Larval dispersal and climate models provide insights into present and future distribution of a tropical sardine

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ABSTRACT

Climate change impacts the distribution of marine organisms and threatens fisheries. Marine protected areas (MPAs) may buffer the detrimental effects of environmental change by acting as biodiversity spillover to neighbouring areas. Yet, it is uncertain whether MPAs in islands favour passive species dispersal through oceanic circulation and how fish abundance and distribution will be impacted by ongoing global warming. Using Brazilian-endemic scaled-sardines (*Harengula* sp.) as a model, we implemented a Lagrangian particle-tracking model to estimate dispersal along the Brazilian coast and four MPAs in islands. Then, we projected an ecological niche model (ENM) of *Harengula* sp. to three climatic scenarios in 2100. Larval dispersal model suggested that three of four MPAs in islands export eggs and larvae of sardines, acting as sources of biomass to the Brazilian coast. ENMs indicated a decrease in environmental suitability for *Harengula* sp. at the Equatorial Brazilian coast and a southward shift in suitability that increases as the climatic scenario modelled is aggravated, mainly driven by changes in sea temperature and depth. Ocean warming may lead to a decrease in abundance of *Harengula* sp. due to lower environmental suitability in the northernmost part of its current distribution, concomitant with an increase in environmental suitability on offshore zones in the south of current distribution. Ecosystem disturbance with environmental suitability shifts can aggravate the isolation of populations in islands.

Keywords: ecological niche modelling; global warming; larval dispersal modelling; Marine Protected Areas; scaled sardines; Tropical Western Atlantic.

1. INTRODUCTION

Global warming is currently a major threat to ecosystem diversity, as well as to the countless goods and services they provide to human communities. In coastal marine systems, it impacts fisheries by decreasing fish abundance (Pörtner & Knust, 2007), compromising recruitment (Walther et al., 2002), dispersal, and shifting species' geographic distribution (Perry et al, 2005). In developing countries, where numerous human communities rely on small-scale fisheries for subsistence, there are weaker management plans focused on sustainable practices, especially those that incorporate scenarios of ongoing climate change (Vilar & Joyeux, 2021; Sumaila et al., 2011; Campredon & Cuq, 2001). This requires coordination between countries when stocks that inhabit international waters or are restricted to a single country might shift distribution to coastal zones of other countries with different regulations (Scheffers & Pecl, 2019). Failing to do so, combined with an unregulated exploration of natural resources, has led once ubiquitous fish species to fisheries collapses (Dickey-Collas et al., 2010; SCFO, 2005). Modelling species occupancy of the environment, their response to future climatic scenarios, and their dispersal potential are a promising aid to tracking marine species' distribution in face of a changing environment. These data provide the basis to plan management strategies that maintain the equilibrium of coastal ecosystems.

Marine Protected Areas (MPAs) play a crucial role in biodiversity conservation. These areas often serve as nursery grounds, where species can feed, reproduce, and increase in density and biomass (Lester et al., 2009). Another important aspect of an effective MPA is their ability to serve as an ecological and fishery spillover (Di Lorenzo et al., 2016), i.e., to act as a source of biodiversity to neighbouring areas. For species with planktonic egg and larval phases, passive dispersion through oceanic currents can allow individuals to reach locations out of the MPA's boundaries in early life stages. This dispersal potential is related to the duration of the larval stage and survival rate, yet, environmental suitability connecting sites is important for individual settlement (Knutsen et al., 2022). As habitats are changing at an incredible pace (Burrows et al., 2011), whether individuals can transit between sites requires assessing their dispersal ability.

Numerous terrestrial and aquatic species have shown a poleward shift in geographic distribution due to global warming (e.g., Poloczanska et al., 2013; Wolkovich et al., 2013). Fish distributions may shift more noticeably because these ectotherms track environmental surroundings closely to thermoregulate (Habary et al., 2017; Burrows et al., 2011; Cossins & Crawford, 2005), leading populations to thrive or perish accordingly. For example, the alternation between an ‘anchovy regime’ and a ‘sardine regime’ in the Pacific is attributable to marked cool versus warm environmental triggers, respectively (Chavez et al., 2003). These regime changes are attributable to cyclical environmental oscillations (e.g., El Niño and La Niña) to which sardines present a marked response (Cabrero et al., 2019). Consequences of such impacts have long been observed in fisheries of sardines (e.g., Radovich, 1982), a common name that refers to small clupeids.

Sardines are abundant in coastal zones, where they influence the abundance of larger fish species, dolphins, and marine birds. Their nutritional and economic value contributes to a significant proportion of employment, nutrition, and cultural value, sustaining numerous traditional fisheries (FAO, 2014; Vasconcellos et al., 2011). In Brazil, the sardine species of the genus *Harengula* are part of popular dishes of cultural value in the northeast region (Ferreira-Araújo et al., 2021) and are often used as bait by artisanal fishermen (Mendes et al., 2020). Specifically, the lineage *Harengula* sp. is the only sardine species in MPAs in the oceanic archipelagos of Fernando de Noronha (FNO), Atol das Rocas (ATR) and Trindade-Martim Vaz (TMV) (Lopes et al., 2017; Pinheiro et al., 2015). This suggests that this species has adaptations that allowed effective colonization of these distant insular habitats, against the main oceanic currents that flow from east to west (i.e., from the oceanic islands to the

Brazilian mainland) (Lumpkin & Garzoli, 2005). However, *Harengula* sp. is absent at the São Pedro e São Paulo archipelago, an oceanic island of the Brazilian EEZ located ca. 630 km northeast of FNO (Pinheiro et al., 2020). Previous modelling and genetic studies with this unique insular sardine have only included data from FNO and mainland coastal sites (Bennemann, 2022; Coelho et al., in prep.). The absence of information from ATR and TMV evidences the difficulties and costly logistics involved in sampling in MPAs in oceanic islands. Besides, whether these MPAs export eggs and larvae of this species to the Brazilian coast is unclear, raising uncertainty about the maintenance of this already exploited fishery at the Brazilian coast (Verba et al., 2020).

An additional issue concerning this fishery is that the lineage occurring along the Brazilian coast is yet undescribed; thus, their vulnerability status is uncertain. Recent molecular studies (Bennemann, 2022; Araújo, 2020) suggested that the *Harengula* lineage occurring in Brazil differs from *H. clupeola* (Cuvier, 1829) and *H. jaguana* Poey 1865, two species that were previously considered vastly and continuously distributed from the USA, Caribbean, to the southeast coast of Brazil (Munroe et al., 2015; 2019). Here, we consider only *Harengula* sp., possibly endemic to the Southwest Atlantic Ocean (SWA) and restricted to the Brazilian Exclusive Economic Zone (EEZ) (Araújo, 2020).

According to the latest assessment of fisheries statistics in Brazil, approximately 282 tons of scaled sardines' species are captured in the Brazilian EEZ (ICMBio, 2011). This number may be underestimated once statistics are only based on popular names and official catches. Verba et al. (2020) analyzed 132 fish species in the Brazilian Exclusive Economic Zone and indicated that those species of smaller body size and exploited by fisheries, such as the scaled sardines, are more prone to collapse. Compared to other sardines of commercial importance in Brazil, e.g., *Sardinella brasiliensis* (Steindachner 1879), *Harengula* sp. is not as explored by large industrial fisheries but for traditional, small-scale fisheries.

Abiotic conditions are important drivers of species distribution and abundance (Ángeles-González et al., 2021; Osorio-Olvera et al., 2020; Waldock et al., 2019). However, climate change can modify a region's environmental settings, reshaping its biotic community. As part of a large and complex ecosystem, lower abundance or the absence of sardines in certain locations in the SWA can influence lower and higher trophic levels. Unfavourable climatic conditions can also decrease fish recruitment, with ecological impacts on the community structure and trophic interactions (Harley, 2011), along with socioeconomic impacts, including the higher cost to harvest fisheries and lower food production (Hilborn et al., 2020).

In the present study, we estimate the extent of passive dispersal of planktonic eggs and larvae of *Harengula* sp. through oceanic currents in the Atlantic Southwest and investigate the potential effects of climate change on the distribution of this species. We focus on the coast of Brazil and its continental and oceanic islands, where this lineage is currently abundant. We also discuss how international cooperation towards sustainable fisheries may arise as a consequence of climate change on the distribution of marine species of ecologic and commercial importance. In addition, we highlight the role of dispersal models to estimate the effectiveness of MPAs in exporting planktonic larvae to other locations.

2. MATERIALS & METHODS

2.1 Ecological Niche Models (ENMs)

2.1.1 Occurrence data

Occurrence records were collected for "*Harengula clupeola*" and "*Harengula jaguana*" from public online databases (speciesLink 2022a, b; GBIF 2021a, b), and the ichthyological collection of the Universidade Federal do Rio Grande do Norte (UFRN), Brazil. Records for *H. clupeola* and *H. jaguana* located at the Brazilian coast were considered as *Harengula* sp., since according to mtDNA data, they represent a different lineage (Bennemann, 2022; Araújo, 2020). We excluded all records on land or within small bodies of water (e.g., lakes, or bays) for which no abiotic data could be extracted (raster data with abiotic information).

Records were filtered to include only data for specimens preserved in biological collections or museums, georeferenced in the study area (Brazilian coast, continental and oceanic islands), and collected after 1945, as older records may be less accurate (Zizka et al., 2020). Once the georeferenced occurrences were heavily biased towards the southern region of Brazil, we applied a spatial filtering technique to improve model performance (Boria et al., 2014). We divided the Brazilian coast latitudinally into north (≤ 10° S) and south (≥ 10° S) regions, then we filtered occurrences every 10 km and 50 km, respectively, with the spThin package v. 0.2.0 (Aiello-Lammens et al., 2015) in R v3.6.3 (R Core Team, 2020). A total of 37 occurrences remained for downstream analyses after the spatial filtering process, which is considered a good number of occurrences for MaxEnt models (Hernandez et al., 2006; Pearson et al., 2006; Wisz et al., 2008) (Figure S1).

2.1.2 Environmental data

Abiotic data to model ecological niches were downloaded from Bio-Oracle (Tyberghein et al., 2012; Assis et al., 2017; 2018) for current (2000-2014) and Representative Concentration Pathways scenarios (RCPs [Period 2090-2100]). The RCP scenarios are estimates of putative environmental conditions considering trends in the emission of greenhouse gases, levels of radiative forcing, energy consumption, land use, as well as human population growth and technology development (van Vuuren et al., 2011). Here we considered three RCP estimates for the period 2090-2100: RCP 2.6, RCP 6.0, and RCP 8.5, which reflect an increase in global mean temperature of up to 1.7°, 2.6°, and 4.8°C, respectively (IPCC 2013). In addition, we downloaded layers of depth (bathymetry) and distance to the coast from MARSPEC (Sbrocco & Barber, 2013). All environmental variables had a resolution of approximately 9 km x 9 km. Uncorrelated variables (Pearson correlation test, $r < |0.8|$; Table 1) of current climate conditions were chosen considering their ecological relevance for the species, that occurs abundantly in shallow, tropical waters of the SWA. The five variables kept to avoid model overfitting and redundancy (see Table S1 for a list of all variables used to test for collinearity) were: depth, mean sea surface temperature, mean current velocity, mean sea surface salinity and range of sea surface salinity (Figure S2). Environmental variables were masked up to 1 km of depth since *Harengula* sp. mostly occurs in shallow waters.

2.1.3 Model calibration and projection

For model calibration, current environmental variables were cropped according to an accessibility hypothesis using the ecoregions by Spalding et al. (2007). This hypothesis aimed to represent the regions explored by the *Harengula* sp., regardless of whether they can establish populations. Such regions are ideal for estimating and testing models (Barve et al., 2011).

ENMs of *Harengula* sp. were estimated using the implementation of Maxent v3.4.4 (maxent.jar) with the ENMeval package v1.3.3 (Kass et al., 2021; Muscarella et al., 2014) in R using a block partition for the dataset of occurrence records. Maxent is a machine-learning algorithm that estimates distribution from presence-only data of a target species (occurrence records) and abiotic features of the environment where it occurs (also called ‘predictors’ or ‘variables’) (Phillips et al., 2006), showing good performance even when sampling data is low (Morales et al., 2017; Wisz et al., 2008).

During the calibration process, we tested 45 models differing in combinations of feature classes (linear [L], quadratic [Q], product [P] and hinge [H] – L, LQ, LQP, LQH and LQHP) and regularization multipliers (1 to 5 by increments of 0.5). The combination of parameters to generate models showing AUC validation higher than 0.80 (AUCv > 0.80) were kept, then evaluated with an omission rate of 10% (OR_{10}). From these, the model with the lowest delta AICc was considered to show the best performance. The ENM selected had a LQH 1 configuration.

The selected model was then projected onto current environmental variables (Table 1), creating a suitability map. We then analyzed the same environmental variables that are expected for the years 2090-2100, based on the Representative Concentration Pathway (RCP) scenarios, to predict the model in future climatic scenarios. It is important to note that the RCP 8.5 scenarios exhibited higher temperatures and salinities compared to the RCP 2.6 and 6.0 scenarios. Despite these changes in environmental conditions, bathymetry remained constant throughout the model projections. We obtained suitability maps for the current and future scenarios (RCP 2.6, 6.0 and 8.5 for the period 2090-2100) and then subtracted the current suitability map against the future scenarios to estimate geographic suitability changes.

2.1.4 Analyses of non-analogous conditions

Different environmental conditions for the calibration and projection areas for the occurrence of *Harengula* sp. were identified with the multivariate environmental similarity surface index (MESS) (Elith et al., 2010). MESS indicates areas of extreme dissimilarity between the climates modelled where caution is needed when interpreting the results as models have been extrapolated to non-analogous conditions (Elith et al., 2010). We also identified the most dissimilar variables (MoD) driving the MESS response in a particular grid cell, and mapped limiting factors as programmed in MaxEnt. MESS and MoD were calculated with ENMeval (Kass et al., 2021).

2.2 Larval dispersal model

Estimations of the dispersal patterns of *Harengula* sp. in the Southwestern Atlantic were done using the Lagrangian particle tracking model ICHTHYOP v. 3.3.3 (Lett et al., 2008), which has been widely implemented to investigate similar problems concerning the dispersal of planktonic stages in marine species (e.g., Lima et al., 2023; Santana-Cisneros et al., 2021; Swearer et al., 2019). The dispersion model was forced by 2-D velocity fields from an ocean circulation model available in the Copernicus Marine Service. Specifically, we accessed surface currents data from GLORYS12V1 (1/12° horizontal daily resolution; Lellouche et al., 2018), a global eddy-resolving physical ocean and sea-ice reanalysis that were reconfigured to a MARS model output structure to make GLORYS12V1 compatible with ICHTHYOP. This hydrodynamic model is adequate to the spatial scale of our question (10 km to 100 km). Using these inputs, the computational domain for the dispersal simulations was set in the south of the Atlantic Ocean between 29°13'W-46°58'W longitude, and 0°16'N-27°47'S latitude, adopting a 600-second time-step within a forward-Euler scheme to track the particles.

We considered ten breeding sites that could help us follow the dispersal routes of *Harengula* sp.: (1) *FNO* Fernando de Noronha (32.5°W, 3.8°S); (2) *ATR* Atol das Rocas (33°48W, 3°51'S); (3) *CE* Ceará (38.3°W, 3.3°S), (4) *RN* Rio Grande do Norte (35.2°W, 5.1°S); (5) *PE* Pernambuco (34°48W, 8°04'S); (6) *BA* Bahia (38.8°W, 13.3°S); (7) *ABR* Abrolhos (38.7°W, 17.9°S); (8) *RJ* Rio de Janeiro (41.6°W, 22.4°S); (9) *SP* São Paulo (46.2°W, 24.1°S); and (10) *TMV* Trindade-Martim Vaz (29.3°W, 20.5°S). Given the uncertain nomenclature regarding the *Harengula* lineage at the Brazilian coast, we approximated the dispersal model parameters according to congeners. Simulations were performed from September (2019) to April (2020) corresponding to the spawning season of *H. pensacolae* Goode & Bean, 1879, later synonymized to *H. jaguana* at the Brazilian coast (Matsuura 1972). Regarding time dispersal, evidence has shown that the period of planktonic duration (eggs and larval stage) is approximately 30 days, based on *H. jaguana* (Houde, 1977) with a conservative approximation of spawning averaged on 200 eggs (Matsuura, 1972; Houde, 1977). This number was considered adequate because although spawning of scaled sardines is estimated to be in the order of thousands, mortality can be up to 99% (Houde, 1977). Thus, we configured model simulations to run forward in time for 30 days by tracking 200 virtual particles by release zone (totalling 2000 particles per model run).

3. RESULTS

3.1 Ecological niche model

ENMs estimate a future decrease in suitability for *Harengula* sp. in the northeast coast of Brazil for all climatic scenarios, while the southeast coast may remain stable (AUCv = 0.82, OR_{10} = 0.06; Figure 1). Under current abiotic conditions, the geographic distribution of this lineage is best predicted by sea surface temperature (SSTmean), followed by depth, mean current velocity (Velmean) and range of sea surface salinity (SSSrange) (permutation importance $\Sigma > 90\%$). The ENM of *Harengula* sp. identified favorable areas with surface temperatures up to 29°C and shallow depths (< 50m). Beyond those thresholds, suitability rapidly diminishes. Furthermore, this species occurs in areas of low mean current velocities and correlates with regions with a high salinity range (0-20 PSU). Notably, this species thrives in habitats with a mean salinity of at least 30 PSU (Figure S3).

3.2. Analyses of non-analogous conditions

Contrasting differences between the current climate and those estimated for the future are prominent in the north, near the Equator, and the south of the *Harengula* sp. distribution (Figure 2). During present-day conditions, offshore habitats along the Brazilian mainland coast are unsuitable while habitats closer to the coast are moderate to highly suitable for *Harengula* sp., except near the Amazon-Orinoco River. Under the future climatic scenarios modelled, environmental suitability will further decrease in the north and central coastal zones, including suitability loss at ABR, while suitability will slightly increase in coastal core habitats located in the south (Figure 2). Along seamounts that connect TMV and the mainland Brazilian coast, environmental suitability decreases and eventually disappears as climatic scenarios for the future are aggravated. Similarly, the MESS index indicates that the northeast coast of Brazil will dramatically change as global warming intensifies, with maps displaying increasingly negative values where larger differences between datasets are seen (Figure S4). The MoD indicates that the mean of sea surface temperature (SSTmean) will be the variable to change the most in the ecoregions where *Harengula* sp. currently occur, followed by SSSmean (Figure S5). The model reported a Gaussian-like response for these variables, reducing uncertainty in predictions (Figure S3).

3.3 Dispersal model

Along the Brazilian mainland coast, virtual eggs and larvae released from the northern release zones (latitudes lower than 5°S) flow northwest, while those released from sites in mid-latitudes, such as BA (13.3°S), retain particles. From southern release zones, as RJ (22.4°S) and SP (24.1°S), particles travel southwards. The six sites at the Brazilian coast where virtual particles were released in the dispersal model are well connected and leading particle trajectory patterns follow the direction of the large-scale circulation in the region, the North Brazil Current and the Brazil Current (Figure 3). The exception is PE, from which virtual particles travelled northwards for seven of the eight months modelled, following the flow of the North Brazil Undercurrent.

The trajectory of the virtual particles varied when released from the MPAs in the continental island (ABR) and the three oceanic islands (ATR, FNO and TMV) observed here. On average, particles travel the farthest when released from ATR (approximately 1055 km), followed by FNO (approximately 1038 km) and ABR (approximately 470 km) (Figure 4). From ATR and FNO, particles travel along the seamounts towards the Brazilian coast, reaching CE and the northern coast of Brazil (Maranhão and Pará, not included here). When released from TMV, on average, particles remain within 200 km of the release area and do not reach the mainland coastal sites in Brazil. From TMV, particles are transported at the shortest distance considering all islands and coastal sites modelled, except SP. From the coastal sites, particles travel farther from CE (660 km on average) and RN (650 km on average), and the least when released from SP (approximately 170 km on average).

No trajectory of particles travelling from the Brazilian coast towards the islands was observed (see animations online: https://doi.org/10.5281/zenodo.8117971), as expected due to the main direction of dominant currents in the region. Monthly travel distances of virtual particles released from all locations are shown in Figures S6 to S13.

4. DISCUSSION

Global assessments of fish species responses to global warming indicate poleward shifts in geographic distribution as a recurring pattern, leading species to go extinct from areas where they were once abundant (Little et al., 2020; Cheung et al., 2013; Perry et al., 2005). Similarly, our models indicate that environmental suitability for the occurrence of the scaled sardine *Harengula* sp. will shift southwards, which may lead this species to become less abundant or even disappear from most of its northern distribution along the Brazilian coast, and become more abundant in coastal zones of the south, where suitability is predicted to increase in the future even under the worst-case scenario of climate change (RCP 8.5). ENMs also show that the high freshwater discharge of the Amazon-Orinoco River plume is an area of low suitability for the occurrence of *Harengula* sp., probably delimiting northern boundary of habitat suitability for this species, as previously suggested (Coelho et al. in prep.). Additionally, we show that MPAs closer to the mainland coast can export sardine' eggs and larvae that could replenish the fishery stock biomass at the Brazilian coast, while such passive dispersal was not detected from more distant MPAs.

4.1 Climate change might shift sardines' distribution

Temporal evaluations of past patterns of occurrence, abundance, and distribution indicate that populations of small pelagic clupeoids such as *H. clupeola* increased with climate warming in locations in the Brazilian southeast coast (Araújo et al., 2018). Models for future scenarios of global warming from the present study indicate similar patterns for *Harengula* sp. in the same area, while the opposite is seen for the northern distribution area of this species. This may indicate that the northern population is already living close to their thermal optima and, as warming progresses, the thermal limits of the species will likely be surpassed in the future as it has been proposed for other species (Doubleday et al., 2016). The disappearance of the scaled sardines from areas where they are currently abundant at the Brazilian coast can lead to a myriad of ecological and socioeconomic impacts, especially in regions that rely on fisheries for subsistence, such as the northeast coast of Brazil and oceanic islands (Ferreira-Araújo et al., 2021; Lopes et al., 2017). However, dissimilarity increases between present and future climates as global warming scenarios intensify, demanding a careful approach as projections to non-analogue climates raise the uncertainty of interpretations of species responses (Fitzpatrick et al., 2018).

Ongoing climate change affects seasonal events that act as triggers of biological processes in fishes, such as reproduction and recruitment, which are crucial sources of variability to populations and key to maintaining stock abundance and biomass (Hsieh et al., 2006). During the critical larval stage, the environment exerts a high direct and indirect influence on an individual. For example, if water temperature rises beyond the performance curve for a given species, there are direct impacts at cellular and organism levels that increase the energetic cost of growth (Little et al., 2020), and indirect ones, such as the availability of prey for larvae. Fluctuations in sea surface temperature can decrease the plankton’s quantity and quality (e.g., size) upon which young fish can prey, compromising their survival and stock recruitment (Beaugrand & Reid, 2003). The projected temperature rise may similarly impact the prey that young individuals of *Harengula* prey upon. Juveniles of *H. clupeola* and *H. jaguana* mainly feed on amphipods and isopods (Arceo-Carranza et al., 2021). These microcrustaceans are vulnerable to warming trends as a poleward shift of more than 10 degrees in latitude has been registered for copepod assemblages related to warming in the North Atlantic (Beaugrand et al., 2002). Although this poleward movement is also predicted for *Harengula* sp., if their prey will move at a similar rate and direction requires investigation.

Poorly regulated fisheries as well as lack of monitoring and management can aggravate the scenario of climate change once current population trends are unknown (Vilar & Joyeux, 2021; Honey et al., 2010). Outdated fisheries statistics in Brazil (ICMBio, 2011), where *Harengula* sp. is currently abundant, constrains managers' ability to plan and implement efforts to ensure sustainable fisheries. Therefore, it is important that authorities in Brazil update fisheries' statistics with as complete sources of information as possible, such as using the Normative Instruction 53, which determines common names and respective scientific names of fishes of commercial interest (MAPA, 2020). Additionally, fisheries statistics should include georeferenced capture records when possible and be made available to environmental managers. Precise occurrence records are valuable data from which other information can be estimated, such as abiotic conditions from where the animals were captured, providing an important basis from which population trends can be assessed and management strategies can be better planned and implemented.

Research in climate sciences improved in the past decades, and the multiple impacts that a changing climate may cause can now be estimated through atmospheric and oceanic models. We recommend including niche modelling tools among environmental management protocols to identify changes in the distribution and abundance of a target species, as implemented for the Pacific sardine (Zwolinski et al., 2011). These tools are also useful to identify populations in areas of climate stability, which have greater capacity for acclimation (Seebacher et al., 2015), and those more exposed to extreme weather events to better plan and implement conservation actions (Andrew et al., 2007). However, cautious interpretation of results is important when extrapolating models to different spaces and time, because non-analogue projections increase uncertainty in estimating species responses (Fitzpatrick et al., 2018).

4.2 The role of larval dispersal connecting populations

The monthly dispersal simulation in the reproduction zones was consistent regardless of the month or year of simulation. As the South Equatorial Current (SEC) bifurcates at the coast of Brazil (5–10°S), particles released from northern areas (< 5°S) follow the direction of the North Brazil Current (NB) and those from the south (> 20°S) follow the Brazil Current (BC) (Lumpkin & Garzoli, 2005). Particles released from PE (8°S) travel northwards, following the North Brazil Undercurrent (Stramma & England, 1999).

Besides achieving a specific set of conservation goals, effective MPAs should act as an ecological and a fishery spillover, exporting biomass of species to neighboring non-protected areas (Di Lorenzo et al., 2016), buffering the negative effects of drift, inbreeding, and potential local extinction (Bell, 2008) aggravated when populations are small and isolated. However, for isolated MPAs to play a role in the passive dispersal of early life stages to other areas depends on the duration of a species planktonic phase (like egg and larval stages), the velocity and direction of oceanic currents. Located approximately 370 km to the northeast of the Brazilian coast, the models suggest that FNO and ATR export eggs and larvae to the northern Brazilian coast, while no particles released from TMV reach the mainland, as this MPA is located about 1,200 km off the Brazilian coast (Pinheiro et al., 2015). Along the Brazilian coast, oceanic currents connect distant sites and aid connectivity within the coastal population.

Models provide an important starting point to analyse the likely impacts of climate change on species distribution, as well as to raise hypotheses that can be tested with other methods. For example, projections of habitat suitability for *Harengula* sp. during the Last Glacial Maximum (ca. 21Kya) indicate narrow suitability along the Brazilian coast, followed by expansion of habitat suitability towards the present climate, agreeing with the signal of population expansion detected by genomic data (Coelho et al., in prep.). Niche models and genetic data (mitochondrial DNA and genomic SNPs) showed that *Harengula* sp. at the Brazilian coast and the oceanic island of FNO are separated by depth, while individuals from the continental island of ABR are connected to those at the Brazilian coast (Bennemann, 2022; Coelho et al., in prep.). Our niche and larval dispersal models also show the connectivity between ABR and the Brazilian coast. However, the larval dispersal model suggests that *Harengula* sp. can reach the northern coast of Brazil when the planktonic stage of egg and larvae are released from the oceanic islands of FNO and ATR, while those released from TMV are isolated from the Brazilian coast (Figure 3). Future studies should include genetic information from individuals further north in Brazil, along the coastal states of Maranhão and Pará, and from the oceanic islands of ATR and TMV, in order to test whether the connectivity between these northern coastal sites and ATR occurs, and whether TMV harbours a separated population, as suggested by the dispersal models.

Finally, it is important to acknowledge that biological and ecologic data used to support our models were estimated from information available on currently called *H. clupeola* and *H. jaguana*, which are the closest relatives of the undescribed species of *Harengula* in Brazil. Once they are different species, data may sometimes be non-congruent regarding the information used to estimate larval dispersal or ecological niche model. In other words, the nature of the information we gathered from the literature is imprecise, as they are often based on studies of size at fecundity, spawning period, larval mortality, and others

(Queiroz et al., 2020; Matsuura, 1972). Even within the same study (e.g., Houde, 1977), estimates of egg and larval duration greatly varied between years, which may reflect annual environmental oscillations in response to varying temperatures, well-known to impact the early stages of development of scaled sardines, such as egg duration (Houde, 1977) and population growth (Araújo et al., 2018). Reassessing these characteristics for *Harengula* sp. once taxonomy and nomenclature are elucidated is fundamental to evaluate our models' assertiveness and to guide more precise estimates of future distribution shift and larval dispersal.

5. CONCLUSION

By considering ecological niche models and particle dispersal models, we provide estimates of global warming impacts on the availability of suitable habitats for *Harengula* sp. at the SWA, in addition to estimates of connectivity by larval dispersal between continent and island locations where this species occurs. We show that aggravated scenarios of global warming may lead to a decrease in environmental suitability for *Harengula* sp. in the north of its current distribution, potentially reducing their abundance and limiting their use and cultural value in the region. In addition, larval dispersal models indicate that MPAs in islands that are geographically close to the Brazilian coast (within ~370 km) may act as a fishery spillover to the coast of Brazil, as seen in Fernando de Noronha, Atol das Rocas and Abrolhos; while those far from the mainland may not export eggs and larvae of scaled sardines through oceanic currents, as seen in the isolated Trindade-Martim Vaz (located ~1,200 km off the Brazilian coast). These islands harbour MPAs that are important feeding and breeding grounds for this species. Under worst-case scenarios of global warming (RCP 8.5), the potential disappearance of environmental suitability in Abrolhos and in seamounts that connect the mainland to distantly located MPAs, such as Trindade-Martim Vaz, may contribute to the isolation of the sardine population in this island. Future studies using genetic data from this distantly located MPA, as well as from ATR and the northern coast of Brazil may shed light on the role of dispersal in establishing gene flow of scaled sardines, elucidating whether populations from oceanic islands are connected to the continental coast. We recommend that Brazilian authorities incorporate tools that consider global warming impacts into the management of marine species of commercial interest.

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Table 1: Abiotic variables used in the ecological niche models. All variables show low correlation (Pearson correlation test, r < |0.8|).

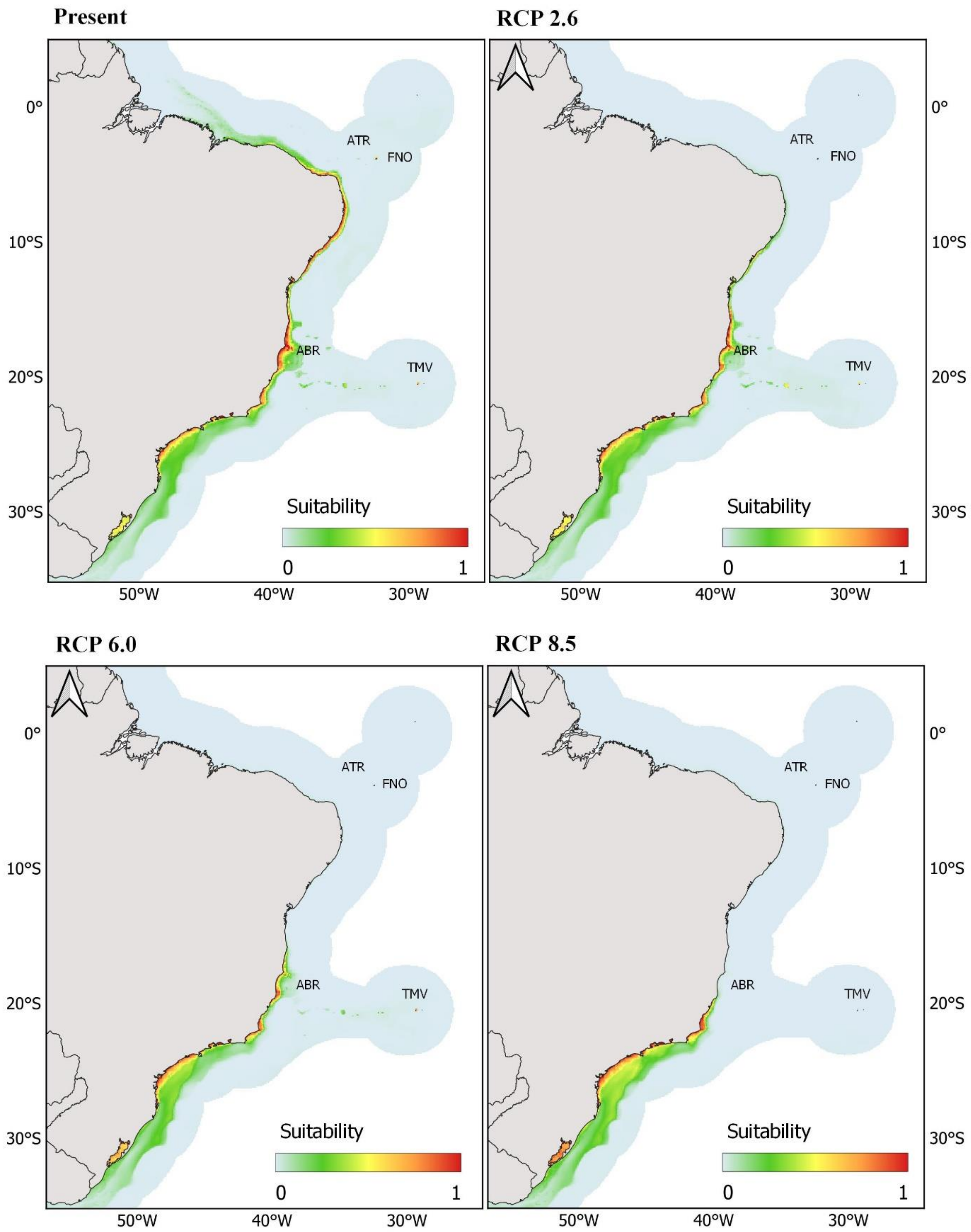
Variable	**Code**	**Unit**	**Database**
Depth	Depth	m	MARSPEC
Mean current velocity	Velmean	$m.s^{-1}$	Bio-ORACLE
Mean of sea surface temperature	SSTmean	°C	Bio-ORACLE
Mean of sea surface salinity	SSSmean	PSS	Bio-ORACLE
Range of sea surface salinity	SSSrange	PSS	Bio-ORACLE

Figure 1: Suitability of ecological niche models (ENMs) for present and three climatic scenarios projected to year 2100: Representative Concentration Pathway (RPC) 2.6, 6.0, and 8.5. Islands: *FNO* Fernando de Noronha, *ATR* Atol das Rocas, *ABR* Abrolhos, and *TMV* Trindade-Martim Vaz.

Figure 2. Differences in suitability between present and each RCP scenario projected. Blue colours indicate an increase in suitability while red colours indicate decrease.

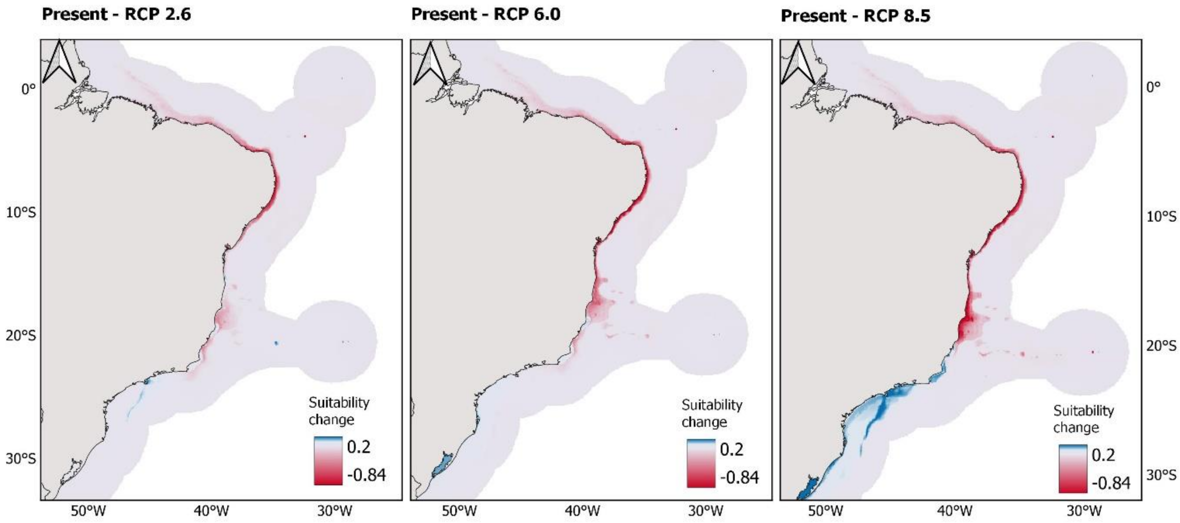
Figure 3: Modelled dispersal patterns and sites where virtual particles were released from in the larval dispersal model of *Harengula* sp. Orange indicates the trajectory of particles released from coastal sites; in blue, the trajectory of particles released from Marine Protected Areas in islands. Grey arrows represent the average direction of main oceanic currents in the region. Islands: *FNO* Fernando de Noronha, *ATR* Atol das Rocas, *ABR* Abrolhos, and *TMV* Trindade-Martim Vaz. Coastal sites: *CE* Ceará, *RN* Rio Grande do Norte, *PE* Pernambuco, *BA* Bahia, *RJ* Rio de Janeiro, and *SP* São Paulo.

Figure 4: Histograms of travelled distance (km) by virtual particles per release zone from September (2019) to April (2020). *CE* Ceará, *ATR* Atol das Rocas, *FNO* Fernando de Noronha, *RN* Rio Grande do Norte, *PE* Pernambuco, *BA* Bahia, *ABR* Abrolhos, *TMV* Trindade-Martim Vaz, *RJ* Rio de Janeiro, and *SP* São Paulo.



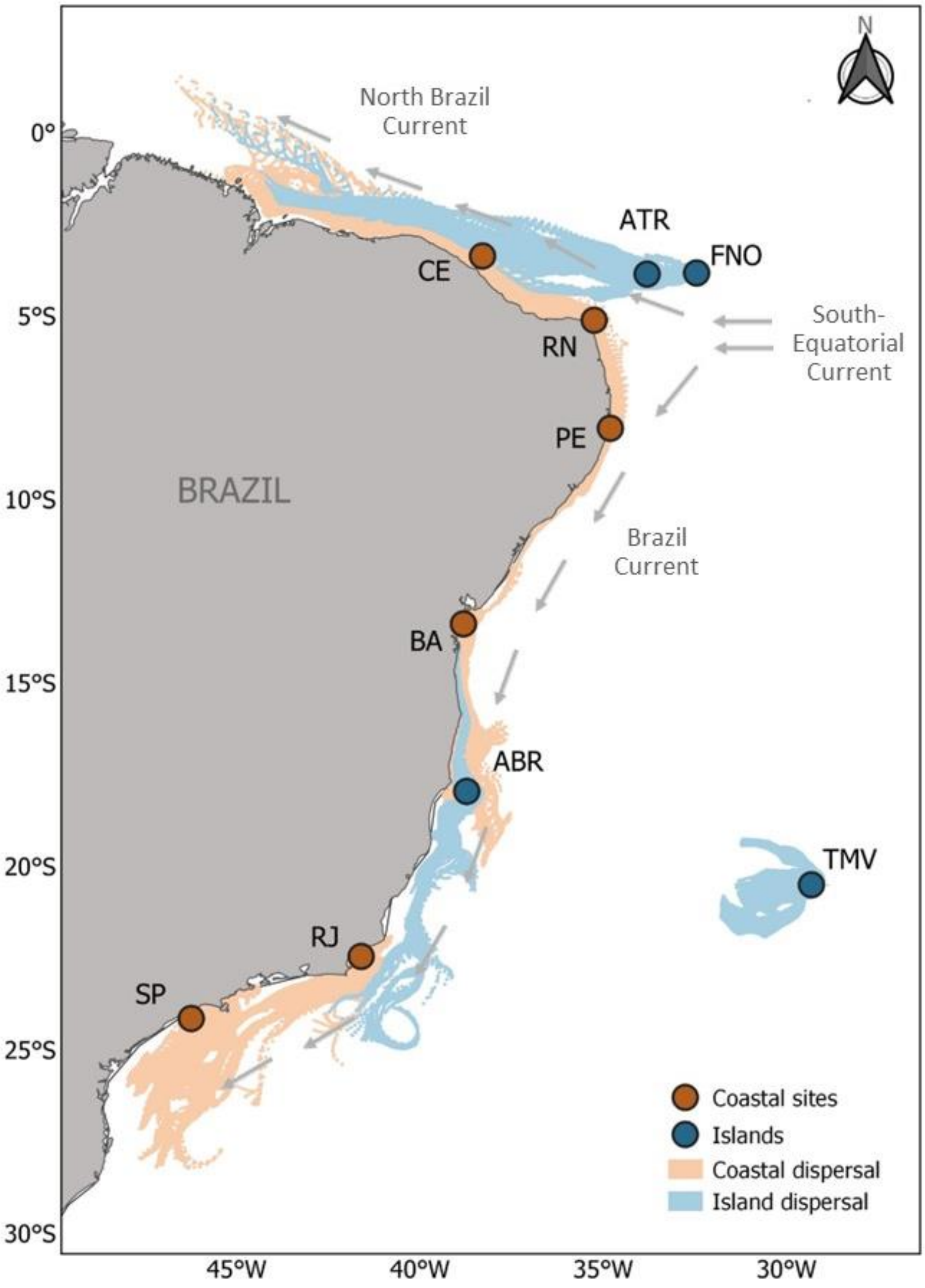
729

730 Figure 1



731

732 Figure 2



733

734 Figure 3

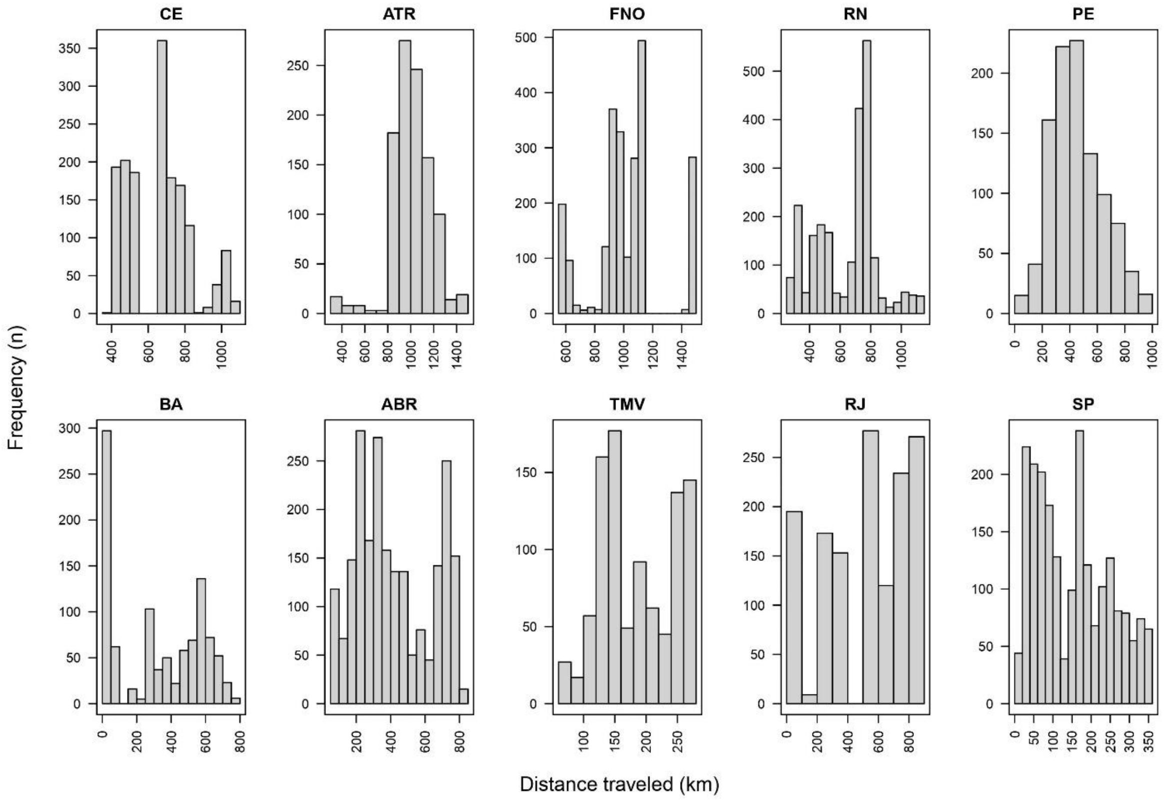

CE
ATR
FNO
RN
PE
BA
ABR
TMV
RJ
SP
Frequency (n)
Distance traveled (km)
0
50
100
150
200
250
300
350
400
500
600
800
1000
1200
1400

Figure 4