Manuscript File Click here to view linked References

Molecular data, ecological niche, and dispersal models reveal a Trans-Atlantic shallow-water octopus species

Françoise D. Lima[a], Luís Enrique Ángeles-González[b], Hugulay Maia[c], Tatiana S. Leite[d], Miguel Cahuich-López[e,f], Ismael Mariño-Tapia[g], Mariana L. Santana-Cisneros[h], Pedro-Luis Ardisson[h], Sergio M. Q. Lima[a]

[a] Department of Botany and Zoology, Universidade Federal do Rio Grande do Norte, 59078-900, Natal/RN, Brazil

[b] Unidad Multidisciplinaria de Docencia e Investigación-Sisal, Facultad de Ciencias, Universidad Nacional Autónoma de México, Puerto de Abrigo s/n, Sisal, Yucatán, México

[c] Departament of Natural Sciences, Life and Environment, Universidade de São Tomé e Príncipe - USTP, São Tomé, São Tomé and Príncipe

[d] Department of Ecology and Zoology, Universidade Federal de Santa Catarina, 88040-900, Florianópolis/SC, Brazil

[e] Institute of Engineering, National Autonomous University of Mexico, Circuito Escolar, CP 04510, Mexico City, Mexico

[f] NOAA/Air Resources Laboratory, and Earth System Science Interdisciplinary Center/Cooperative Institute for Satellite Earth System Studies, University of Maryland

[g] Escuela Nacional de Estudios Superiores-Mérida,Universidad Nacional Autónoma de México, 97357, Ucú,Yucatán, México

[h] Departamento de Recursos del Mar, Cinvestav. Carretera antigua a Progreso. 97310 Mérida, Yucatán, México

Corresponding author: limad.francoise@gmail.com

ABSTRACT

The tropical *Octopus insularis* is a shallow-water species widely distributed in the western Atlantic. Recent studies of niche models have identified suitable habitats for its settlement

also on the east coast of the Atlantic. Considering the pelagic larval period and the high tolerance of this species to environmental variations, this study aimed to analyze the possibility of *O. insularis* occurrence in the West Atlantic (São Tomé Island) through molecular analyses, dispersion, and niche models. The molecular analyses were performed using fragments of 481 bp of the mitochondrial gene (cox1) from three muscle samples collected in São Tomé Island. The *O. insularis* long-range connectivity between South America and Western Africa was analyzed using the Lagrangian tool. Additionally, *O. insularis* records across its entire known distribution were applied to run the ecological niche model (ENM) using the Maxent algorithm. The Bayesian phylogenetic reconstruction showed that two of the three octopus sequences from São Tomé island (Central-Western Africa) belong to a monophyletic and well-supported *O. insularis* clade. The third octopus sample revealed a new species related to the clade with the *Octopus vulgaris* species complex. The dispersal models pointed out that passive particles could potentially reach the seamounts region at Africa coast via oceanic currents (mainly the North Equatorial Countercurrent) from São Pedro and São Paulo archipelago (Central-Western Region of the Atlantic) in a period of ~30-60 days. This suggests that São Pedro and São Paulo archipelago could act as a potential source of paralarvae to Western Africa, although we hypothesize that this connection was more common during the Pleistocene, when sea level was around 120 meters lower. In addition to the already known areas of *O. insularis* occurrence, the ENM pointed suitable habitats to the octopus settlement from Guinea-Bissau down to Equatorial Guinea and Gabon, and African Islands, such as São Tomé and Príncipe. The new record of *O. insularis* in Africa raises important questions regarding regional fisheries management. Considering that *O. insularis* is highly tolerant to environmental variations and very adapted to warm shallow waters, there is a possibility that octopus fisheries stocks on the African coast have a mixed composition (*O. vulgaris*, *O. insularis,* and *Octopus* sp.) and therefore the fisheries must follow management measures suitable for each species. In addition, further studies should be carried out in order to characterize and describe the potential new octopus species found only in São Tomé Island according to our genetic survey.

Keywords: *Octopus insularis*, dispersion, oceanic currents, molecular genetics, niche modeling

1. Introduction

Dispersal in the marine environment allows individuals (especially in its planktonic stages) to reach long distances and move within and among populations (Cowen and Sponaugle 2009). The ocean circulation, river outflows, thermoclines, and depth can act as “soft” aquatic barriers or even pathways that regulate marine species’ movements in the oceanic environment (Hedgecock 1986; Hellberg 2009). Thus, understanding the drivers of larval dispersal in the ocean is a crucial goal for studies on population dynamics, community structure, adaptation, and speciation (Álvarez-Noriega et al. 2020).

Widely distributed species can be interconnected through dispersive processes that promote gene flow among meta-populations. These processes allow populations greater genetic diversity and, consequently, less susceptibility to adverse genetic drift and disappearance by local catastrophes (Hellberg 2009; Nunes et al. 2011). Conversely, isolated populations usually have low genetic diversity, mainly due to genetic drift. However, they may undergo local adaptation processes and give rise to new species along the evolutionary scale, increasing the local diversity of species (Gaither et al. 2015).

Oceanic circulation is one of the main drivers to understanding marine organisms' long-range dispersal. In the tropical Atlantic, surface ocean circulation is delimited by subtropical gyres to the north and south (Lumpkin and Garzoli 2005). The South Equatorial Current (SEC) flows westward and divides into the northern and southern branches at about 12–14°S on the Brazilian coast (Peterson and Stramma 1991). The north branch becomes the North Brazil Current (NBC), which flows bordering the Brazilian coast until the Guyana Current (GC). The south branch of SEC becomes Brazil Current (BC), the western boundary of the South Atlantic subtropical gyre. The retroflection of the NBC flows eastward and forms the North Equatorial

Countercurrent (NECC), which extends towards the African coast, turning into the GC (Lumpkin and Garzoli 2005) (Fig. 1).

Passive and active trans-Atlantic dispersal processes have been documented for several marine species, including fish, turtles, corals, mollusks, and crustaceans (Joyeux et al. 2001; Lapègue et al. 2002; Rocha et al. 2008; Rudorff et al. 2009; Nunes et al. 2011; Lalire and Gaspar 2019), as well as for some terrestrial groups (Houle 1998; Carranza and Arnold 2003; Renner et al. 2004). Three routes seem to be the main pathway for transoceanic dispersal: from the Caribbean to the Northeast Atlantic, from northern Brazil to the Gulf of Guinea, and from Africa to southern Brazil (Joyeux et al. 2001).

Ecological niche modeling performed by Lima et al. (2020) showed suitable areas for *Octopus insularis* Leite & Haimocivi, 2008 occurrence along the African coast. However, this species is distributed mainly in the western Atlantic, with the easternmost records in Saint Helena and Ascension islands in the mid-Atlantic (Amor et al. 2017; Lima et al. 2017). Its dispersion ability, generalist diet, and high tolerance level to environmental variation have contributed to its spreading in the West and Mid-Atlantic Ocean waters (Leite et al. 2016; Lima et al. 2020). Paralarvae, after hatching, as in many *Octopus* species, spend some time in the water column (1 – 3 months for *O. vulgaris* and *O. americanus*) (Villanueva et al. 1997; Bastos and Vieira 2018; Roura et al. 2019), and are carried by ocean currents across long distances, until settling on the seabed (Boyle and Rodhouse 2005).

Octopus insularis, most common octopus species in the tropical Atlantic, inhabits shallow waters in a wide range of temperatures and salinities (Leite et al. 2018; Lima et al. 2017). It is found from the subtropical oceanic islands, such as Trindade and Martim Vaz archipelago (20°31'17" S -29°19'18" W), at sea surface temperatures (SST) between 23 and 27 °C (Leite et al. 2009; Leite et al. 2016), to tropical islands such Rocas Atoll (3°51'59" S -33°48'59" W), where the SST reaches up to 36 °C in tide pools inside the atoll ring (Bouth et al. 2011). The embryos of this species also have high thermal tolerance, developing in optimum temperatures around 24-29 °C (Ángeles-González et al. 2020). In addition, *O. insularis* also

seems to have a high salinity tolerance (Amado et al. 2015), since it has been recorded in estuaries of the Northeastern coast of Brazil and tide pools with high salinities in the Rocas atoll (36 - 42 PSU) (Bouth et al. 2011; Lima et al. 2017).

Although *O. insularis* has a wide distribution in the Tropical Atlantic Ocean (Santana-Cisneros et al. 2021; Lima et al. 2022), its long-range transport mechanisms in the Atlantic are still unknown. Previous studies have already pointed out the possibility of *O. insularis* occurrence in the eastern Atlantic (Lima et al. 2020). Therefore, considering the ability of this species to disperse and its wide tolerance for environmental variation, this study aims to use molecular biology methods to confirm the taxonomic status of octopus samples collected on a tropical African island. We also used particle dispersal models to simulate the movement of *O. insularis* paralarvae across the tropical Atlantic Ocean and ecological niche models (ENM) to identify regions where it could establish populations in the Americas and Western Africa.

2. Material & methods

2.1 Phylogenetic analyses

2.1.1 Genetic sample collection

Muscle tissue samples from the arms of three octopus specimens were collected in the Praia Muteca (00° 05' 59.39" N, 06° 37' 34.40" E), Messias Alves (00° 14' 42.56" N, 06° 44' 48.83" E), and Porto Alegre (00° 01' 41.67" N, 06° 30' 44.10" E) from São Tomé Island, about 250 km off the African coast, in February 2016. São Tomé Island is characterized by rocky volcanic reefs with limited coral growth. The SST ranges around 26-29°C from September to May and decreases to approximately 25°C from June to August (Maia et al. 2018a). The samples were preserved in 95% ethanol and stored at -10° C. Additional 37 sequences of 14 species were obtained from GenBank to evaluate the phylogenetic relationships among octopod species (Table S1).

2.1.2 Molecular analysis

The genomic DNA of octopus specimens was extracted using the GF-1 Nucleic Acid Extraction Kit (Vivantis, Malaysia) following the manufacturer's instructions. Fragments of cytochrome oxidase subunit I gene (*cox*1) were amplified using the universal primers LCO1490 and HCO2198 (Folmer et al. 1994). The PCR amplification reactions were conducted in a final volume of 25 µL containing 1 µL forward primer (10 mM), 1 µL reverse primer, 12.5 µL Taq DNA Polymerase Master Mix (Amplicon A/S, Copenhagen), 8.5 µL H_2O, and 2 µL DNA. PCR cycle parameters used to amplify *cox*1 were 3 min at 95 °C for denaturation, followed by 40 cycles of 1 min at 94 °C, 1 min at 45 °C for annealing, 1.5 min at 72 °C for extension, and a final extension step of 4 min at 72 °C. The PCR products were purified and sequenced by Macrogen Inc, Seoul, South Korea.

The electropherograms were edited in Geneious 9.0.2 (Kearse et al. 2012), and sequences were aligned using MEGA 6 (Tamura et al. 2013). After sequence alignment, a haplotype distribution was generated using the DNAsp v.5.0 software (Librado and Rozas 2009). The substitution model GTR+G+I was chosen using the software jModeltest (Posada 2008).

Bayesian phylogenetic inferences were carried out in BEAST 1.8.4 (Drummond et al. 2012). An uncorrelated lognormal relaxed clock model was used. Monte Carlo Markov Chain (MCMC) runs were performed for 1×10^8 generations, sampling one tree every 1×10^4 runs. The convergence of MCMC runs, effective sample size, and the correct 'burn–in' for the analysis were assessed using Tracer v1.6 (Rambaut et al. 2014). A consensus tree accessing the posterior probability values of each clade was generated using TreeAnnotator 1.8.3 (Drummond et al. 2012) and displayed using FigTree 1.4.3. Pairwise genetic distances of an *Octopus* species subset were calculated using Tamura-Nei model distance in MEGA 6 (Tamura et al. 2013).

2.2 Ecological Niche Models (ENMs)

2.2.1 Occurrence data

Octopus insularis records were obtained from the studies of Lima et al. (2020) and Obrien et al. (2021) and combined with supposed occurrences downloaded from the Global Biodiversity Information Facility (GBIF) and Ocean Biodiversity Information System (OBIS) using the libraries rgbif 3.6.0 (Chamberlain et al. 2022) and robis 2.10.1 (Provoost and Bosch 2022) respectively from the software R 4.1.2 (R Core Team 2022). Duplicated, land, or far away records from where *O. insularis* is reported (e.g., depths or latitudes deemed too high) were excluded. In addition, to address the sampling bias of occurrence databases, a random spatial thinning (1000 iterations) with a buffer of 50 km was used with the help of the spThin library (Aiello-Lammens et al. 2015). A total of 54 occurrences remained after the cleaning process.

2.2.2 Environmental layers and calibration region

Maximum, mean, and minimum layers of temperature and salinity were downloaded from Bio-ORACLE (Assis et al. 2017), while bathymetry data and distance to the coast were obtained from MARSPEC (Sbrocco and Barber 2013) at a resolution of ~9 km^2. Five uncorrelated environmental layers (Pearson correlation test, $r < |0.8|$ - Table 1) were kept to avoid model overfitting or wrongly calculated coefficients, as they could hinder the interpretation of our results (Sillero and Barbosa 2021).

For model calibration, it is necessary to generate an accessibility hypothesis for model development and testing that represents areas explored by the *O. insularis*. Briefly, the calibration region needs to consider areas within the species' capability of movement, whether it can establish a population or not, allowing us to characterize suitable and unsuitable regions for the species (Barve et al. 2011). Therefore, environmental layers were cropped according to the accessibility hypothesis using the ecoregions by Spalding et al. (2007) (Fig. 1). In addition, variables were masked up to 500 m depth since literature suggests that *O. insularis* benthonic phase is mainly a shallow water species (Batista and Leite 2016; Leite et al. 2009).

Table 1. Environmental variables used to generate a calibration region and develop the ecological niche models (ENM) tested. The asterisk (*) identifies variables used in the ENM after eliminating correlated environmental variables with a Pearson correlation (r > 0.8).

Variable	Key	Measurement unit	Database
Bathymetry*	Bathymetry	m	MARSPEC
Maximum sea surface temperature*	SST_Max	°C	Bio-ORACLE
Mean sea surface temperature	SST_Mean	°C	Bio-ORACLE
Minimum sea surface temperature*	SST_Min	°C	Bio-ORACLE
Range of sea surface temperature	SST_Ran	°C	Bio-ORACLE
Maximum sea surface salinity*	SSS_Max	PSS	Bio-ORACLE
Mean sea surface salinity	SSS_Mean	PSS	Bio-ORACLE
Minimum sea surface salinity*	SSS_Min	PSS	Bio-ORACLE
Range of sea surface salinity*	SSS_Ran	PSS	Bio-ORACLE

2.2.3. Model selection and projection

Forty-five Ecological Niche Models (ENMs) of *O. insularis* were generated and selected using the algorithm Maxent v3.4.4 (maxent.jar) via ENMeval library (Kass et al. 2021; Muscarella et al. 2014). Different combinations of features (linear [L], quadratic [Q], product [P], and hinge [H] – L, LQ, LQH, LQP, LQHP) and regularization multipliers (1 to 5 by a sequence of 0.5) were tested for model selection. We used a block partition that divides the data into k-bins (four in this work) based on latitude and longitude (Fig. 1), where occurrences are divided equally as possible (Muscarella et al. 2014), with each bin providing spatially independent evaluation data for models generated by the training data (Radosavljevic and Anderson, 2014). This procedure is recommended when extrapolating ENM (Muscarella et al. 2014; Radosavljevic and Anderson 2014).

Regarding metrics used for selection, first, we considered models with the lowest omission rate of 10% (OR10); posteriorly, from the remaining models, we selected the ones with the highest AUC validation values (AUCval). Finally, we considered the goodness-of-fit and the complexity, selecting the model with the lowest delta Akaike (delta AIC). The selected model was projected to the East Atlantic region to obtain a suitability map. Later, we created binary maps (presence-absence) based on the minimum presence threshold. This method binarizes the suitability maps based on the lowest value known of an occurrence, allowing us to consider all the information available from known records of *O. insularis*. Since models projections were made in regions away from where the model is calibrated (higher and lower latitudes in the Americas and from Southern Europe to Southern Africa), we used the multivariate environmental similarity surface index (MESS) (Elith et al. 2010) to identify areas of strict extrapolation (i.e., environmental distinct of calibration region) and where caution is needed while interpreting the results.

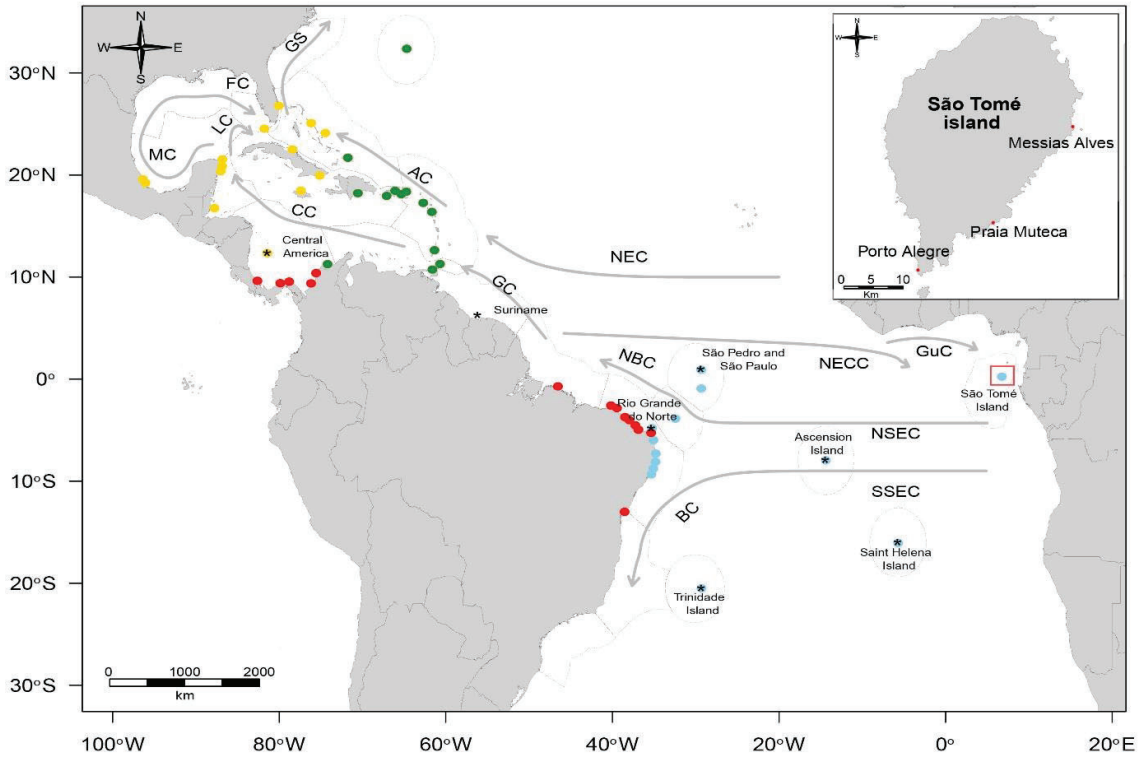


Fig. 1. Occurrences of *Octopus insularis* used for the ecological niche model. Colour dots (yellow, green, red, and blue) indicate the four bins used for model training and testing. Ecoregions by Spalding et al. (2007) used for model calibration are shown as dashed lines. The red square represents São Tome Island (in detail). Ocean currents: northern branch of South Equatorial Current (NSEC), southern branch of South Equatorial Current (SSEC), Brazil Current (BC), North Brazil Current (NBC), Guyana Current (GC), North Equatorial Countercurrent (NECC), Guinea Current (GuC), Caribbean Current (CC), Antilles Current (AC), Loop Current (LC), Mexico Current (MC), Florida Current (FC) and Gulf Stream (GS). Black asterisks indicate release zones used for dispersal models.

2.3 Dispersal model

2.3.1 Dispersal model tool

The *O. insularis* potential long dispersal between South America and Western Africa was analyzed using passive particles from the Lagrangian tool ICHTHYOP v. 3.3.3 (Lett et al.,

2008) coupled with a hydrodynamic model. ICHTHYOP assesses the effects of physical and biological factors on plankton/particles dynamics and uses as inputs ocean circulation models such as ROMS and MARS (Lett et al. 2008). This software has been extensively used to estimate transport pathways in different organisms (Cabral et al. 2021; Gray et al. 2021; Jordan et al. 2021; Lima et al. 2021; Macías et al. 2021; Santana-Cisneros et al. 2021).

2.3.2 Hydrodynamic model

The hydrodynamic model to drive the dispersal model comes from the product GLORYS12V1, a global eddy-resolving physical ocean and sea-ice reanalysis (https://doi.org/10.48670/moi-00021) available in the Copernicus Marine Service (https://www.copernicus.eu/en - CMEMS) with a reliable level of performance reproducing oceanic features such as eddies (Lellouche et al. 2021b, 2021a). This product is based on the current real-time forecasting of the CMEMS system with a model component of NEMO, with the observations assimilated using a reduced-order Kalman filter. The simulation covered the surface waters of the North Atlantic and South Atlantic oceans between 100° W, 20° E and 50° N, 40° S in 1/12° resolution for the period 2006-2016 with a daily frequency. The models were reconfigured to a MARS 2D model structure to make them compatible with ICHTHYOP in 2D and tabulated in monthly files.

2.3.3 Dispersal model configuration and scenarios

The dispersal implemented a passive Forward Euler time-stepping scheme for advection with a time step of 600 s. With the above configuration, we set seven release zones to seed the initial positions of particles: Rio Grande do Norte, São Pedro and São Paulo archipelago, and Trindade and Martin Vaz, all in Brazil; Suriname; Ascension and Saint Helena islands, and Central America (Fig. 1). The areas were selected aiming to include regions that could help to understand how *O. insularis* disperse in their known distribution (i.e., the whole range of

species distribution) and detect potential release regions where sea currents could facilitate a potential connectivity between South America and Africa.

In general, there is no evident hatching season for *O. insularis*. Studies on reproduction of this species in the Northeast Brazil found mature males and mature and spawned females occurring year-round (Lima et al. 2014b; Batista et al. 2021). In the Gulf of Mexico, mature and spent females were observed from late spring to autumn, mostly in winter and mature males are present year-round (González-Gómez et al. 2020). Therefore, the models were configured in a forward dispersion approach using a bimonthly simulation starting each month (60 days of time simulation – 12 runs per year, a total of 120 simulations) for the period to establish the potential dates of connectivity between South America and Western Africa. We also accounted for horizontal dispersion in the advection process caused by the turbulent process following Peliz et al. (2007).

One hundred thousand particles were released in total for all seven zones, randomly placed in the release zones for each simulation based on *O. insularis* fecundity (68,502 to 120,166 oocytes, eggs size ~ 2.5 mm – Lima et al. 2014a, Lenz et al. 2015). It must be pointed out that no study has described the duration of the paralarvae phase of *O. insularis*. However, studies with the related species *O. vulgaris* have demonstrated a planktonic period between 1-3 months (Villanueva and Norman 2008). Since *O. insularis* probably has a life cycle shorter than *O. vulgaris* (Lima et al. 2014b, Batista et al. 2021), we decided to settle its planktonic period as 60 days to perform the model simulation.

3. Results

3.1 Genetic analysis

Fragments of 481 bp of the mitochondrial *cox1* gene were used to analyze the phylogenetic relationships among the octopod species. The samples used in the genetic analysis resulted in 30 haplotypes. The Bayesian phylogenetic reconstruction showed that two of the three

octopus sequences from São Tomé island belong to a monophyletic and well-supported *O. insularis* clade (posterior probability, PP = 1). These specimens are more closely related to the Ascension and Saint Helena individuals, sharing the same haplotype. The *Octopus insularis* group splits into two main clades: one with individuals from Trindade and Martin Vaz island and Bahia and the other including octopuses from Northeast Brazil and the Caribbean, where the African samples were placed. The genetic distances between the *O. insularis* individuals from Brazil and Caribbean and the samples from Africa varied between 0.21 to 0.84% (Tamura-Nei model) (Table 2), confirming that they belong to the same species.

The third octopus sample seems to be a new species related to the clade with the *Octopus vulgaris* species complex. Molecular distance analysis showed *O. tetricus* and *O. vulgaris* as the most closely related to this new species, with 91.52% and 91.31% of genetic similarity, respectively (Table 2). A similar analysis performed using BLAST on the NCBI platform revealed a similar result indicating that *O. tetricus* is the most similar species with a 7.55% of genetic distance.

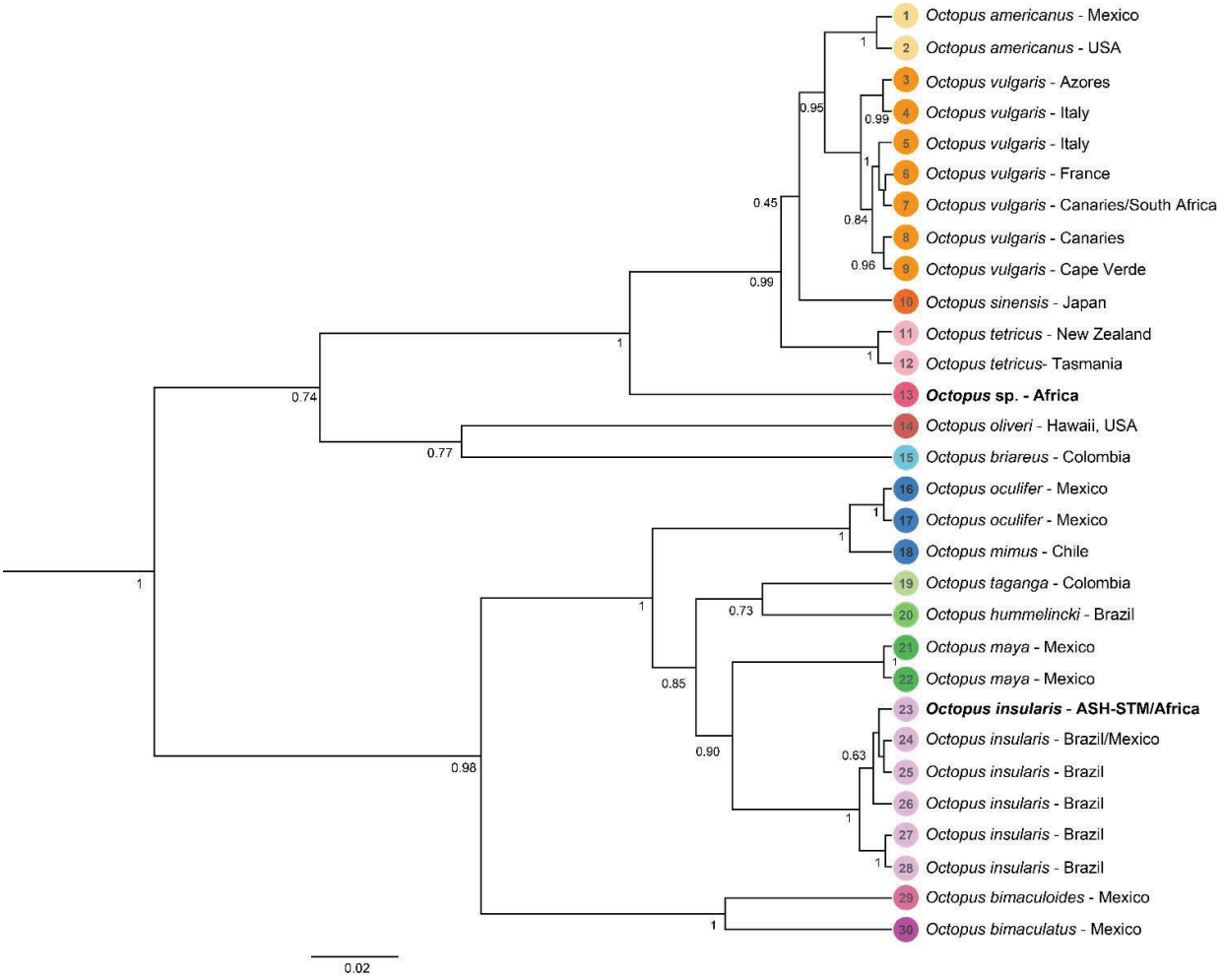


Fig. 2. Bayesian phylogenetic tree constructed with *Octopus cox1* sequences. The Bayesian posterior probabilities of the clades are shown below the nodes. Each color represents a different species. The haplotype number is shown in the circles and detailed in Table S1. In bold are the haplotypes of the African samples collected in this study. ASH = Ascension and St. Helena Islands, STM = São Tomé Island.

Table 2. Estimates of evolutionary divergence between sequences of *cox*1 using Tamura-Nei distance. In bold blue are the molecular distances among *O. insularis* sequences. The genetic distances are estimated in percentage (%). ASH = Ascension and St. Helena Islands, STM = São Tomé Island

Haplotype/Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1. *O. americanus* (Mexico)																													
2. *O. americanus* (USA)	0.4																												
3. *O. vulgaris* (Azores)	2.4	2.4																											
4. *O. vulgaris* (Italy)	2.2	2.1	0.2																										
5. *O. vulgaris* (Italy)	2.4	2.4	0.8	0.6																									
6. *O. vulgaris* (France)	2.4	2.4	0.8	0.6	0.4																								
7. *O. vulgaris* (Canaries/South Africa)	2.2	2.1	0.6	0.4	0.2	0.2																							
8. *O. vulgaris* (Canaries)	2.4	2.4	0.8	0.6	0.4	0.4	0.2																						
9. *O. vulgaris* (Cape Verde)	2.8	2.8	1.3	1.1	0.8	0.8	0.6	0.4																					
10. *O. sinensis* (Japan)	3.0	3.0	3.0	2.8	3.0	3.0	2.8	2.6	3.0																				
11. *O. tetricus* (New Zealand)	3.5	3.5	4.2	3.9	4.2	4.2	3.9	3.7	4.2	3.5																			
12. *O. tetricus* (Tasmania)	3.1	3.0	3.7	3.5	3.7	3.7	3.5	3.3	3.7	3.0	0.4																		
13. ***Octopus* sp. (STM-Africa)**	8.7	8.7	9.2	9.0	9.2	8.7	9.0	8.8	9.3	9.5	9.0	8.5																	
14. *O. oliveri* (Hawaii, USA)	16.3	16.2	16.7	16.5	16.1	16.1	15.8	15.6	16.1	16.3	15.5	15.0	16.1																
15. *O. briareus* (Colombia)	15.8	15.7	17.3	17.6	17.9	17.3	17.6	17.4	17.3	17.1	15.8	15.5	16.7	15.9															
16. *O. oculifer* (Mexico)	13.4	13.3	15.0	14.7	15.0	15.0	14.7	14.5	14.0	14.0	13.9	13.4	13.5	16.4	16.4														
17. *O. oculifer* (Mexico)	13.6	13.6	14.7	14.4	14.7	14.7	14.4	14.2	13.7	13.7	13.6	13.1	13.8	16.8	16.7	0.2													
18. *O. mimus* (Chile)	13.0	13.0	14.6	14.4	14.6	14.7	14.4	14.2	14.1	13.7	13.6	13.0	13.8	15.8	16.0	1.1	1.3												
19. *O. taganga* (Colombia)	14.2	14.1	15.2	15.0	15.8	15.3	15.6	15.3	15.3	14.9	14.1	13.6	14.0	15.1	14.9	4.7	4.9	4.4											
20. *O. hummelincki* (Brazil)	14.3	14.3	14.8	14.5	15.4	15.4	15.1	15.4	15.3	14.6	14.7	14.2	15.2	16.5	16.4	6.6	6.9	6.3	4.9										
21. *O. maya* (Mexico)	16.3	16.2	16.4	16.2	17.1	16.5	16.8	16.6	16.5	16.6	16.8	16.3	15.0	17.9	17.3	8.1	7.8	7.8	7.6	8.7									
22. *O. maya* (Mexico)	16.6	16.5	16.7	16.5	17.4	16.8	17.1	16.9	16.8	16.9	17.2	16.6	15.3	18.3	17.6	8.4	8.1	8.0	7.9	8.9	0.2								
23. ***O. insularis* (ASH-STM/Africa)**	12.0	11.9	12.4	12.2	13.0	13.0	12.7	12.5	12.5	12.6	13.0	12.5	15.0	16.3	17.4	6.4	6.6	6.1	6.5	7.5	8.8	9.1							
24. *O. insularis* (Brazil)	12.3	12.2	12.7	12.5	13.3	13.3	13.0	12.8	12.7	12.9	13.3	12.8	14.7	16.0	17.7	6.1	6.4	5.8	6.2	7.2	8.6	8.8	**0.2**						
25. *O. insularis* (Brazil)	12.5	12.5	13.0	12.7	13.6	13.6	13.3	13.1	13.0	13.2	13.6	13.1	15.0	16.0	18.0	6.4	6.6	6.1	6.5	7.5	8.3	8.5	**0.4**	**0.2**					

26. *O. insularis* (Brazil)	12.5	12.5	13.0	12.7	13.6	13.6	13.3	13.1	13.0	13.2	13.6	13.1	14.4	16.3	18.0	6.4	6.6	6.1	6.5	7.5	8.3	8.5	0.4	0.2	0.4				
27. *O. insularis* (Brazil)	12.8	12.7	13.0	12.7	13.5	13.6	13.3	13.1	13.0	13.2	13.3	12.8	14.7	15.7	18.3	6.3	6.6	6.0	6.4	7.4	8.7	9.0	0.8	0.6	0.8	0.8			
28. *O. insularis* (Brazil)	12.8	12.7	13.0	12.7	13.5	13.6	13.3	13.1	13.0	13.2	13.3	12.8	14.7	15.7	18.3	6.3	6.6	6.0	6.4	7.4	8.9	9.2	1.1	0.8	1.1	1.1	0.2		
29. *O. bimaculoides* (Mexico)	15.7	16.3	17.1	16.9	17.8	17.2	17.5	17.3	17.2	16.5	17.6	17.0	15.9	19.1	15.7	11.5	11.8	11.7	11.1	12.5	12.6	12.9	11.4	11.1	11.4	11.4	11.8	11.8	
30. *O. bimaculatus* (Mexico)	15.2	15.1	15.9	15.7	16.6	16.0	16.3	16.1	16.0	16.6	17.7	17.1	15.6	15.9	16.4	11.6	11.9	10.7	11.1	12.0	12.4	12.7	11.7	11.4	11.7	11.7	11.6	11.6	6.7

3.2 Ecological Niche Model

The ENM with the best overall performance had an L configuration (AUCval = 0.78, OR10 = 0.05 and delta AIC = 5.69). The permutation importance analysis indicates that the variables that most contributed to the model were SST_Min (44.1%), SSS_Min (27.9%), and Bathymetry (26.6%). Conversely, SST_Max contributed little (1.4%), while SSS_Max and SSS_Ran effect on the model was negligible (0%). Suitability maps were binarized according to a value of 0.19 (Fig. S1), meaning that any value below was considered an absence. Response curves (Fig. S2) show that *O. insularis* has high thermal (from 20 °C to temperatures above 30 °C) and salinity tolerances (20 PSS – Fig. S2).

Suitability (Fig. 3) and binary map (Fig. S2) suggest that the distribution of *O. insularis* in America occurs from Florida, USA (~30°N) to São Paulo and Paraná, Brazil (~25°S – however, such southern regions have lower suitability) with Amazon River acting as a soft barrier. This species could also find potentially suitable regions throughout the Gulf of Mexico (except the Northern Gulf of Mexico) and the Caribbean. The Mid-Atlantic islands like São Pedro and São Paulo, Ascension, Saint Helena, and Trindade and Martin Vaz may harbor octopus populations. Regarding Western Africa, suitable regions are found from Guinea-Bissau (~12°N) down to Equatorial Guinea and Gabon (~1°N), with a break of suitability in front of coastal Cameroon (~3°N). Finally, the ENM also suggests that the African Islands such as São Tomé and Príncipe, and Cabo Verde have favorable environmental conditions. High extrapolation risk was detected in northern and southern Africa (Fig. S3).

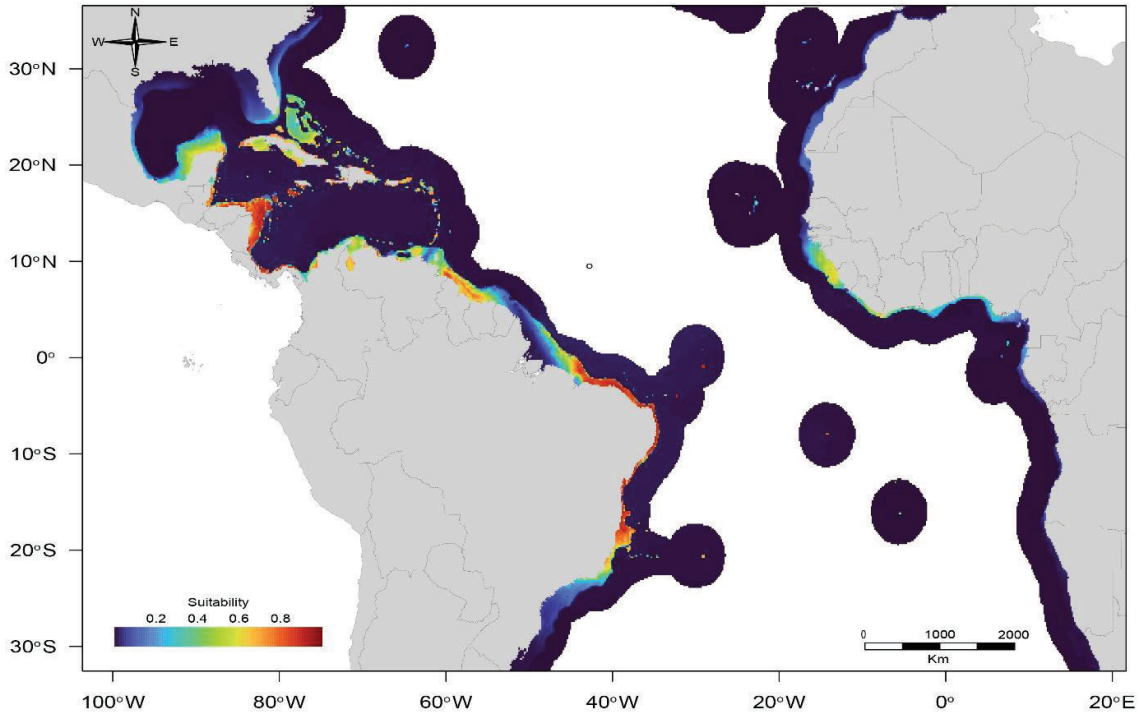


Fig. 3. Distribution of suitable climatic niche for *Octopus insularis* in the Atlantic Ocean

3.3 Dispersal models

3.3.1 Bimonthly dispersal simulations

The bimonthly simulations (simulations of 60 days) showed that particles from northeast coast of Brazil, Suriname, Caribbean regions of Colombia, and Central America tend to disperse toward the northwest Atlantic, the latter arriving in Florida. In addition, the São Pedro and São Paulo archipelago could have acted as a stepping-stone between South America and Western Africa thanks to the Equatorial Countercurrent, allowing particles to get closer to seamounts region at Central-West Africa in 30-60 days approximately. May and June are the months that showed higher potential connectivity between São Pedro and São Paulo and the African coast, mainly in 2009 when particles reach close the African Shelf. Finally, Trindade and Martim Vaz, Ascension, and Saint Helena islands greatly differed from the other release zones since the dispersion was almost non-existent (Fig. 4), with no connectivity between them or other

release regions. The gifs animation files of bimonthly dispersal simulations for the years 2006 to 2015 are shown in Supplementary 4.

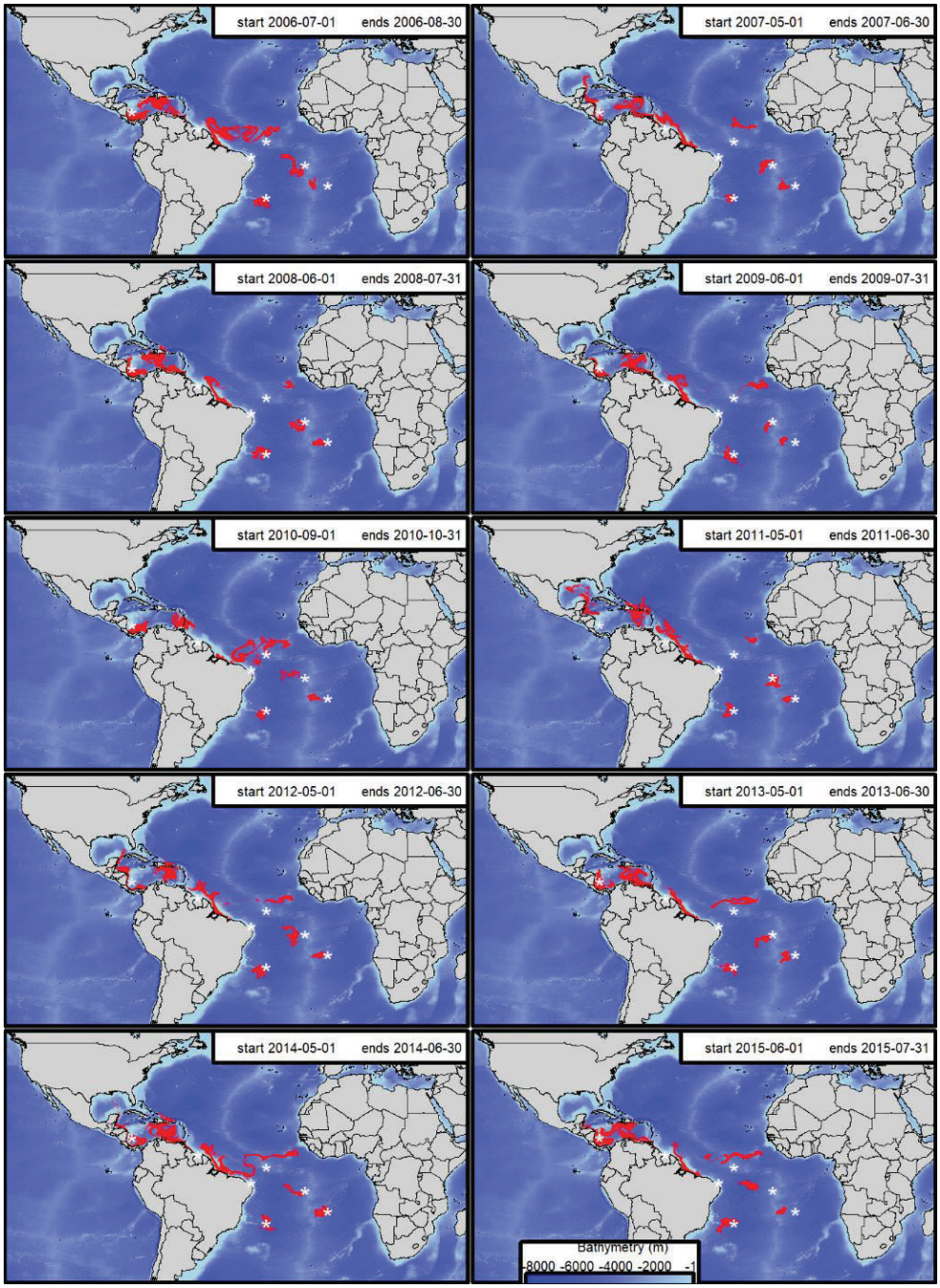


Fig. 4. Bimonthly dispersal simulations of *Octopus insularis* paralarvae. The stars indicated the released areas.

4. Discussion

The genetics analysis using fragments of the *cox1* gene, ENM, and dispersal models performed in this study showed that the dominant octopus species in the shallow waters of Western Tropical Atlantic also inhabit the shallow waters of tropical Eastern Atlantic. The Bayesian phylogenetic reconstruction revealed that two octopus samples collected in São Tomé Island belong to a monophyletic and well-supported *O. insularis* clade. In addition, ENM showed that Suriname, São Pedro and São Paulo archipelago, and Western Africa had highly suitable regions (~0.40 of suitability). At the same time, dispersal models pointed out that Suriname, São Pedro and São Paulo archipelago could have been a source of paralarvae to Western Africa.

The long dispersal route from West to East Atlantic could impede the species population settlement on the African islands. However, considering the duration of the species larval period (Roura et al. 2019), high fecundity (Lima et al. 2014a), and the high tolerance of paralarvae to environmental variations (Ángeles-González et al. 2020), the dispersal model demonstrated that *O. insularis* paralarvae could potentially reach Atlantic African seamounts via ocean currents under optimal current conditions after 30-50 days.

Previous studies applying species distribution modeling have pointed out the possibility of *O. insularis* suitable niche in the eastern Atlantic (Lima et al. 2020); nevertheless, this study provides the first evidence of *O. insularis* as a trans-Atlantic species. Updated results of ENM obtained here corroborate the study by Lima et al. (2020) as they show that *O. insularis* can be widely distributed in the Americas and African coast due to its high temperatures (32 °C) and salinities (36-42 PSU) tolerances as observed in the field. Indeed, according to the ENM, the *O. insularis* distribution may be limited mainly by low temperatures and salinities; however, as temperatures increase due to climate change, this species may likely invade higher latitudes (Lima et al. 2020).

The North Equatorial Countercurrent (NECC) influences the connectivity dispersal route towards western Africa. The mean eastward velocity for the NECC is 42 cm s^{-1}, and maximum

velocities of up 147 cm s^{-1} in the western section of the current (Fratantoni 2001). The hatchlings from São Pedro and São Paulo would arrive at the African coast after 30 (maximum velocity) to 116 days (mean velocity), hypothetically within the larval duration range of the species and in agreement with the dispersal models results. Moreover, the connectivity route coincides with the region of high primary productivity in the Atlantic (Tilstone et al. 2009), which may favor paralarvae survival due to greater food availability. It is important to point out that NECC eastern flow is higher during the boreal summer (June-August) and early fall (September) (Carton and Katz, 1990). Such trends could explain the higher potential connectivity during May-June-July for most years, as paralarvae dispersing thorough NECC could travel eastward faster. The high fecundity of *O. insularis* (68,502 to 120,166) (Lima et al. 2014a) and the small eggs size (~ 2.5 mm) (Lenz et al. 2015) facilitate the paralarvae to be faster carried out by the currents. In addition, the high thermal tolerance of the embryos (Ángeles-González et al. 2020), possibly allows the paralarvae to survive in a wide range of temperatures.

Both phylogenetic reconstruction and genetic distance analyses (Tamura-Nei model) pointed out that *O. insularis* from São Tomé Island is part of the Ascension and Saint Helena populations. The African haplotype is also in the same clade of *O. insularis* from Brazil's Northeast coast and oceanic islands. These findings suggest that the African population probably originated from the dispersion of individuals from the Western Atlantic, which agrees with the results of the dispersal model. The haplotype network constructed by Lima et al. (2022) also showed that Saint Helena and Ascension specimens are closely related to individuals from Northeast Brazil. The phylogenetic analysis performed in this study also showed low genetic distances between *O. oculifer* and *O. mimus* (1.06-1.27%), indicating they belong to the same species, which is in agreement with Acosta-Jofré et al. (2012) and Vandez-Cibrián et al. (2020) findings.

The planktonic larvae of many other marine species can successfully travel long distances until finding a suitable area for settlement (Cowen and Sponaugle 2009). According to Joyeux

et al. (2001), five species of marine fishes have apparently made the eastward transatlantic crossing, two of which are probably recent arrivals, and three established local populations. Lessios et al. (1999) suggest that populations of the sea urchin *Eucidaris tribuloides* (Lamark, 1816) from the west coast of Africa and the Caribbean Sea are also connected by recent gene flow. Nunes et al. (2011) assessed connectivity patterns in broadly distributed amphi-Atlantic corals and found species from Brazil and Africa with identical alleles or 1–2 mutations differences.

The genetic analyses of these trans-Atlantic taxa aforementioned show low current connectivity between distant populations. The gene flow was probably more frequent in the Pleistocene during the Last Glacial Period (LGP) (110,00-15,000 kya), when the sea level was approximately 120 m lower than today, rising again around 14.5 kya (Lambeck et al. 2014; Ludt & Rocha 2015). Throughout this period, the ocean thermohaline circulation were similar to present days (Yu et al. 1996; Watkins et al. 2007). The shallow ocean depths on continental shelves and seamounts probably favoured transcontinental movement and population expansions. During the trajectory to Western Africa, paralarvae may find seamounts that could be useful as stepping-stones to reach African islands. However, they are currently too deep (bathymetry > 100 m) for settlement to occur. The populations of octopus species with wide distribution are commonly structured over a geographic area (Van Nieuwenhove et al. 2019). Indeed, Lima et al. (2022) demonstrated that populations of *O. insularis* are genetically structured along their distribution range, with low gene flow between both Atlantic coasts. Therefore, considering the current low genetic connectivity between Africa and South America (Lima et al. 2022), we can hypothesize that seamounts in the tropical Atlantic were essential pathways of population connectivity during the LGP.

Although our dispersal model was helpful to propose the hypothesis of potential connectivity between South America and Africa, there is a lack of information about the paralarva stage of *O. insularis,* which difficult the addition of biological parameters to the model to increase reliability. For instance, studies have shown that paralarvae vertical diel behaviour can lead to

different dispersal patterns, allowing retention or oceanic dispersal of paralarvae (Roura et al. 2016, 2019). Particularly, Roura et al. (2019) identified a coastal-oceanic dispersal pattern for *O. vulgaris* (paralarvae were reported between the continental shelf and continental slope), suggesting that the dispersal capacity would be lower for biological entities than for particle simulations (Freire et al. 2021). However, the paralarvae ability to reach seamounts less than 100 m depth may have been higher during the Pleistocene, reducing the time necessary for the paralarva to drift.

The particles released in Trindade and Martim Vaz archipelago (SW Atlantic) differed greatly from the other zones since the dispersal was almost non-existent, suggesting self-recruitment in this region. These islands are under the influence of the South Atlantic Subtropical Gyre, which originated from the Brazil Current and the South Equatorial Current (Lumpkin and Garzoli 2005; Silveira et al. 2000). The interaction of the Brazil Current with the region's complex topography (Victoria-Trindade seamount) promotes the formation of cyclonic and anticyclonic meanders that can give rise, among others, to the Vitória Vortex (Schmid et al. 1995; Campos 2006). The formation of these vortices and closed recirculation cells may be responsible for larval retention in the region, making it difficult for paralarvae to disperse to distant areas (Swearer et al. 1999). Lima et al. (2022) showed that the populations of *O. insularis* from Alagoas, Bahia, and Trindade and Martin Vaz are highly structured compared to populations from the other locations of the Northeast Coast of Brazil, probably due to the low potential for dispersion caused by the presence of these eddies. Using genetic data and Lagrangian dispersal models, Freire et al. (2021) also identified the same pattern for the crustacean *Grapsus grapsus* (Linnaeus, 1758) in the Trindade and Martin Vaz islands.

The octopus fisheries in some African countries of the eastern Atlantic coast have been under-reported on a massive scale (Sauer et al. 2021), mainly in the Gulf of Guinea countries, where São Tomé and Príncipe islands are located (Area 34 FAO). There are three main stocks of "*Octopus vulgaris*" in the FAO area 34: Dakhla, Cape Blanc, and Senegal-Gambia, reported either as fully exploited or overexploited (Alder and Sumalia 2004**)**. The estimate of the *O.*

vulgaris total catch in this area is around 60,000 t on average, with a peak of over 330,000 t per year (FAO 2011; Sauer et al. 2021).

The new record of *O. insularis* in Africa raises important questions regarding regional fisheries management. The octopus fisheries in São Tomé and Príncipe islands are performed mainly by spearfishing in shallow waters (Maia et al. 2018b). There is little information on the number of octopuses captured through this fishery. Still, according to Porriños (2021), fishers can catch up to 100 to 500 kg of octopuses in a single fishing trip. In addition, the new octopus species indicated in this study may also be part of the target octopus stock in São Tomé Island. There is no specific regulation for octopus fishing in São Tomé and Príncipe, and little is known about the biology and ecology of octopus species in this region. For this reason, it is urgent that further studies on cephalopod diversity, as well as the species composition of the octopus fishery stock, are carried out for the successful management of this important fishery resource.

Considering that *O. insularis* is highly tolerant to environmental variations and very adapted to warm shallow waters, there is a possibility that these stocks have a mixed composition (*O. vulgaris*, *O. insularis*, and the new species) and therefore, the octopus fisheries must follow management measures suitable for each species.

5. Conclusion

The genetic results of this study extended the distribution of *O. insularis* to São Tomé and Príncipe islands, confirming that this is the most widely distributed octopus species in the tropical Atlantic. The ENM suggests that the Americas and Western Africa tropical regions are suitable for the species. Finally, the passive dispersal model showed that the *O. insularis paralarvae* could potentially cross the Atlantic Ocean and reach the African coast, even though we hypothesized that the current dispersal is occasional and was more common during the lower sea-level glaciation periods in the Miocene–Pliocene.

Studies on the biology, ecology, and fishing of octopus in the Gulf of Guinea are scarce. However, correctly identifying the species that compose a fishery stock is crucial for monitoring population fluctuations and preventing species overexploitation (Lima et al. 2017; Tillet et al. 2012; Ward 2000). New studies on integrative taxonomy and fishery biology can correctly identify the species that compose these octopus stocks so effective management measures can be applied, ensuring the sustainable exploitation of these species.

Acknowledgements

We are thankful to the Brazilian National Research Council (CNPq 481492/2013-9) and Coordination for the Improvement of Higher Education Personnel (Ciências do Mar II - CAPES) for financial support to run the analyses and research grant (F.D.L.), and the productivity research grant (CNPq 312066/2021-0).

References

Acosta-Jofré, M.S., Sahade, R., Laudien, J., Chiappero, M.B., 2012. A contribution to the understanding of phylogenetic relationships among species of the genus *Octopus* (Octopodidae: Cephalopoda). Sci. Mar. 76, 311–318. https://doi.org/10.3989/scimar.03365.03B

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., Anderson, R.P., 2015. spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography. 38, 541–545. https://doi.org/10.1111/ecog.01132

Alder, J., Sumaila, U.R., 2004. Western Africa: A fish basket of Europe past and present. J. Environ. Dev. 13, 156–178. https://doi.org/10.1177/1070496504266092

Allcock, A.L., Strugnell, J.M., Ruggiero, H., Collins, M.A., 2006. Redescription of the deep-sea octopod *Benthoctopus normani* (Massy 1907) and a description of a new species

from the Northeast Atlantic. Mar. Biol. Res. 2, 372–387. https://doi.org/10.1080/17451000600973315

Álvarez-Noriega, M., Burgess, S.C., Byers, J.E., Pringle, J.M., Wares, J.P., Marshall, D.J., 2020. Global biogeography of marine dispersal potential. Nat. Ecol. Evol. 4, 1196–1203. https://doi.org/10.1038/s41559-020-1238-y

Amado, E.M., Souza-Bastos, L.R., Vidal, E.A.G., Leite, T.S., Freire, C.A., 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. https://doi.org/10.1080/10236244.2015.1024078

Amor, M.D., Norman, M.D., Cameron, H.E., Strugnell, J.M., 2014. Allopatric speciation within a cryptic species complex of Australasian octopuses. PLoS One 9, 1–6. https://doi.org/10.1371/journal.pone.0098982

Amor, M.D., Laptikhovsky, V., Norman, M.D., Strugnell, J.M., 2017. Genetic evidence extends the known distribution of *Octopus insularis* to the mid-Atlantic islands Ascension and St Helena. J. Mar. Biol. Assoc. United Kingdom 97, 753–758. https://doi.org/https://doi.org/10.1017/S0025315415000958

Ángeles-González, L.E., Lima, F.D., Caamal-Monsreal, C., Díaz, F., Rosas, C., 2020. Exploring the effects of warming seas by using the optimal and pejus temperatures of the embryo of three Octopoda species in the Gulf of Mexico. J. Therm. Biol. 94, 102753. https://doi.org/10.1016/j.jtherbio.2020.102753

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., 2017. Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. Glob. Ecol. Biogeogr. 27, 277–284. https://doi.org/10.1111/geb.12693

Avendaño, O., Roura, Á., Cedillo-Robles, C.E., González, Á.F., Rodríguez-Canul, R., Velázquez-Abunader, I., Guerra, Á., 2020. *Octopus americanus*: a cryptic species of the O. vulgaris species complex redescribed from the Caribbean. Aquat. Ecol. 54, 909–

925. https://doi.org/10.1007/s10452-020-09778-6

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J., Villalobos, F., 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol. Modell. 222, 1810–1819. https://doi.org/10.1016/j.ecolmodel.2011.02.011

Bastos, P., Vieira, G.C., 2018. Maintenance of *Octopus vulgaris* Type II paralarvae in an estuarine area. Rev. Bras. Zootec. 47, 1-7. https://doi.org/10.1590/rbz4720170009

Batista, A.T., Leite, T.S., 2016. *Octopus insularis* (Cephalopoda: Octopodidae) on the tropical coast of Brazil: Where it lives and what it eats. Brazilian J. Oceanogr. 64, 353–364. https://doi.org/10.1590/S1679-87592016123406404

Batista, B.B., Matthews-Cascon, H., Marinho, R.A., Kikuchi, E., Haimovici, M., 2021. The growth and population dynamics of *Octopus insularis* targeted by a pot longline fishery in north-eastern Brazil. J. Mar. Biol. Assoc. United Kingdom 101, 935–946. https://doi.org/10.1017/S0025315421000898

Bouth, H.F., Leite, T.S., de Lima, F.D., Oliveira, J.E.L., 2011. Atol das Rocas: An oasis for *Octopus insularis* juveniles (Cephalopoda: Octopodidae). Zoologia 28, 45–52. https://doi.org/10.1590/S1984-46702011000100007

Boyle, P., Rodhouse, P.G., 2005. Cephalopods: ecology and fisheries. Blackwell Science, Oxford.

Cabral, H., Drouineau, H., Teles-Machado, A., Pierre, M., Lepage, M., Lobry, J., Reis-Santos, P., Tanner, S.E., 2021. Contrasting impacts of climate change on connectivity and larval recruitment to estuarine nursery areas. Prog. Oceanogr. 196, 102608. https://doi.org/10.1016/j.pocean.2021.102608

Campos, E.J.D., 2006. Equatorward translation of the Vitoria Eddy in a numerical simulation. Geophys. Res. Lett. 33, 1–5. https://doi.org/10.1029/2006GL026997

Carranza, S., Arnold, E.N., 2003. Investigating the origin of transoceanic distributions: mtDNA shows *Mabuya* lizards (Reptilia, Scincidae) crossed the Atlantic twice. Syst. Biodivers. 1, 275–282. https://doi.org/10.1017/S1477200003001099

Carton, J.A., Katz, E.J., 1990. Estimates of the Zonal Slope and Seasonal Transport of the Atlantic North Equatorial Countercurrent. J. Geophys. Res. 95, 3091–3100. https://doi.org/doi.org/10.1029/JC095iC03p03091

Chamberlain, S., Barve, V., Mcglinn, D., Oldoni, D., Desmet, P., Geffert, L., Ram, K., 2022. rgbif: Interface to the Global Biodiversity Information Facility API_. R package version 3.6.0.

Cowen, R.K., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. Ann. Rev. Mar. Sci. 1, 443–466. https://doi.org/10.1146/annurev.marine.010908.163757

Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A., 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol. Biol. Evol. 29, 1969–1973. https://doi.org/10.1093/molbev/mss075

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods Ecol. Evol., 1, 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

FAO, 2011. Review of the state of world marine fishery resources. FAO Fish. Aquac. Tech. Pap. 569. FAO, Rome.

Flores-Valle, A., Pliego-Cárdenas, R., Jiménez-Badillo, L., Arredondo-Figueroa, J.L., Barriga-Sosa, I.D.L.A., 2018. First Record of *Octopus insularis* Leite and Haimovici, 2008 in the Octopus Fishery of a Marine Protected Area in the Gulf of Mexico. J. Shellfish Res. 37, 221–227. https://doi.org/10.2983/035.037.0120

Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial Cytochrome c Oxidase Subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. Biotechnol. 3, 294–299.

Fratantoni, D.M., 2001. North Atlantic Surface Circulation during the 1990's Observed with Satellite-Tracked Drifters. J. Geophys. Res. 22, 22067–22093.

Freire, A.S., Teschima, M.M., Brandão, M.C., Iwasa-Arai, T., Sobral, F.C., Sasaki, D.K., Agostinis, A.O., Pie, M.R., 2021. Does the transport of larvae throughout the south Atlantic support the genetic and morphometric diversity of the Sally Lightfoot Crabs

Grapsus grapsus (Linnaeus, 1758) and *Grapsus adscensionis* (Osbeck, 1765) (Decapoda: Grapsidae) among the oceanic islands. J. Mar. Syst. 223. https://doi.org/10.1016/j.jmarsys.2021.103614

Gaither, M.R., Bernal, M.A., Coleman, R.R., Bowen, B.W., Jones, S.A., Simison, W.B., Rocha, L.A., 2015. Genomic signatures of geographic isolation and natural selection in coral reef fishes. Mol. Ecol. 24, 1543–1557. https://doi.org/10.1111/mec.13129

Gray, L.A., Bisonó León, A.G., Rojas, F.E., Veroneau, S.S., Slocum, A.H., 2021. Caribbean-Wide, Negative Emissions Solution to Sargassum spp. Low-Cost Collection Device and Sustainable Disposal Method. Phycology 1, 49–75. https://doi.org/10.3390/phycology1010004

González-Gómez, R., Meiners-Mandujano, C., Morillo-Velarde, P.S., Jiménez-Badillo, L., Markaida, U., 2020. Reproductive Dynamics and Population Structure of *Octopus insularis* From the Veracruz Reef System Marine Protected Area, Mexico. Fish. Res. 221, 105385. https://doi.org/10.1016/j.fishres.2019.105385

Hedgecock, D., 1986. Is Gene Flow From Pelagic Larval Dispersal Important in the Adaptation and Evolution of Marine Invertebrates? Bull. Mar. Sci. 39, 550–564.

Hellberg, M.E., 2009. Gene Flow and Isolation among Populations of Marine Animals. Annu. Rev. Ecol. Evol. Syst. 40, 291–310. https://doi.org/10.1146/annurev.ecolsys.110308.120223

Houle, A., 1998. Floating Islands: A Mode of Long-Distance Dispersal for Small and Medium- Sized Terrestrial Vertebrates. Divers. Distrib, 4, 201–216.

Jordan, C., Cusack, C., Tomlinson, M.C., Meredith, A., McGeady, R., Salas, R., Gregory, C., Croot, P.L., 2021. Using the Red Band Difference Algorithm to Detect and Monitor a Karenia spp. Bloom Off the South Coast of Ireland, June 2019. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.638889

Joyeux, J., Floeter, S.R., Ferreira, C.E.L., Gasparini, J.L., 2001. Biogeography of tropical reef fishes: the South Atlantic puzzle. J. Biogeogr. 28, 831–841. https://doi.org/10.1046/j.1365-2699.2001.00602.x

Juárez, O., Rosas, C., Arenta-Ortiz, M., 2012. Phylogenetic relationships *of Octopus maya* revealed by mtDNA sequences. Ciencias Mar. 38, 563–575. https://doi.org/10.7773/cm.v38i3.1962

Kaneko, N., Kubodera, T., Iguchis, A., 2011. Taxonomic study of shallow-water octopuses (Cephalopoda: Octopodidae) in Japan and adjacent waters using mitochondrial genes with perspectives on octopus DNA barcoding. Malacologia 54, 97–108. https://doi.org/10.4002/040.054.0102

Kass, J.M., Muscarella, R., Galante, P.J., Bohl, C.L., Pinilla-Buitrago, G.E., Boria, R.A., Soley-Guardia, M., Anderson, R.P., 2021. ENMeval 2.0: Redesigned for customizable and reproducible modeling of species' niches and distributions. Methods Ecol. Evol. 12, 1602–1608. https://doi.org/10.1111/2041-210X.13628

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., Drummond, A., 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28, 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Lalire, M., Gaspar, P., 2019. Modeling the active dispersal of juvenile leatherback turtles in the North Atlantic Ocean. Mov. Ecol. 7, 1–18. https://doi.org/doi.org/10.1186/s40462-019-0149-5

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. PNAS 111, 15296–15303. https://doi.org/10.1073/pnas.1411762111

Lapègue, S., Boutet, I., Leitão, A., Heurtebise, S., Garcia, P., Thiriot-Quiévreux, C., Boudry, P., 2002. Trans-Atlantic Distribution of a Mangrove Oyster Species Revealed by 16S mtDNA and Karyological Analyses. Biol. Bull. 202, 232–242. https://doi.org/10.2307/1543473

Leite, T.S., 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. https://doi.org/10.1093/mollus/eym050

Leite, T.S., Haimovici, M., Mather, J., Oliveira, J.E.L., 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. https://doi.org/10.1016/j.fishres.2009.04.001

Leite, T.S., Batista, A.T., Lima, F.D., Barbosa, J.C., Mather, J., 2016. Geographic variability of *Octopus insularis* diet: From oceanic island to continental populations. Aquat. Biol. 25, 17–27. https://doi.org/10.3354/ab00655

Lellouche, J.-M., Bourdallé-Badie, R., Greiner, E., Garric, G., Melet, A., Bricaud, C., Legalloudec, O., Hamon, M., Candela, T., Regnier, C., Drevillon, M., 2021a. The Copernicus global 1/12° oceanic and sea ice reanalysis. https://doi.org/10.5194/egusphere-egu21-14961, 2021

Lellouche, J.M., Greiner, E., Bourdallé-Badie, R., Garric, G., Melet, A., Drévillon, M., Bricaud, C., Hamon, M., Le Galloudec, O., Regnier, C., Candela, T., Testut, C.-E., Gasparin, F., Ruggiero, G., Benkiran, M., Drillet, Y., Pierre-Yves, L.T., 2021b. The Copernicus Global 1/12° Oceanic and Sea Ice GLORYS12 Reanalysis. Front. Earth Sci. 9, 1–27. https://doi.org/10.3389/feart.2021.698876

Lenz, T.M., Elias, N.H., Leite, T.S., Vidal, E.A.G., 2015. First description of the eggs and paralarvae of the tropical octopus, *Octopus insularis*, under culture conditions. Am. Malacol. Bull. 33, 101–109. https://doi.org/10.4003/006.033.0115

Lessios, H.A., Kessing, B.D., Robertson, D.R., Paulay, G., 1999. Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. Evolution (N. Y). 53, 806–817. https://doi.org/10.1111/j.1558-5646.1999.tb05374.x

Lett, C., Verley, P., Mullon, C., Parada, C., Brochier, T., Penven, P., Blanke, B., 2008. A Lagrangian tool for modelling ichthyoplankton dynamics. Environ. Model. Softw. 23, 1210–1214. https://doi.org/10.1016/j.envsoft.2008.02.005

Librado, P., Rozas, J.,2009. DnaSP v5: a software for comprehensive analysis of DNA

polymorphism data. Bioinformatics 25:1451–1452. https://doi.org/10.1093/bioinformatics/ btp187

Lima, F.D., Leite, T.S., Haimovici, M., Lins Oliveira, J.E., 2014a. Gonadal development and reproductive strategies of the tropical octopus (*Octopus insularis*) in northeast Brazil. Hydrobiologia 725, 7–21. https://doi.org/10.1007/s10750-013-1718-z

Lima, F., Leite, T., Haimovici, M., Nobrega, M., Lins Oliveira, J., 2014b. Population structure and reproductive dynamics of *Octopus insularis* (Cephalopoda: Octopodidae) in a coastal reef environment along northeastern Brazil. Fish. Res. 152, 86–92. https://doi.org/10.1016/j.fishres.2013.08.009

Lima, F.D., Berbel-Filho, W.M., Leite, T.S., Rosas, C., Lima, S.M.Q., 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. https://doi.org/10.1007/s12526-017-0638-y

Lima, F., Ángeles-González, L., Leite, T., Lima, S., 2020. Global climate changes over time shape the environmental niche distribution of *Octopus insularis* in the Atlantic Ocean. Mar. Ecol. Prog. Ser. 652, 111–121. https://doi.org/10.3354/meps13486

Lima, L.S., Gherardi, D.F.M., Pezzi, L.P., Passos, L.G. dos, Endo, C.A.K., Quimbayo, J.P., 2021. Potential changes in the connectivity of marine protected areas driven by extreme ocean warming. Sci. Rep. 11, 1–12. https://doi.org/10.1038/s41598-021-89192-6

Lima, F.D., Leite, T.S., Lima, S.M.Q., 2022. Seamounts and oceanic currents drive the population structure of *Octopus insularis* in the Southwest Tropical Atlantic. Aquat. Ecol. https://doi.org/10.1007/s10452-022-09955-9

Ludt, W.B., Rocha, L.A., 2015. Shifting seas: The impacts of Pleistocene sea-level fluctuations on the evolution of tropical marine taxa. J. Biogeogr. 42, 25–38. https://doi.org/10.1111/jbi.12416

Lumpkin, R., Garzoli, S.L., 2005. Near-surface circulation in the Tropical Atlantic Ocean. Deep. Res. Part I 52, 495–518. https://doi.org/10.1016/j.dsr.2004.09.001

Macías, D., Prieto, L., García-Gorriz, E., 2021. A model-based management tool to predict the spread of Physalia physalis in the Mediterranean Sea. Minimizing risks for coastal activities. Ocean Coast. Manag. 212, 105810. https://doi.org/10.1016/j.ocecoaman.2021.105810

Maia, H.A., Morais, R.A., Quimbayo, J.P., Dias, M.S., Sampaio, C.L.S., Horta, P.A., Ferreira, C.E.L., Floeter, S.R., 2018a. Spatial patterns and drivers of fish and benthic reef communities at São Tomé Island, Tropical Eastern Atlantic. Mar. Ecol. 39. https://doi.org/10.1111/maec.12520

Maia, H.A., Morais, R.A., Siqueira, A.C., Hanazaki, N., Floeter, S.R., Bender, M.G., 2018b. Shifting baselines among traditional fishers in São Tomé and Príncipe islands, Gulf of Guinea. Ocean Coast. Manag. 154, 133–142. https://doi.org/10.1016/j.ocecoaman.2018.01.006

Melis, R., Vacca, L., Cuccu, D., Mereu, M., Cau, A., Follesa, M.C., Cannas, R., 2018. Genetic population structure and phylogeny of the common octopus *Octopus vulgaris* Cuvier, 1797 in the western Mediterranean Sea through nuclear and mitochondrial markers. Hydrobiologia 807, 277–296. https://doi.org/10.1007/s10750-017-3399-5

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for <scp>Maxent</scp> ecological niche models. Methods Ecol. Evol. 5, 1198–1205. https://doi.org/10.1111/2041-210X.12261

Nunes, F.L.D., Norris, R.D., Knowlton, N., 2011. Long distance dispersal and connectivity in Amphi-Atlantic corals at regional and basin scales. PLoS One 6. https://doi.org/10.1371/journal.pone.0022298

O'brien, C.E., Bennice, C.O., Leite, T., 2021. A field guide to distinguishing *Octopus insularis* and *Octopus americanus* (Octopoda: Octopodidae). Zootaxa 5060, 589–594.

https://doi.org/10.11646/zootaxa.5060.4.8

Peliz A, Dubert J., Marchesiello P., Teles-Machado A., (2007) Surface circulation in the Gulf of Cadiz: Model and mean flow structure. J Geophys Res Ocean 112:1–20. https://doi.org/10.1029/2007JC004159

Peterson, R.G., Stramma, L., 1991. Upper-level circulation in the South Atlantic Ocean. Prog. Oceanogr. 26, 1–73. https://doi.org/10.1016/0079-6611(91)90006-8

Pliego-Cárdenas, R., Hochberg, F.G., León, F.J.G. De, Barriga-Sosa, I.D.L.A., 2014. Close genetic relationships between two American cctopuses: *Octopus hubbsorum* Berry, 1953, and *Octopus mimus* Gould, 1852. J. Shellfish Res. 33, 293–303. https://doi.org/10.2983/035.033.0128

Posada, D., 2008. jModelTest: Phylogenetic model averaging. Mol. Biol. Evol. 25, 1253–1256. https://doi.org/10.1093/molbev/msn083

Porriños, G., da Rocha, N., da Graça, M., Santos, A., Nazaré, L., Espírito-Santo, S., Madruga, L., 2021. Characterisation of artisanal fisheries in São Tomé and Príncipe through participatory, smartphone-based landing surveys, Report for Fauna and Flora International.

Provoost, P., Bosch, S., 2022. robis: Ocean Biodiversity Information System (OBIS) Client. R package version 2.10.1.

Quinteiro, J., Rodríguez-Castro, J., Rey-Méndez, M., Henríquez, N.G., 2020. Phylogeography of the insular populations of common octopus, *Octopus vulgaris* cuvier, 1797, in the atlantic macaronesia. PLoS One 15, 1–19. https://doi.org/10.1371/journal.pone.0230294

Ramos, J.E., Pecl, G.T., Moltschaniwskyj, N.A., Semmens, J.M., Souza, C.A., Strugnell, J.M., 2018. Population genetic signatures of a climate change driven marine range extension. Sci. Rep. 8, 9558. https://doi.org/10.1038/s41598-018-27351-y

R Core Team, 2022. R: A Language and Environment for Statistical Computing.

Radosavljevic, A., Anderson, R.P., 2014. Making better Maxent models of species

distributions: Complexity, overfitting and evaluation. J. Biogeogr. 41, 629–643. https://doi.org/10.1111/jbi.12227

Rambaut, A., Suchard, M.A., Xie, D., Drummond, A.J., 2014. Tracer v1.6.0. Available at http://tree.bio.ed.ac.uk/software/tracer/.

Renner, S., 2004. Plant dispersal across the tropical Atlantic by wind and sea currents. Int. J. Plant Sci. 165. https://doi.org/10.1086/383334

Ritschard, E.A., Guerrero-Kommritz, J., Sanchez, J.A., 2019. First molecular approach to the octopus fauna from the southern Caribbean. PeerJ 2019, 1–14. https://doi.org/10.7717/peerj.7300

Rocha, L.A., Rocha, C.R., Robertson, D.R., Bowen, B.W., 2008. Comparative phylogeography of Atlantic reef fishes indicates both origin and accumulation of diversity in the Caribbean. BMC Evol. Biol. 8, 1–16. https://doi.org/10.1186/1471-2148-8-157

Roura, Á., Antón Álvarez-Salgado, X., González, Á.F., Gregori, M., Rosón, G., Otero, J., Guerra, Á., 2016. Life strategies of cephalopod paralarvae in a coastal upwelling system (NW Iberian Peninsula): Insights from zooplankton community and spatio-temporal analyses. Fish. Oceanogr. 25, 241–258. https://doi.org/10.1111/fog.12151

Roura, Á., Amor, M., González, Á.F., Guerra, Á., Barton, E.D., Strugnell, J.M., 2019. Oceanographic processes shape genetic signatures of planktonic cephalopod paralarvae in two upwelling regions. Prog. Oceanogr. 170, 11–27. https://doi.org/10.1016/j.pocean.2018.10.005

Rudorff, C.A.. G., Lorenzzetti, J.A., Gherardi, D.F.M., Lins-Oliveira, J.E., 2009. Modeling spiny lobster larval dispersion in the Tropical Atlantic. Fish. Res. 96, 206–215. https://doi.org/10.1016/j.fishres.2008.11.005

Santana-Cisneros, M.L., Ardisson, P.L., González, Á.F., Mariño-Tapia, I., Cahuich-López, M., Ángeles-González, L.E., Ordoñez-López, U., Velázquez-Abunader, I., 2021. Dispersal modeling of octopoda paralarvae in the Gulf of Mexico. Fish. Oceanogr. 1–14. https://doi.org/10.1111/fog.12555

Sauer, W.H.H., Gleadall, I.G., Downey-Breedt, N., Doubleday, Z., Gillespie, G., Haimovici, M., Ibáñez, C.M., Katugin, O.N., Leporati, S., Lipinski, M.R., Markaida, U., Ramos, J.E., Rosa, R., Villanueva, R., Arguelles, J., Briceño, F.A., Carrasco, S.A., Che, L.J., et al., 2021. World Octopus Fisheries. Rev. Fish. Sci. Aquac. 29, 279–429. https://doi.org/10.1080/23308249.2019.1680603

Sbrocco, E.J., Barber, P.H., 2013. MARSPEC: Ocean climate layers for marine spatial ecology. Ecology 94, 979. https://doi.org/10.1890/12-1358.1

Sillero, N., Barbosa, A.M., 2021. Common mistakes in ecological niche models. Int. J. Geogr. Inf. Sci. 35, 213–226. https://doi.org/10.1080/13658816.2020.1798968

Silveira, I.C.A., Schmidt, A.C.K., Campos, E.J.D., Godoi, S.S., Ikeda, Y., 2000. A Corrente do Brasil ao Largo da Costa Leste Brasileira. Rev. bras. Ocean. 48, 171–183. https://doi.org/10.1136/bmj.j3567

Schmid, C., Schäfer, H., Zenk, W., Podestá, G., 1995. The Vitória eddy and its relation to the Brazil Current. J. Phys. Oceanogr. 25, 2532–2546. https://doi.org/https://doi.org/10.1175/1520-0485(1995)025<2532:TVEAIR>2.0.CO;2

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A.., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C., Robertson, J., 2007. Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. Bioscience 57, 573–583. https://doi.org/10.1641/B570707

Swearer, S.E., Caselle, J.E., Lea, D.W., Warner, R.R., 1999. Larval retention and recruitment in an island population of a coral-reef fish. Nature 402, 799–802. https://doi.org/10.1038/45533

Tamura, K., Stecher, G., Peterson, D., Filipski, A., Kumar, S., 2013. MEGA6: Molecular evolutionary genetics analysis version 6.0. Mol. Biol. Evol. 30, 2725–2729. https://doi.org/10.1093/molbev/mst197

Teske, P.R., Oosthuizen, A., Papadopoulos, I., Barker, N.P., 2007. Phylogeographic structure of *Octopus vulgaris* in South Africa revisited: Identification of a second lineage

near Durban harbour. Mar. Biol. 151, 2119–2122. https://doi.org/10.1007/s00227-007-0644-x

Tillett, B.J., Field, I.C., Bradshaw, C.J.A., Johnson, G., Buckworth, R.C., Meekan, M.G., Ovenden, J.R., 2012. Accuracy of species identification by fisheries observers in a north Australian shark fishery. Fish. Res. 127–128, 109–115. https://doi.org/10.1016/j.fishres.2012.04.007

Tilstone, G., Smyth, T., Poulton, A., Hutson, R., 2009. Measured and remotely sensed estimates of primary production in the Atlantic Ocean from 1998 to 2005. Deep. Res. Part II Top. Stud. Oceanogr. 56, 918–930. https://doi.org/10.1016/j.dsr2.2008.10.034

Valdez-Cibrián, A., Díaz-Santana-iturrios, M., Landa-Jaime, V., Michel-Morfín, J.E., 2020. First detection of an ocellate octopus in the revillagigedos ecoregion, a biodiversity hotspot located in the tropical east Pacific Province. Zookeys 2020, 81–100. https://doi.org/10.3897/zookeys.986.53250

Van Nieuwenhove, A.H.M., Ratsimbazafy, H.A., Kochzius, M., 2019. Cryptic diversity and limited connectivity in octopuses: Recommendations for fisheries management. PLoS One 14, 1–20. https://doi.org/10.1371/journal.pone.0214748

Villanueva, R., Nozais, C., Boletzky, S. V., 1997. Swimming behaviour and food searching in planktonic *Octopus vulgaris* Cuvier from hatching to settlement. J. Exp. Mar. Bio. Ecol. 208, 169–184. https://doi.org/10.1016/S0022-0981(96)026706

Villanueva, R., Norman, M.D., 2008. Biology of the planktonic stages of benthic octopuses. Oceanogr. Mar. Biol. An Annu. Rev. 46, 105–202.

Ward, R.D., 2000. Genetics in fisheries management. Hydrobiologia 420, 191–201. https://doi.org/10.1023/A:1003928327503

Watkins, S.J., Maher, B.A., Bigg, G.R., 2007. Ocean circulation at the Last Glacial Maximum: A combined modeling and magnetic proxy-based study. Paleoceanography 22, 1–20. https://doi.org/10.1029/2006PA001281

Ylitalo, H. a., Watling, L., Toonen, R.J., 2014. First description of hatchlings and eggs of *Octopus oliveri* (Berry, 1914) (Cephalopoda: Octopodidae). Molluscan Res. 34, 79–83. https://doi.org/10.1080/13235818.2013.860871

Yu, E.F., Francois, R., Bacon, M.P., 1996. Similar rates of modern and last-glacial ocean thermohaline circulation inferred from radiochemical data. Nature. https://doi.org/10.1038/379689a0

SUPPLEMENTARY MATERIAL

Molecular data, ecological niche, and dispersal models reveal a Trans-Atlantic shallow-water octopus species

Françoise D. Lima, Luís Enrique Ángeles-González, Hugulay Maia, Tatiana S. Leite, Miguel Cahuich-López, Ismael Mariño-Tapia, Mariana L. Santana-Cisneros, Pedro-Luis Ardisson, Sergio M. Q. Lima

Table S1.

Sequences of *cox1* gene of octopods species retrieved from GenBank and this study used in the phylogenetic analyses.

Species	Local	Accession number	Haplotype	Reference
Octopus americanus	Mexico	MT022413	1	Avendaño et al. 2020
Octopus americanus	United States - Virginia	MH087637	2	Aguilar et al. 2018 (*Unpublished*)
Octopus vulgaris	Azores	MN705281	3	Quinteiro et al. 2020
Octopus vulgaris	Italy	KT008577	4	Melis et al. 2018
Octopus vulgaris	Italy	KT008578	5	Melis et al. 2018
Octopus vulgaris	France	EF016328	6	Allcock et al. 2006
Octopus vulgaris	Canaries	MN705287	7	Quinteiro et al. 2020
Octopus vulgaris	South Africa	DQ683213	7	Teske et al. 2007
Octopus vulgaris	South Africa	DQ683212	7	Teske et al. 2007
Octopus vulgaris	Canaries	MN705309	8	Quinteiro et al. 2020
Octopus vulgaris	Cabo verde	MN705290	9	Quinteiro et al. 2020
Octopus sinensis	Japan	AB430548	10	Kaneko et al. 2011
Octopus tetricus	New Zealand	KJ605259	11	Amor et al. 2014
Octopus tetricus	Autralia - Tasmania	MH289820	12	Ramos et al. 2018
Octopus sp	São Tomé Island	OQ361634	13	present study
Octopus oliveri	Hawaii - USA	KC848885	14	Ylitalo et al. 2014

Octopus briareus	Colombia	MG778069	15	Ritschard et al. 2019
Octopus oculifer	Revillagigedos, Mexico	MN259102	16	Valdez-Cibrián et al. 2020
Octopus oculifer	Revillagigedos, Mexico	MN259101	17	Valdez-Cibrián et al. 2020
Octopus mimus	Chile	GU355924	18	Acosta-Jofré et al. 2012
Octopus taganga	Colombia	MG778063	19	Ritschard et al. 2019
Octopus hummelincki	Brazil	MN933640	20	Lima et al. 2020
Octopus maya	Mexico	KY492363	21	Flores-Valle et al. 2018
Octopus maya	Mexico	GU362545	22	Juarez et al. 2012
Octopus insularis	São Tomé Island	OQ361632	23	present study
Octopus insularis	São Tomé Island	OQ361633	23	present study
Octopus insularis	Ascension and St Helena	KP056552	23	Amor et al. 2017
Octopus insularis	Ascension and St Helena	KP056553	23	Amor et al. 2017
Octopus insularis	Ascension and St Helena	KP056554	23	Amor et al. 2017
Octopus insularis	Ascension and St Helena	KP056555	23	Amor et al. 2017
Octopus insularis	Veracruz/Mexico	MH550422	24	González-Gomez et al. 2018
Octopus insularis	Veracruz/Mexico	MH550423	24	González-Gomez et al. 2018
Octopus insularis	Veracruz/Mexico	MH550424	24	González-Gomez et al. 2018
Octopus insularis	Ceará - Brazil	OM307333	24	Lima et al. 2022
Octopus insularis	Rio Grande do Norte - Brazil	OM307355	25	Lima et al. 2022
Octopus insularis	São Pedro and São Paulo - Brazil	OM307298	26	Lima et al. 2022
Octopus insularis	Trindade island - Brazil	OM307377	27	Lima et al. 2022
Octopus insularis	Bahia - Brazil	OM307312	28	Lima et al. 2022
Octopus bimaculatus	Mexico - Sonora	KT335828	30	Pliego-Cárdenas et al. 2014
Octopus bimaculoides	Mexico	MN180721	31	Pliego-Cárdenas et al. 2020

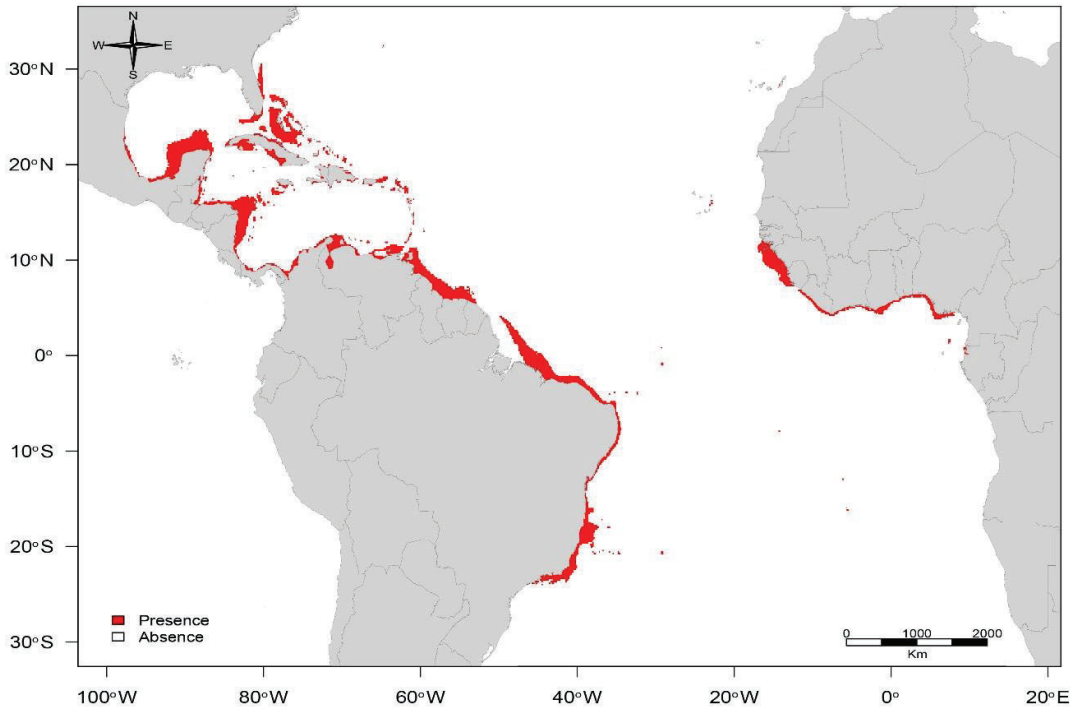


Figure S1. Binary map of *O. insularis* niche suitability obtained from the suitability map.

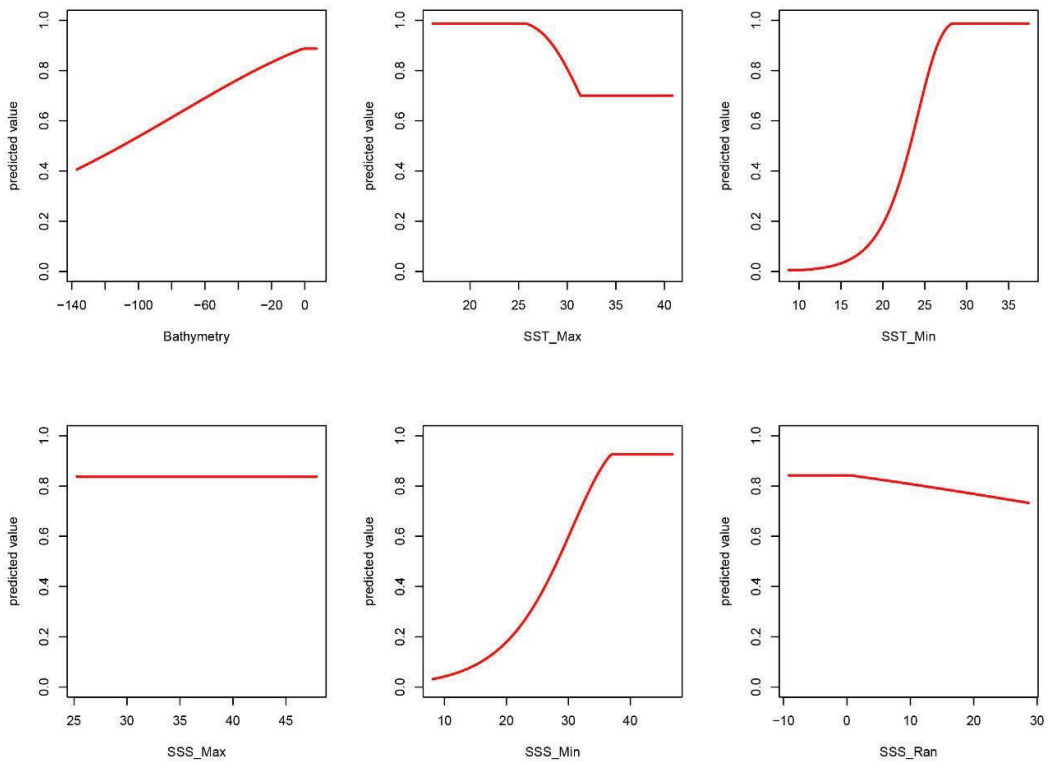


Figure S2. Response curves of the environmental and physical variables.

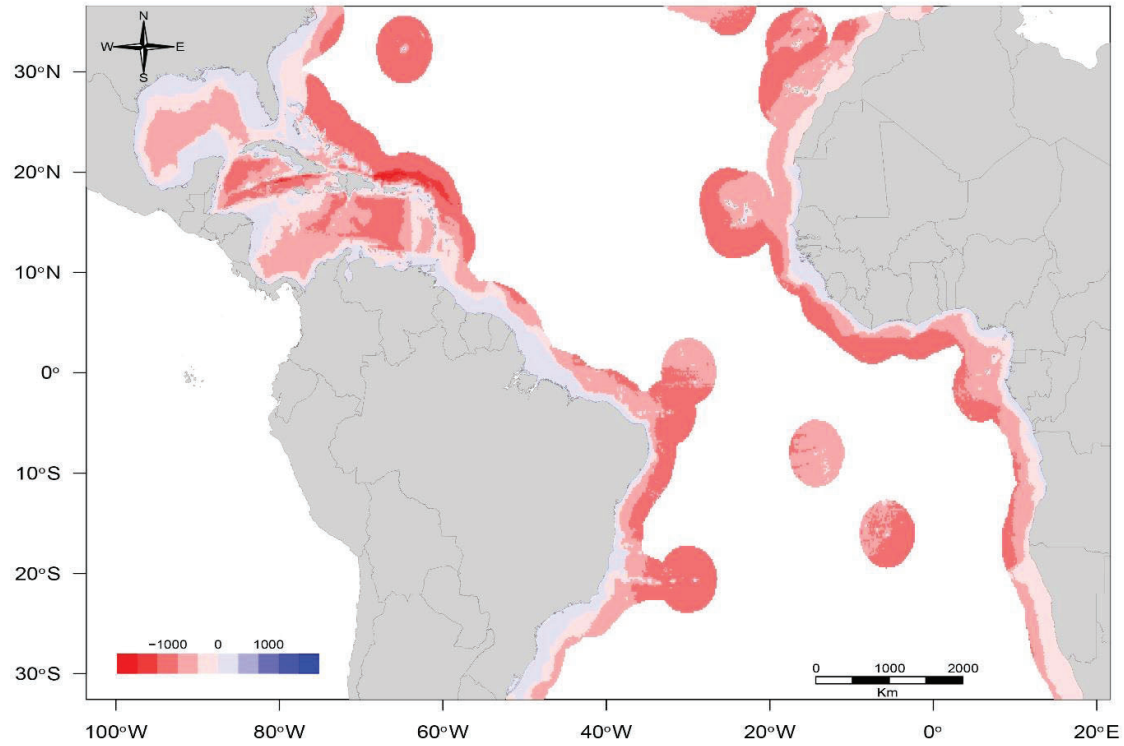


Figure S3. Extrapolation risk map. Positive values indicate no extrapolation risk while red ones indicate risk.

Supplementary 4:

Gifs animation of bimonthly dispersal simulations for the years 2006 to 2015:

https://doi.org/10.5281/zenodo.7596276

Figure1

Click here to access/download;Figure;Fig1.tif

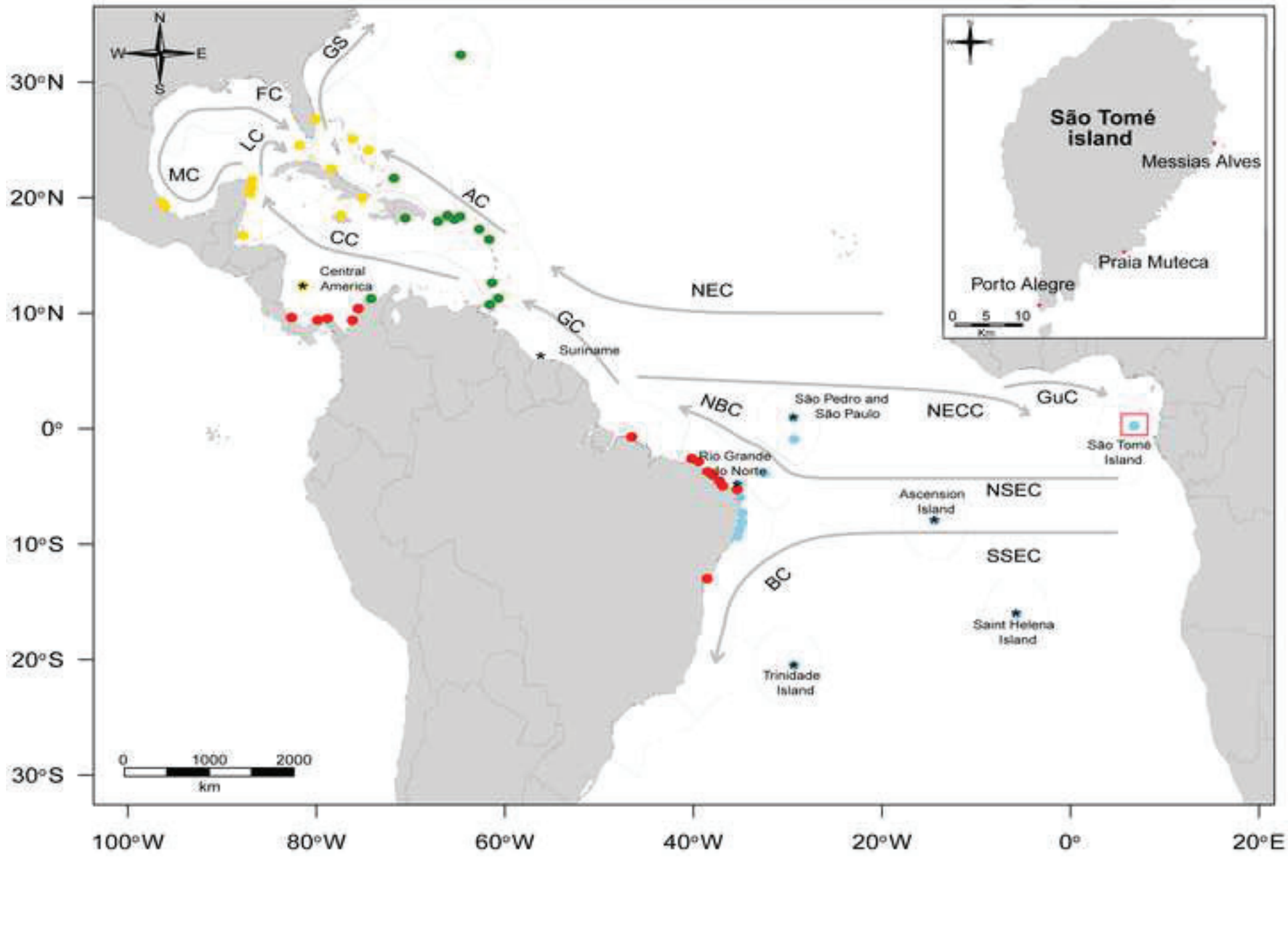


Figure2

Click here to access/download;Figure;Fig2.tif

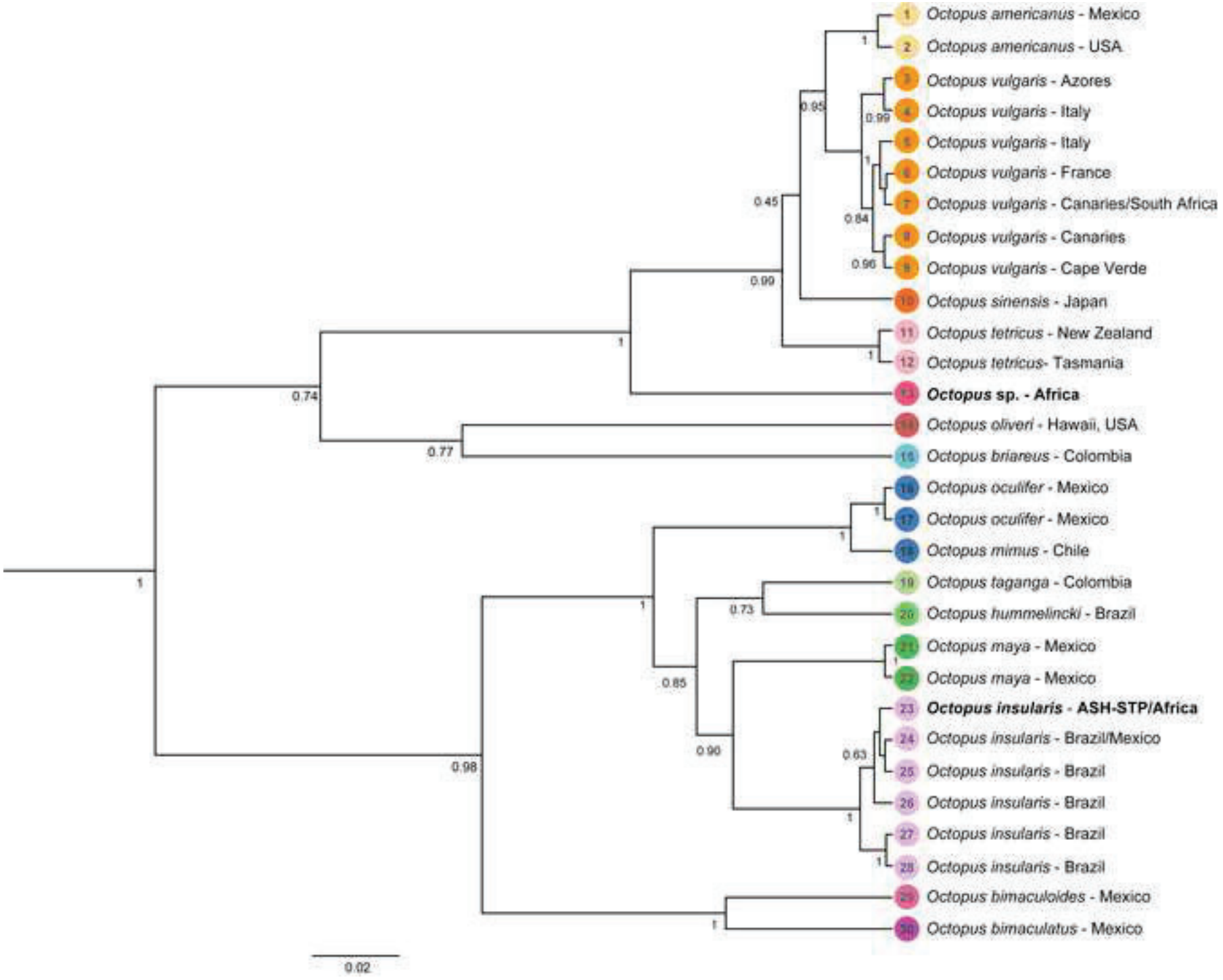


Figure3

Click here to access/download;Figure;Fig3.tif

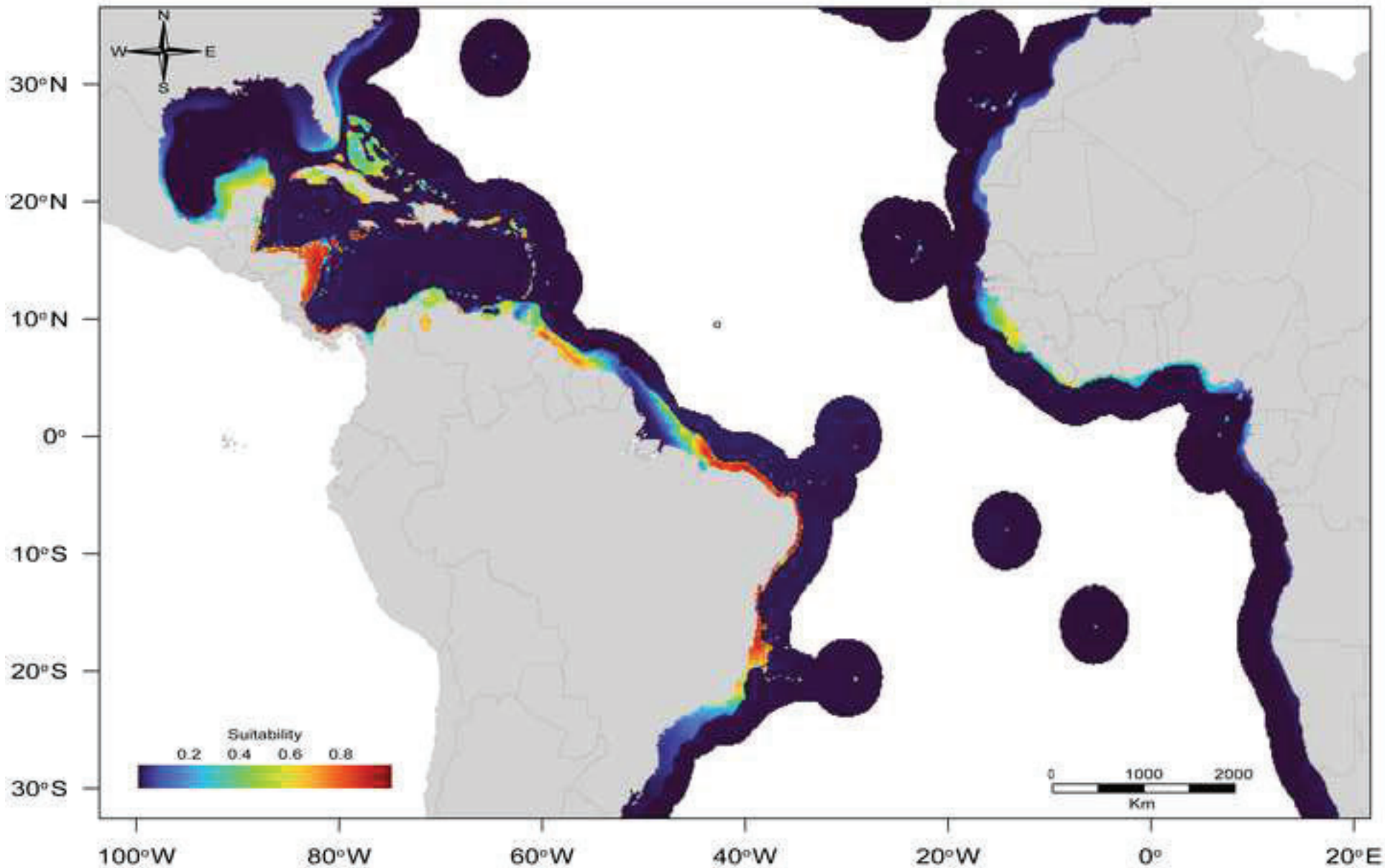


Figure4

Click here to access/download;Figure;Fig4.tif

