mexico. Thus, this tropical species dominates an immense area along the coast of the central and western Atlantic and around oceanic islands. In addition, *O. insularis* seems to be tolerant of a wide range of temperature and salinity (Amado et al. 2015). In the wild, it has been recorded in extreme conditions, such as estuarine regions, very warm tide pools at Rocas Atoll (31°C), and in subtropical waters (22°C) (Trindade and Martim Vaz Archipelago) (Leite et al. 2016).

The wide geographic distribution of *O. insularis* in tropical Atlantic waters and its high thermal and osmotic tolerance make it an excellent example to study the consequences of global climate changes in natural populations. Considering the life history of O. insularis, an increase in its distribution can be expected as sea temperature rises. Thus, in this study we aimed to model suitable areas for O. insularis in 5 different scenarios, including past (Last Glacial Maximum, LGM, and Mid-Holocene, MH), modern (current time), and future (2050 and 2100) scenarios to understand how climate change has historically shaped the ranges of the Grinnellian niche (also known as the abiotic niche) for this species. Additionally, we intended to identify the main environmental variables associated with its settlement in a region and the potential occurrence of the species in non-sampled areas.

2. MATERIALS AND METHODS

2.1. Species dataset

Occurrence records were obtained from a scientific literature search in the web search engine 'Google Scholar' using the species name 'Octopus insularis' as a keyword. A total of 374 occurrences were registered from the literature. Occurrences were recorded if the coordinates of the sampling area were described or shown on maps. If this was not possible, the coordinates were estimated from the information given in the articles (for example, the capture localities or depth). Additionally, we obtained more occurrences from the repositories of the Global Biodiversity Information Facility (GBIF, https://www.gbif. org/) and the Ocean Biodiversity Information System (OBIS, https://obis.org/). The occurrence data used in this study encompass the whole occurrence range of O. insularis recorded to date (Fig. 1).

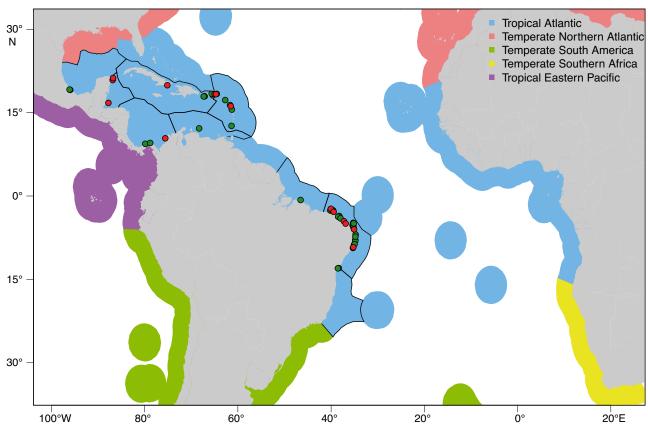


Fig. 1. Octopus insularis occurrence used to model the suitable niche for this species in different climatic scenarios. The marine realms according to Spalding et al. (2007) are indicated by colors. Green dots: training data; red dots: testing data; black lines: calibration areas

2.2. Environmental variables

Environmental variables for modern and representative concentration pathway (RCP) 4.5 and 6.0 scenarios (2050 and 2100) were downloaded from Bio-ORACLE (Assis et al. 2018) (Fig. 2). Additionally, the paleoclimate data for MH and the LGM were obtained from Ocean Climate Layers for Marine Spatial Ecology (MARSPEC) calculated from the Paleoclimate Modeling Intercomparison Project (PMIP2) (Sbrocco & Barber 2013, Sbrocco 2014). Four environmental variables were chosen to model the distribution of *O. insularis*: depth, slope, SST, and sea surface salinity. All environmental variables had a resolution of 5 arcminutes (~10 km by pixel).

To model the species distribution in MH, 2050, and 2100 scenarios, we used the modern depth and slope variables, assuming that sea-level fluctuation from the MH to present was low (global sea level rose around 4 m for the past 6400 yr) (Lambeck et al. 2014) to influence the *O. insularis* distribution in the scale of this study.

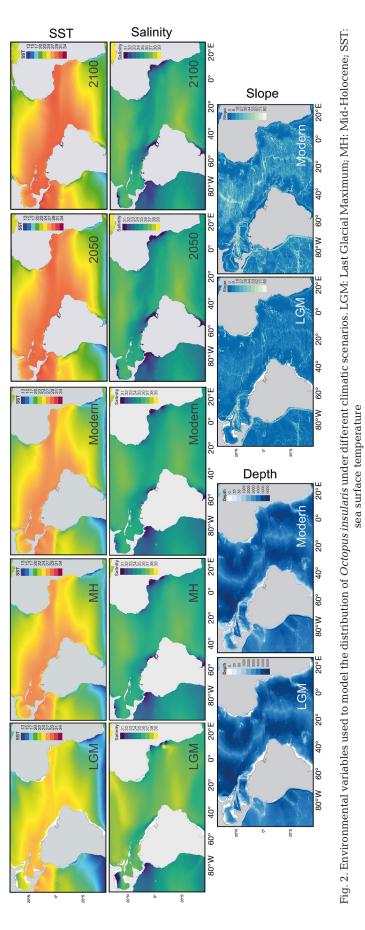
2.3. Model calibration

2.3.1. Algorithm

To correlate the occurrence records with environmental variables we used the maximum entropy model 'Maxent' (Phillips et al. 2006). Maxent models estimate a target probability of distribution closer to the most spread-out distribution (maximum entropy) by using environmental variables as the set of information available about the target distribution and species occurrence data (Elith et al. 2011).

2.3.2. Spatial filtering of occurrences

To avoid the problem of the over-representation of environments due to sample bias (Boria et al. 2014) we used a method of spatial thinning through an iterative method of minimum nearest-neighbor distance (15 km) with the library 'spThin.' This analysis was done with the programming language R v. 4.0.0 (R Core Team 2020). A total of 54 occurrences remained



after the spatial thinning (Table S1 in the Supplement at www.int-res.com/articles/suppl/m652p111 _supp.pdf). We randomly extracted 75% of occurrences (40 points) to calibrate the model while the remaining 25% (14) were used to evaluate the model performance, taking advantage of all available data without having an independent dataset (Phillips & Dudík 2008).

2.3.3. Calibration area

A relevant calibration area to train and validate the models was chosen. Such a decision is important, since a poorly defined region greatly affects the output of the models (Barve et al. 2011). This region is represented as a polygon that reflects a hypothetical accessibility area that has been explored and tested by the species, the 'M area' (Soberón & Peterson 2005).

The models were calibrated in the marine ecoregions proposed by Spalding et al. (2007) in which the occurrences are reported (Fig. 1); in the Discussion (Section 4), we consider the marine realms suggested in their work. Furthermore, because this species is restricted to the top 100 m of the water column (Leite et al. 2009, Batista & Leite 2016), the models were not calibrated at greater depths. The environmental layers were cropped according to this 'M area' using the function 'CropRaster' in the library ENMGadgets (Barve & Barve 2013).

2.3.4. Model calibration, evaluation, and selection

To select a parsimonious model with statistical significance and good performance, we tested 32 different combinations of features (linear, L; quadratic, Q; product, P; and hinge, H) and regularization multipliers (RMs, 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4). These models were first filtered based on their statistical significance (p < 0.05) via partial receiver operating characteristics (pROCs), an analysis derived from the classical ROC, where the x-axis represents a proportion of the overall area predicted as present and the y-axis evaluates an acceptable level of omission error (E = 5% in this work) (Peterson et al. 2008). The remaining models were analyzed via omission rates (ORs), a metric that indicates the percent of test occurrences left out if a binarization of the training data is done (Peterson et al. 2011). To retain as much niche information as possible, we used an OR of 5% (OR_5), so models with values >5% were eliminated. Finally, the complexity of the remaining group of models was evaluated with the difference in Akaike's information criterion (delta AIC), a metric that reflects the goodness-of-fit and complexity of the model, where models with a delta AIC ≤ 2 have substantial support. The remaining model was projected to past, present, and future scenarios. For this process, we used the library 'kuenm' in R (Cobos et al. 2019). We projected the selected model onto future and past climate scenarios; a total of 15 runs (replicates) were done to provide sufficient variability to perform the statistical tests of the predictions.

Additionally, jackknife tests were performed to evaluate the importance of each environmental variable (Elith et al. 2011). This test shows the training gain (how good an environmental variable may improve the fit of the occurrence data compared to a uniform distribution) by running the model excluding 1 variable in each run, then running the model with only 1 variable, and comparing these runs to the training gain of the model with all variables. Response curves for each environmental variable were generated showing how the logistic prediction of the model changes as each environmental parameter varied, keeping the remaining variables at their average value.

Finally, we created binary maps (presence–absence) from the methods of binarization offered by the results of Maxent. We used the method of the minimum presence threshold, which equals the minimum model suitability value for any training occurrence.

2.3.5. Non-analogous conditions

Taking into consideration that interpretation of a model outside the range of calibration can be perilous, we calculated the non-analogous conditions using a multivariate environmental similarity surfaces (MESS) analysis. The MESS maps measure the similarity of the calibration area with a set of points of a chosen environmental variable of the different scenarios. Negative values indicate a dissimilarity (Elith et al. 2011). Additionally, we report which environmental variables are the most dissimilar.

3. RESULTS

A model of 'LQTH' configuration with an RM of 4 was chosen. According to the pROC, this model

showed statistical significance (p < 0.05), had a good performance based on the OR_5 (OR of 0), and a delta AIC value of 0. Moreover, the test of OR versus predicted area (as a function of the cumulative threshold) for all replicate runs showed that the average OR is close to the predicted omission (Fig. S1). The AUC (area under the curve) mean score of the replicated runs achieved a high value (mean \pm SD: 0.880 \pm 0.02), which indicates that the predicted distribution is very different from random sampling.

According to the jackknife test of the regularized training gain, variables that most contributed to the model were SST (37.2%), depth (26.4%), salinity (20.9%), and slope (15.5%) (Fig. S2). The environmental variable with the highest gain, when used in isolation, was SST, which therefore appears to have the most useful information by itself. The suitability is higher in warm (26.5–28°C), shallow (10–30 m) waters, and in regions with high values of salinity (36–40 PSU). It appears that the species also prefers sloping areas over flat bottoms (Fig. S3).

3.1. Suitable niche areas

The occurrence of the *Octopus insularis* in the study area during the LGM was very restricted (Fig. 3). Although the model showed small areas with suitable niches in the tropical Atlantic realm, the highest suitability was in the Caribbean Sea. Within the Gulf of Mexico, the suitable areas for the species were near zero.

During the MH, the potentially suitable areas of *O. insularis* were distributed closer to the equator, such as the northern coast of Brazil and the central Caribbean Sea (coasts of Honduras and Nicaragua). Suitable areas for the settlement of this species were also identified in the southern part of the Gulf of Mexico and northeast Brazil, whereas low suitability was evident along the African coast (from Senegal to Liberia).

At present, the potentially suitable areas of *O. insularis* are concentrated in the western tropical Atlantic (along with shallow waters of the Caribbean Sea, Brazilian northeast coast, and oceanic islands) and the Gulf of Mexico (coasts of Campeche, Tabasco, and Veracruz). The modeling also showed suitable areas for species occurrence along the African coast (from Senegal to Liberia), Cape Verde, and Canary Islands (Fig. 3). According to the model, there is low suitability in the southeast of Brazil, northern Florida, northern Gulf of Mexico, and northern and southern African coast.

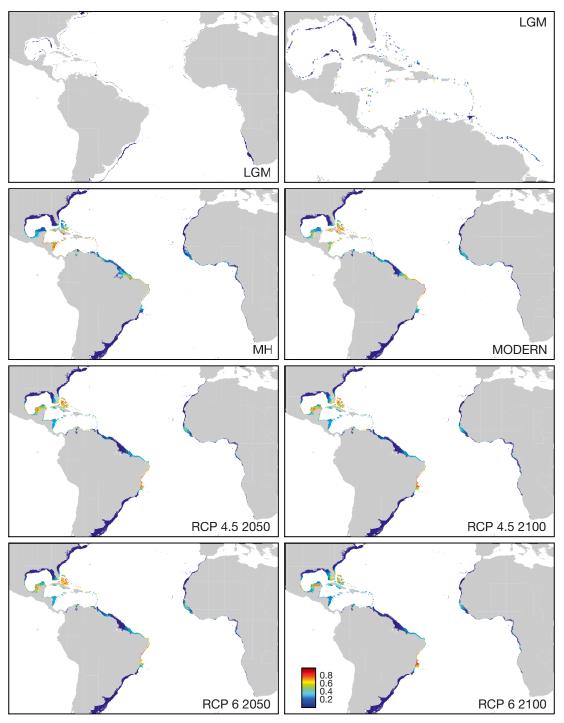


Fig. 3. Distribution of suitable climatic niche for *Octopus insularis* under 2 past scenarios, (Last Glacial Maximum [LGM] and Middle-Holocene), present (modern) conditions, and 2 future projections (2050 and 2100 under scenarios RCP 4.5 and 6). Topright panel shows details of the Caribbean region for LGM predictions, since the species distribution is very restricted in this scenario. The abiotic niche predictions range from 0 (low suitability areas) to 1 (high suitability areas)

The models for both RCP 4.5 and RCP 6.0 scenarios were quite similar, with a slight increase in suitable areas in the RC6 scenario compared to RC4. Suitable niche space in low latitudes would be reduced in

global warming scenarios (2050 and 2100). Therefore, the potential distribution of *O. insularis* would expand from the equator to higher latitudes. Modeling for the future scenarios also showed an increase

in suitable niche areas in the tropical Atlantic realm and high suitability for the temperate northern Atlantic realm (Warm Temperate Northwest Atlantic Province). It is important to highlight the expansion of the suitable niche into the Gulf of Mexico and areas off the coast of Florida, where *O. insularis* occupied only a small region in the modern scenario. The same trend was observed for the southeast coast of Brazil, where the abiotic niche will potentially expand to sub-temperate areas, on the coast of São Paulo and Rio de Janeiro. Suitable areas for *O. insularis* in all scenarios can be better visualized in the binary maps (Fig. S4).

3.2. Non-analogous conditions

Non-analogous conditions were detected at higher latitudes for all scenarios. Moreover, during the RCP 6 scenario for the year 2100, non-analogous conditions appear in the Caribbean region and Brazil near the Amazon River (Fig. S5). These non-analogous conditions are caused mainly by the temperature (Fig. S6); nonetheless, the response curve of temperature obtained in our analysis is Gaussian-like, so the risk of extrapolation is low (Owens et al. 2013).

4. DISCUSSION

Our study provides important insight into the suitable niche dynamics of a widely distributed octopus species across the tropical Atlantic under progressive global warming, from the LGM to future projections.

Climate changes since the LGM have had strong impacts on the dynamics of marine species (Maggs et al. 2008, Hoegh-Guldberg & Bruno 2010). The present study reveals that it is no different for the tropical *Octopus insularis*. Modeling of the species distribution in different climatic scenarios showed an increase in suitable niche space for its establishment, from the LGM up to future projections, and a displacement from the equator towards higher latitudes. To our knowledge, this is the first study to model a cephalopod species widely distributed over different climatic scenarios.

The suitable niche areas for *O. insularis* progressively increase across the climatic scenarios, mainly due to the warming of the SST, which is the variable that most influences the distribution of the species. *O. insularis* has a broad thermal tolerance, being found across a wide range of SST (23–32°C) (Leite et al. 2009, Amado et al. 2015). The species also

appears to have a high salinity tolerance, as it has been recorded from estuaries of rivers to small tide pools with high salinity in the oceanic islands of Brazil, such as Rocas Atoll (36–42 PSU) (Longo et al. 2015). Hermosilla et al. (2011) also reported that temperature and salinity are important variables to predict the suitable abiotic niche of *O. vulgaris*.

The model indicated that the current distribution of O. insularis is concentrated along the coasts and around oceanic islands of the western tropical Atlantic, and the southern Gulf of Mexico, which is in agreement with the known range of this species (Leite et al. 2009, Lima et al. 2017). Furthermore, modeling also indicated the possibility of species occurrence in the eastern tropical Atlantic along the central African coast (Nigeria, Liberia, Guinea, and Sierra Leone). Except for Ascension and St. Helena Islands, there are no records of O. insularis on the African coast and islands to date, although the model indicates that the climatic conditions are appropriate for settlement of the species. Thus, more taxonomic and molecular studies with octopus species should be conducted on the central African coast, using an integrative approach (morphology and genetics) to verify whether or not *O. insularis* occurs in this region.

It is important to highlight unsuitable niches in areas in the Amazon river mouth, probably due to very low salinity and strong water discharge in this region. However, Sales et al. (2013) found *O. insularis* in the stomach contents of a red snapper in Pará State, near the Amazon River mouth, indicating that the species can tolerate living in areas near large river discharges.

Throughout the LGM, the distribution of *O. insularis* was considerably narrowed compared to modern occurrence areas. The suitable niche availability was constricted, likely due to sea-level fluctuations that restricted shallow areas in the continental shelf (Braconnot et al. 2007, Clark et al. 2009). The sea level at 21 kya was around 120 m lower than today, and an abrupt rise started around 14.5 kya (Lambeck et al. 2014, Ludt & Rocha 2015). Furthermore, the global SST cooling of 4.5°C compared to preindustrial conditions (Otto-Bliesner et al. 2006) also contributed to the reduction of suitable areas for *O. insularis* settlement.

The predictions of species distribution in the MH were very similar to modern time, except for the suitable areas closer to the equator in this scenario. In this period, global, annual cooling was <0.1°C compared to preindustrial conditions. Much larger and significant changes occurred regionally and seasonally (Otto-Bliesner et al. 2006). The range of

SST variation was less than in LGM conditions, and the climatic oceanic variables were close to the present situation. Thus, no major variations on *O. insularis* distribution occurred during this time. Considering that the sea level was around 4 m lower than at present (Lambeck et al. 2014), the prediction must be slightly inflated because we used the modern depth layer to model the suitable niche in this period.

Several studies using niche modeling and mostly genetic reconstruction of historical demography indicated a significant expansion of shallow-water benthic and pelagic populations after the LGM up to the present, especially for corals (Kleypas 1997), mollusks (Cordellier & Pfenninger 2009, González-Wevar et al. 2012), and fishes (Rose 2005, Hattab et al. 2014, Ceballos et al. 2016). Population genetics studies of *O. insularis* have been conducted, which can also detect population expansion across the climate changes scenarios. This highlights the importance of integrative studies of phylogeography and ENM to predict global warming effects on wild populations (Alvarado-Serrano & Knowles 2014).

The predictions of O. insularis distribution for the future scenarios (2050 and 2100) showed an increase in suitable niche areas in the tropical Atlantic and an expansion of its niche to higher latitudes. Under these climate change scenarios, many marine species shift their ranges to higher latitudes or are displaced away from the center of their original distribution (Pecl & Jackson 2008, Pandolfi et al. 2011, Perry et al. 2005). Despite the displacement from the equator, as temperature rises in the future, O. insularis appears to increase its distribution, maintaining its occurrence in most of the suitable areas observed in the modern scenario. The increase in temperature accelerates the process of gonadal development in O. insularis and could greatly enhance growth rates in cephalopods (Mangold 1986). Since the species has already been recorded in areas with a wide variation of temperature and salinity, plus its fast growth rates, high fecundity (~95000 eggs during the unique spawning lifetime event), and short life cycle (<1 yr) (Lima et al. 2014a, Lenz et al. 2015), it is likely that the species may successfully expand its distribution towards higher latitudes under global warming scenarios. This trend was recorded in *O. tetricus* Gould, 1852, which extended its distribution several hundred kilometers polewards and maintained a successful reproductive population in the new environment (Ramos et al. 2018). The trend was also observed for fast-growing Humboldt squid Dosidicus gigas Steenstrup, 1857, in the eastern North Pacific (Zeidberg & Robison 2007) and for the Australian sea urchin Centrostephanus rodgersii A. Agassiz, 1864, which has exhibited poleward range expansion to eastern Tasmania (Ling 2008) as have 4 coral species in tropical Indo-Pacific regions (Yamano et al. 2011).

Range expansion of species with a broad spectrum of tolerance, such as O. insularis, may induce the competitive exclusion of native species and reduce local biodiversity (Sexton et al. 2009). Furthermore, synergistic effects may arise from climate warming and overfishing of top predators, causing profound changes in the trophic structure (Lenoir et al. 2011, Perry et al. 2005). The spread of O. insularis inside the Gulf of Mexico could endanger O. maya, the endemic species that occurs in this region (Ángeles-González et al. 2020). This species has similar habitat requirements as O. insularis, such as the same rock-bottom preference and diet components (crabs, bivalves, and gastropods) (Rosas et al. 2007, Zarco-Perelló et al. 2013, de Souza Dantas et al. 2020). Currently, there is no record of O. insularis in the Yucatán Peninsula, probably due to the low sea temperatures caused by the Yucatan upwelling. However, as the sea temperature increases, O. insularis may occupy that region. According to Juárez et al. (2015), higher temperatures impair fertilization and egg development of O. maya, and any modification in its habitat that interrupts the continuity of the Yucatan upwelling could affect the population abundance (Angeles-Gonzalez et al. 2017). Thus, O. maya may shift to deeper waters or even be competitively excluded due to its low tolerance to environmental changes and limited ability to disperse. Moreover, the species expansion of O. insularis towards the south of Brazil could cause habitat displacement of O. cf. vulgaris (the most common octopus species in this region). In this case, it is possible that both species could share the same region but live in different thermal habitats (depths), since O. vulgaris prefers colder waters. However, this new scenario may force the restructuring of trophic relations in this subtropical ecosystem with unknown consequences for the environment.

These are considered suitable areas for *O. insularis* settlement based on only 4 environmental variables. Although they are important conditions for its life cycle and we know that *O. insularis* is very competitive and tolerant, other factors such as ocean currents, habitat, and biotic interactions may restrict the occurrence of the species in certain areas. Moreover, the increase in temperature can promote physiological changes in the species, and have considerable impacts on the population dynamics of different species. André et al. (2010) claimed that increasing water temperatures may not be as beneficial to

cephalopods as previously thought. Their models revealed that the thermal stress could promote a decrease in the incubation time of the eggs, hatchling size, weight at first sexual maturity, and average generation time. Furthermore, synergistic effects may arise between climate warming and overfishing of top predators, causing unknown changes in the marine trophic chain (Lenoir et al. 2011).

ENM is an important tool to predict local and global shifts or expansion of suitable habitat for marine organisms and to understand how species will respond to climate changes (Nogués-Bravo 2009, Provan 2013). However, it is difficult to predict how communities will behave, as they are a complicated systems subject to many ecological processes. A more complete analysis would require in-depth knowledge of physiology, ecology, and evolution, but such processes are beyond the capacity of our statistical approach (Dormann 2007, Fitzpatrick & Hargrove 2009). Regardless of such difficulties, thermal preferences obtained for O. insularis embryos in the aquaculture facilities of the Universidad Nacional Autónoma de Mexico (C. Rosas unpubl. data) are consistent with our results, indicating that our models are useful to evaluate the response of O. insularis under different scenarios until more dynamic approaches are developed.

The impact of climate change on population fluctuations in *Octopus* species may also be detrimental to several artisanal fishing communities along the west coast of the Atlantic. Although management depends on the challenging evaluation of habitat responses to new climatic conditions, the predictions of species distribution under different climatic scenarios can help to prompt further discussion about integrated ecosystem management (Marzloff et al. 2016) and help both the species and the fishing communities which depend on this important marine resource.

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LITERATURE CITED

Alabia ID, Saitoh SI, Igarashi H, Ishikawa Y, Imamura Y (2020) Spatial habitat shifts of oceanic cephalopod (Ommastrephes bartramii) in oscillating climate. Remote Sens 12:521

- Alvarado-Serrano DF, Knowles LL (2014) Ecological niche models in phylogeographic studies: applications, advances and precautions. Mol Ecol Resour 14:233–248
- Amado EM, Souza-Bastos LR, Vidal EAG, Leite TS, Freire CA (2015) Different abilities to regulate tissue hydration upon osmotic challenge *in vitro*, in the cephalopods *Octopus vulgaris* and *O. insularis*. Mar Freshw Behav Physiol 48:205–211
- Amor MD, Laptikhovsky V, Norman MD, Strugnell JM (2017) Genetic evidence extends the known distribution of *Octopus insularis* to the mid-Atlantic islands Ascension and St Helena. J Mar Biol Assoc UK 97:753–758
- André J, Haddon M, Pecl GT (2010) Modelling climatechange-induced nonlinear thresholds in cephalopod population dynamics. Glob Change Biol 16:2866–2875
- Angeles-Gonzalez LE, Calva R, Santos-Valencia J, Avila-Poveda OH, Olivares A, Diaz F, Rosas C (2017) Temperature modulates spatio-temporal variability of the functional reproductive maturation of *Octopus maya* (Cephalopoda) on the shelf of the Yucatan Peninsula, Mexico. J Molluscan Stud 83:280–288
- Ángeles-González LE, Martínez-Meyer E, Yañez-Arenas C, Velázquez-Abunader I and others (2020) Using realized thermal niche to validate thermal preferences from laboratory studies. How do they stand? Ecol Indic 118:106741
- Assis J, Tyberghein L, Bosch S, Verbruggen H, Serrão EA, De Clerck O (2018) Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. Glob Ecol Biogeogr 27:277–284
 - Barve N, Barve V (2013) ENMGadgets: tools for pre and post processing in ENM workflows. https://github.com/vijay-barve/ENMGadgets
- *Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A and others (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol Model 222:1810–1819
- Batista AT, Leite TS (2016) *Octopus insularis* (Cephalopoda: Octopodidae) on the tropical coast of Brazil: where it lives and what it eats. Braz J Oceanogr 64:353–364
- Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecol Model 275: 73–77
- Braconnot P, Otto-Bliesner B, Harrison S, Joussaume S and others (2007) Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum. 2. Feedbacks with emphasis on the location of the ITCZ and mid- and high latitudes heat budget. Clim Past 3:279–296
- Ceballos SG, Lessa EP, Licandeo R, Fernández DA (2016)
 Genetic relationships between Atlantic and Pacific populations of the notothenioid fish *Eleginops maclovinus*: the footprints of Quaternary glaciations in Patagonia. Heredity 116:372–377
- Chen IC, Hill JK, Ohlemuller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026
- Clark PU, Dyke AS, Shakum JD, Carlson AE and others (2009) The Last Glacial Maximum. Science 325:710–714
- Cobos ME, Peterson AT, Barve N, Osorio-Olvera L (2019) kuenm: an R package for detailed development of ecological niche models using Maxent. PeerJ 7:e6281
- Cordellier M, Pfenninger M (2009) Inferring the past to predict the future: climate modelling predictions and phylogeography for the freshwater gastropod *Radix balthica* (Pulmonata, Basommatophora). Mol Ecol 18:534–544

- Dambach J, Rödder D (2011) Applications and future challenges in marine species distribution modeling. Aquat Conserv 21:92–100
 - De Souza dantas RJ, Leite TS, de Albuquerque CQ (2020) Assessing the diet of octopuses: traditional techniques and the stable isotopes approach. J Molluscan Stud 86: 210–218
- Dormann CF (2007) Promising the future? Global change projections of species distributions. Basic Appl Ecol 8: 387–397
- Doubleday ZA, Prowse TAA, Arkhipkin A, Pierce GJ and others (2016) Global proliferation of cephalopods. Curr Biol 26:R406–R407
- Elith J, Graham CH (2009) Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. Ecography 32:66–77
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17:43–57
- Fitzpatrick MC, Hargrove WW (2009) The projection of species distribution models and the problem of non-analog climate. Biodivers Conserv 18:2255–2261
- González-Gómez R, Barriga-Sosa IDLA, Pliego-Cárdenas R, Jiménez-Badillo L, Markaida U, Meiners-Mandujano C, Morillo-Velarde PS (2018) An integrative taxonomic approach reveals *Octopus insularis* as the dominant species in the Veracruz Reef System (southwestern Gulf of Mexico). PeerJ 6:e6015
- González-Írusta JM, González-Porto M, Sarralde R, Arrese B, Almón B, Martín-Sosa P (2015) Comparing species distribution models: a case study of four deep sea urchin species. Hydrobiologia 745:43–57
- González-Wevar CA, Hüne M, Cañete JI, Mansilla A, Nakano T, Poulin E (2012) Towards a model of post-glacial biogeography in shallow marine species along the Patagonian Province: lessons from the limpet *Nacella magellanica* (Gmelin, 1791). BMC Evol Biol 12:139
- Hattab T, Albouy C, Lasram FBR, Somot S, Le Loch F, Leprieur F (2014) Towards a better understanding of potential impacts of climate change on marine species distribution: a multiscale modelling approach. Glob Ecol Biogeogr 23:1417–1429
- *Heneghan RF, Hatton IA, Galbraith ED (2019) Climate change impacts on marine ecosystems through the lens of the size spectrum. Emerg Top Life Sci 3:233–243
- Hermosilla C, Rocha F, Valavanis VD (2011) Assessing *Octopus vulgaris* distribution using presence-only model methods. Hydrobiologia 670:35–47
- Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. Science 328: 1523-1528
- Horton BP, Rahmstorf S, Engelhart SE, Kemp AC (2014) Expert assessment of sea-level rise by AD 2100 and AD 2300. Quat Sci Rev 84:1–6
- Juárez OE, Galindo-Sánchez CE, Díaz F, Re D, Sánchez-García AM, Camaal-Monsreal C, Rosas C (2015) Is temperature conditioning *Octopus maya* fitness? J Exp Mar Biol Ecol 467:71–76
- Kleypas JA (1997) Modeled estimates of global reef habitat and carbonate production since the last glacial maximum. Paleoceanography 12:533–545
- *Lambeck K, Rouby H, Purcell A, Sun Y, Sambridge M (2014) Sea level and global ice volumes from the Last Glacial Maximum to the Holocene. Proc Natl Acad Sci USA 111: 15296–15303

- Leite TS, Haimovici M, Molina W, Warnke K (2008) Morphological and genetic description of *Octopus insularis*, a new cryptic species in the *Octopus vulgaris* complex (Cephalopoda: Octopodidae) from the tropical southwestern Atlantic. J Molluscan Stud 74:63–74
- Leite TS, Haimovici M, Mather J, Oliveira JEL (2009) Habitat, distribution, and abundance of the commercial octopus (*Octopus insularis*) in a tropical oceanic island, Brazil: information for management of an artisanal fishery inside a marine protected area. Fish Res 98:85–91
- Leite TS, Batista AT, Lima FD, Barbosa JC, Mather J (2016) Geographic variability of *Octopus insularis* diet: from oceanic island to continental populations. Aquat Biol 25: 17–27
- Lenoir S, Beaugrand G, Lecuyer É (2011) Modelled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. Glob Change Biol 17:115–129
- Lenz TM, Elias NH, Leite TS, Vidal EAG (2015) First description of the eggs and paralarvae of the tropical octopus, *Octopus insularis*, under culture conditions. Am Malacol Bull 33:101–109
- Lima FD, Leite TS, Haimovici M, Nóbrega MF, Oliveira JEL (2014a) Population structure and reproductive dynamics of *Octopus insularis* (Cephalopoda: Octopodidae) in a coastal reef environment along northeastern Brazil. Fish Res 152:86–92
- Lima FD, Leite TS, Haimovici M, Oliveira JEL (2014b) Gonadal development and reproductive strategies of the tropical octopus (*Octopus insularis*) in northeast Brazil. Hydrobiologia 725:7–21
- Lima FD, Berbel-Filho WM, Leite TS, Rosas C, Lima SMQ (2017) Occurrence of *Octopus insularis* Leite and Haimovici, 2008 in the Tropical Northwestern Atlantic and implications of species misidentification to octopus fisheries management. Mar Biodivers 47:723–734
- Ling SD (2008) Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. Oecologia 156:883–894
- Liscovitch-Brauer N, Alon S, Porath HT, Elstein B and others (2017) Trade-off between transcriptome plasticity and genome evolution in Cephalopods. Cell 169:191–202
- Longo GO, Morais RA, Martins CDL, Mendes TC and others (2015) Between-habitat variation of benthic cover, reef fish assemblage and feeding pressure on the benthos at the only atoll in South Atlantic: Rocas atoll, NE Brazil. PLOS ONE 10:e0127176
- Ludt WB, Rocha LA (2015) Shifting seas: the impacts of Pleistocene sea-level fluctuations on the evolution of tropical marine taxa. J Biogeogr 42:25–38
- Maggs CA, Castilho R, Foltz D, Henzler C and others (2008) Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. Ecology 89:S108–S122
 - Mangold K (1986) Reproduction. In: Boyle PR (ed) Cephalopod life cycles. II. Comparative reviews. Academic Press, London, p 157–200
- Marzloff MP, Melbourne-Thomas J, Hamon KG, Hoshino E, Jennings S, van Putten IE, Pecl GT (2016) Modelling marine community responses to climate-driven species redistribution to guide monitoring and adaptive ecosystembased management. Glob Change Biol 22:2462–2474
- Nogués-Bravo D (2009) Predicting the past distribution of species climatic niches. Glob Ecol Biogeogr 18:521–553
- Otto-Bliesner BL, Brady EC, Clauzet G, Tomas R, Levis S, Kothavala Z (2006) Last glacial maximum and Holocene climate in CCSM3. J Clim 19:2526–2544

- Owens HL, Campbell LP, Dornak LL, Saupe EE and others (2013) Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. Ecol Model 263:10–18
- Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011)
 Projecting coral reef futures under global warming and
 ocean acidification. Science 333:418–422
- Pecl GT, Jackson GD (2008) The potential impacts of climate change on inshore squid: biology, ecology and fisheries. Rev Fish Biol Fish 18:373–385
- Pecl GT, Araújo MB, Bell JD, Blanchard J and others (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science 355: eaai9214
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308: 1912–1915
- Peterson AT, Papeş M, Soberón J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol Model 213:63–72
 - Peterson TA, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011) Ecological niches and geographic distributions. Princeton University Press, Princeton, NJ
- Phillips SJ, Dudík M (2008) Modeling of species distribution with Maxent: new extensions and a comprehensive evaluation. Ecography 31:161–175
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259
- Provan J (2013) The effects of past, present and future climate change on range-wide genetic diversity in northern North Atlantic marine species. Front Biogeogr 5:60–66
 - R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ramos JE, Pecl GT, Moltschaniwskyj NA, Semmens JM, Souza CA, Strugnell JM (2018) Population genetic signatures of a climate change driven marine range extension. Sci Rep 8:9558
- Reiss H, Cunze S, König K, Neumann H, Kröncke I (2011) Species distribution modelling of marine benthos: a North Sea case study. Mar Ecol Prog Ser 442:71–86
- Rosa R, Pissarra V, Borges FO, Xavier J and others (2019) Global patterns of species richness in coastal cepha-

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- lopods. Front Mar Sci 6:469
- Rosas C, Cuzon G, Pascual C, Gaxiola G and others (2007) Energy balance of *Octopus maya* fed crab or an artificial diet. Mar Biol 152:371–381
- Rose GA (2005) Capelin (*Mallotus villosus*) distribution and climate: a sea 'canary' for marine ecosystem change. ICES J Mar Sci 62:1524–1530
- Saeedi H, Basher Z, Costello MJ (2017) Modelling present and future global distributions of razor clams (Bivalvia: Solenidae). Helgol Mar Res 70:23
- Sales JBDL, Rego PS, Hilsdorf AWS, Moreira AA and others (2013) Phylogeographical features of *Octopus vulgaris* and *Octopus insularis* in the Southeastern Atlantic based on the analysis of mitochondrial markers. J Shellfish Res 32:325–339
- Sbrocco E (2014) Paleo-MARSPEC: gridded ocean climate layers for the mid- Holocene and Last Glacial Maximum. Ecology 95:1710
- Sbrocco EJ, Barber PH (2013) MARSPEC: ocean climate layers for marine spatial ecology. Ecology 94:979
- Schwartz MW, Iverson LR, Prasad AM, Matthews SN, Connor RJO (2006) Predicting extinctions as a result of climate change. Ecology 87:1611–1615
- Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range limits. Annu Rev Ecol Evol Syst 40:415–436
- Soberón J, Peterson TA (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers Inform 2:1–10
- Spalding MD, Fox HE, Allen GR, Davidson N and others (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57:573–583
- Tittensor DP, Baco AR, Brewin PE, Clark MR and others (2009) Predicting global habitat suitability for stony corals on seamounts. J Biogeogr 36:1111-1128
- Yamano H, Sugihara K, Nomura K (2011) Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. Geophys Res Lett 38:L04601
 - Zarco-Perelló S, Mascaró M, Garza-Pérez R, Simoes N (2013) Topography and coral community of the Sisal Reefs, Campeche Bank, Yucatán, México. Hidrobiologica 23: 28–41
- Zeidberg LD, Robison BH (2007) Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. Proc Natl Acad Sci USA 104:12948–12950

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