



Forecasting shifts in habitat suitability across the distribution range of a temperate small pelagic fish under different scenarios of climate change

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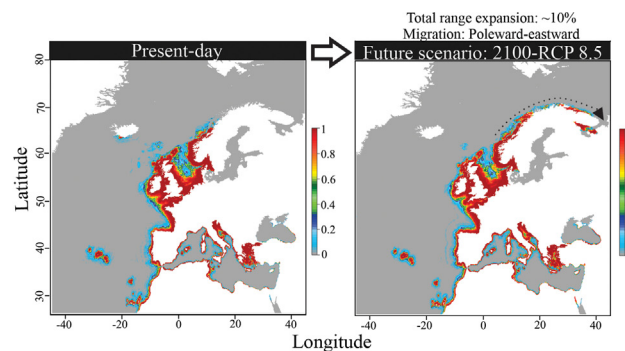
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HIGHLIGHTS

- Climate change may cause a poleward shift in sardine distribution.
- Mean SST, SSS, current velocity and distance to the coast explained distribution.
- Future climate scenarios suggest new suitable habitats at high latitudes.
- By 2100, sardine range is projected to expand in the Norwegian and White Seas.
- Habitat loss is projected on African Coast, in the British Isles and North Sea.

GRAPHICAL ABSTRACT

Sardina pilchardus
68,767 occurrence records
Selected model: GAM
Predictors:
Sea surface temperature
Sea surface salinity
Current velocity
Distance to the coast



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ABSTRACT

Climate change often leads to shifts in the distribution of small pelagic fish, likely by changing the match-mismatch dynamics between these sensitive species within their environmental optima. Using present-day habitat suitability, we projected how different scenarios of climate change (IPCC Representative Concentration Pathways 2.6, 4.5 and 8.5) may alter the large scale distribution of European sardine *Sardina pilchardus* (a path species) by 2050 and 2100. We evaluated the variability of species-specific environmental optima allowing a comparison between present-day and future scenarios. Regardless of the scenario, sea surface temperature and salinity and the interaction between current velocity and distance to the nearest coast were the main descriptors responsible for the main effects on sardine's distribution. Present-day and future potential "hotspots" for sardine were neritic zones (<250 km) with water currents <0.4 m s⁻¹, where SST was between 10 and 22 °C and SSS > 20 (PSU), on average. Most variability in projected shifts among climatic scenarios was in habitats with moderate to low suitability. By the end of this century, habitat suitability was projected to increase in the Canary Islands, Iberian Peninsula, central North Sea, northern Mediterranean, and eastern Black Sea and to decrease in the Atlantic African coast, southwest Mediterranean, English Channel, northern North Sea and Western U.K. A gradual poleward-eastward shift in sardine distribution was also projected among scenarios. This shift was most pronounced in 2100 under RCP 8.5. In that scenario, sardines had a 9.6% range expansion which included waters along the entire coast of Norway up and into the White Sea. As habitat suitability is mediated by the

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synergic effects of climate variability and change on species fitness, it is critical to apply models with robust underlying species-habitat data that integrate knowledge on the full range of processes shaping species productivity and distribution.

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1. Introduction

Climatic fluctuations enhanced by anthropogenic activities are resulting in shifts in atmosphere-ocean physical forcing, leading to critical changes in biogeochemical processes that poses a major threat to global marine biodiversity in the long-term (Ramírez et al., 2017). The most recent models of the Intergovernmental Panel on Climate Change (IPCC) project that the average global ocean temperature will increase between 1 and 4 °C by the end of this century. The 3 °C range depends on different scenarios of greenhouse gases concentrations, termed Representative Concentration Pathways (RCPs; IPCC, 2013). For instance, climate change is acknowledged to promote changes in air-sea interactions leading to ocean warming, inputs of new CO₂ in the water column and intensification or smoothening of wind-driven ocean currents (Doney et al., 2020; Yang et al., 2020). The changes translate into O₂ depletion (often causing coastal hypoxia), ocean acidification, sea level rise and shifts in upwelling intensity with multiple potential effects on ocean food webs at global and regional scales (Xiu et al., 2018; Claireaux and Chabot, 2019). Consequences of these “new” oceanic dynamic on the ecology of organisms have been extensively reported for a wide range of marine taxa (Brander et al., 2003; Doney et al., 2012; Poloczanska et al., 2013; Ramírez et al., 2017). However, the magnitude of such impacts is challenging to forecast in the marine environment since responses to climate change are species-specific, and plants and animals may adapt to/tolerate new conditions or shift their distribution to follow environmental optima (Melo-Merino et al., 2020).

Due to their tight coupling to physical and biogeochemical processes impacting the base of marine food webs, small pelagic fish (SPF) display rapid changes in their distribution and productivity linked to climate variability (Alheit et al., 2014; Garrido et al., 2017). Characteristics such as protracted spawning season, short lifespan, high dependence on productive areas and large distribution range suggest that they are a strong bio-indicator of climate variability and change in marine systems (Peck et al., 2013). Similar to the vast majority of fish, SPF are ectothermic and their body temperature and metabolic requirements depend on ambient temperature. In addition to the direct effect of temperature on physiological performance, environmental variability can affect the distribution, growth, recruitment and spawning of SPF via indirect, trophodynamic processes impacting prey availability (bottom-up control) and intensity of predation (top-down control) (Costalago et al., 2015; Basilone et al., 2017; Peck et al., 2021). Moreover, these fish act as conduits of energy from lower to upper trophic levels in marine food webs of coastal ecosystems (Zwolinski et al., 2010; Pikitch et al., 2012; Chauvelon et al., 2014), highlighting the importance of understanding and projecting how climate variability and change impacts on their populations.

The European sardine (*Sardina pilchardus*) inhabits waters in the northeast Atlantic from the North Sea to Senegal, the eastern Atlantic islands, and across the Mediterranean and the Black Seas (Giannoulaki et al., 2014). Although widely distributed, a high connectivity along its distribution range supports the hypothesis that this SPF has a nearly panmictic stock (Baibai et al., 2012; Baltazar-Soares et al., 2021). Sardines generally inhabit waters with temperatures ranging from 8 °C to 26 °C, and salinities from 30 to 38 (PSU) and use a more narrow range in temperatures (13 to 18 °C) when spawning (Giannoulaki et al., 2005; Coombs et al., 2006; Stratoudakis et al., 2007; Tugores et al., 2011). The largest sardine stocks are located in central Morocco, with landings around 700,000 t, while landings from all Mediterranean

stocks are ~80,000 t, at the level of landings from European Atlantic stocks (Silva et al., 2015). Off Europe, sardine is mainly abundant off the Atlanto-Iberian upwelling ecosystem where it represents nearly 40% of the total catch in this sub-region (ICES, 2006; DGRM, 2016). Biomass of the Iberian stock have declined since 2006 (ICES, 2020) due to a long period of time without good recruitment years, which is thought to be the result of previous negative sardine regimes due to climate variability (Almeida et al., 2014; Cabrero et al., 2019). Controversially, as sardines re-invaded the North Sea since the 1990's (Alheit et al., 2012), an increase of 35% in the fishery activity is reported for the northern stocks (from the Bay of Biscay up to the North Sea). Increases in fishing effort (FAO, 2018) combined with climate change (ICES, 2015) have been attributed to severe declines in Mediterranean stocks of European sardine. From both social (economic) and ecological perspectives, it is critical to make robust projections of how climate change may cause decreases and increases in local populations based on a thorough understanding of the factors and processes that drive changes in productivity to make climate-ready management of living marine resources.

Habitat Suitability Models (HSMs) [also named Species Distribution Models (SDMs)] have been commonly applied to predict how environmental change will impact the future geographic range of different species based on the niche-biotope duality (Beaugrand et al., 2019). These models establish correlative relationships between species' occurrence and environmental characteristics to create habitat suitability maps for present-day conditions which are combined with physical and biogeochemical climate model projections to estimate the location of future, suitable habitats (Hollowed et al., 2013) and, hence, shifts in distribution (Sinclair et al., 2010). Thus, HSMs provide estimates of future locations having a high probability of the occurrence of species to support conservation and management actions (Raybaud et al., 2017; Schickele et al., 2021). Given large differences in ocean warming associated with different RCP scenarios and thermal performance of species, a large range of potential outcomes for the future changes in the distribution of SPF often exist (Tugores et al., 2010; Peck et al., 2013; Jghab et al., 2019).

Here, HSMs were used to (I) evaluate the influence of environmental factors on the occurrence of the European sardine along its distribution range, and to create present-day, habitat suitability maps. Next, we (II) examined projected changes in key habitats in 2050 and 2100 within three different IPCC scenarios (RCPs 2.6, 4.5 and 8.5) using the same environmental variables selected under the present-day condition. Therefore, it is evaluated whether the spatial variability of the same environmental forcing under different climate change scenarios will structure the probability of occurrence of the European sardine based on the variability of environmental optima over large scale spatial projections.

2. Material and methods

2.1. Study area and occurrence data selection

Historical geo-referenced occurrence data (spatial points from 2009 to 2020) of large juvenile and adult European sardine were compiled. Protocols to avoid duplicated data among different databases and the exclusion of spatial points located outside the distribution range of the species were performed. The large spatial extent of available data was assumed to cover all of the known, present-day habitats utilized by this species in the Atlantic Ocean and regional seas. Data were available for the northeast Atlantic Ocean, including the Canary, Madeira and

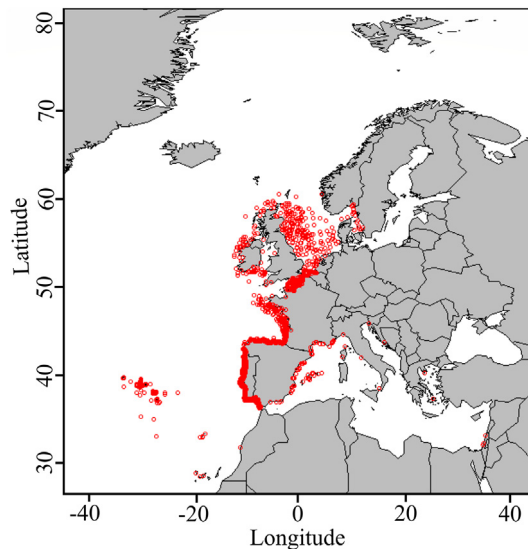


Fig. 1. Map of spatial points representing the occurrence of *Sardina pilchardus* along its distribution range. Geographic coordinate system: WGS 1984. R package: Maptools (<https://cran.r-project.org/web/packages/maptools/index.html>).

Azores archipelagos, Iceland and the western Mediterranean Sea (Fig. 1). Data from the southern Mediterranean, Baltic and Black Seas were either not available or the occurrence of this species was rare. Occurrence data along the adult sardine's distribution range were provided by the Portuguese Institute for the Sea and the Atmosphere (IPMA) and the Instituto Español de Oceanografía (IEO), as well as downloaded from open science databases [i.e. International Council for the Exploration of the Sea (ICES), Ocean Biodiversity Information System (OBIS) and Global Biodiversity Information Facility (GBIF)] (Table S1). A total of 68,767 geo-referenced occurrence data (i.e. pelagic hauls and scientific acoustic data) were used to develop habitat suitability models, being 64,177 located in the northeast Atlantic and 4590 in the Mediterranean Sea (Fig. 1).

2.2. Environmental data selection for the present-day suitability models

We considered 59 oceanographic variables among biological, chemical, and physical (remotely sensed) data as explanatory variables to statistically describe the present-day distribution of the European sardine (Table S2). Specifically, 44 relate to the average, maximum, minimum and range of sea surface temperature ($^{\circ}\text{C}$), sea surface salinity (PSU), current velocity (m s^{-1}), dissolved molecular oxygen (mol m^{-3}), nutrients [phosphate, silicate, nitrate, iron (mol m^{-3})], chlorophyll (mg m^{-3}), phytoplankton ($\mu\text{mol m}^{-3}$) and primary productivity ($\text{g m}^{-3} \text{ day}^{-1}$) (Assis et al., 2017). These variables are known to directly influence the habitat suitability of the European sardine (Giannoulaki et al., 2011; Tugores et al., 2011; Peck et al., 2021). The remaining 13 variables are represented by northward/eastward wind and current components (m s^{-1}) (Rio et al., 2014), sea surface density (kg m^{-3}) (Droghei et al., 2016) and sea level anomaly (m) (Mertz and Legeais, 2019). These variables were used as proxies for casual factors such as dispersal ability

and preferences of sardines for upwelling regions (Santos et al., 2004; Tugores et al., 2011). Finally, bathymetry (km) (GEBCO, 2020) and the distance to the nearest coast (km) (NASA, 2009) were used as proxies for the affinity of sardines to areas closer to the coast (Giannoulaki et al., 2011; Schickele et al., 2021). Each variable consists of annual raster layers based on monthly-averaged satellite images from daily measurements reanalysed as regular grids under Geographic Information Systems (e.g. Assis et al., 2017; Mertz and Legeais, 2019). The satellite variables were downloaded from open databases according to their best resolution to obtain grid cells representing the environmental characteristics around each sampling point (Table S2). We fitted kriging interpolations [spatial analyst tools in ArcGis 10.4.1 (<https://www.esri.com/>)] and the raster package [(Hijmans et al., 2020) in R 3.6.2 (R Core Team, 2020)] to downscale all raster layers to a common spatial resolution of 0.083° (~ 9 arcmin) to reproduce the characteristics of the raster with the highest resolution possible (Table S2).

Sets of environmental predictors were constructed to describe present-day habitat suitability of European sardine. To avoid the use of highly correlated predictors in the same analysis, the correlation among layers was checked using a Pearson's correlation matrix. Only layers with correlation coefficient below 0.45 ($P > 0.05$) were included in the same set. To evaluate which were the most important predictors to be maintained in each previously established set, we calculated the respective explanatory power of the variables using the function "get_variable_importance" in the biomod2 package, without interaction between variables and 1000 permutations (Thuiller et al., 2020). It is computed a simple correlation (Pearson's by default) between reference predictions and shuffled predictions. The return score is $1 - \text{cor}$ (0 to 1), which was then normalized to percentages. The highest the value, the more influence the variable has on the model. Backward selections progressively excluded variables whose explanatory power was below 10% and new sets were built. The average sea surface temperature (SST), the average sea surface salinity (SSS), the average current velocity (CVEL) and the distance to the nearest coast (DIST) were the final set of predictors as these variables were maintained in most sets and had the highest explanatory power (Table 1 and Fig. S1).

2.3. Environmental data selection for future suitability models

To forecast the effects of climate change and to investigate potential changes in the spatial distribution of the European sardine (i.e. present-day vs. future conditions) under several climate change scenarios, three greenhouse gas emission scenarios were considered (the IPCC Representative Concentration Pathways; RCPs) for both 2050 and 2100: (I) the optimistic scenario of peak-and-decline ending in very low greenhouse gas concentration levels by the end of the 21st century (RCP 2.6), (II) the intermediate scenario of stabilization (RCP 4.5) and (III) the pessimistic scenario of increasing emissions over time ending in high greenhouse gas concentration levels (RCP 8.5) (Assis et al., 2017; Moss et al., 2010). Environmental variables for future scenarios were the same considered for the present-day condition to allow comparisons among scenarios (Table 1 and Fig. S1). Rasters simulating future averages of SST, SSS and CVEL were retrieved from Bio-oracle.org (Assis et al., 2017). We considered DIST constant over time because sea level rise (SLR) for the study area is expected to increase at a

Table 1

Description of environmental satellite parameters used into modelling. MODIS: Moderate-resolution Imaging Spectroradiometer, WOD: World Ocean Database, ARMOR: Global Observed Ocean Physics Reprocessing, ORAP: Global Ocean Physics Reanalysis, NASA: National Aeronautics and Space Administration, GODDARD: NASA's Goddard Space Flight Center.

| Parameter | Abbreviation | Units | Sensor/model | Resolution | Source of climate data | Sources of reanalyses | References |
|--|--------------|--------------------|-----------------------|-----------------|------------------------|--------------------------|--------------------|
| Average sea surface temperature ^a | SST | $^{\circ}\text{C}$ | Aqua-MODIS | 0.083° | ARMOR | bio-oracle.org | Assis et al., 2017 |
| Average sea surface salinity ^a | SSS | PSU | WOD 2009 | | | | |
| Average current velocity ^a | CVEL | m s^{-1} | Multiple | | ORAP | | |
| Distance to the nearest coast | DIST | km | Generic Mapping Tools | 0.01° | GODDARD | oceancolor.gsfc.nasa.org | NASA, 2009 |

^a Parameters represented by the contemporary and future scenarios (RCP 2.6, RCP 4.5 and RCP 8.5 by 2050 and 2100).

Table 2

Results of the 12 best GAMs (Method: Restricted maximum likelihood). s: natural cubic spline based smooth term, D%: deviance explained, AIC: Akaike's information criterion, SP: *Sardina pilchardus* (presence/absence), SST: Sea surface temperature (°C), SSS: Sea surface salinity, CVEL: Current velocity (m s⁻¹), DIST: Distance to the nearest coast (km). Bold: selected model.

| Models | Present-day | | 2050 RCP 2.6 | | 2100 RCP 2.6 | | 2050 RCP 4.5 | | 2100 RCP 4.5 | | 2050 RCP 8.5 | | 2100 RCP 8.5 | |
|---|-------------|---------------|--------------|---------------|--------------|---------------|--------------|---------------|--------------|---------------|--------------|---------------|--------------|---------------|
| | D% | AIC | D% | AIC | D% | AIC | D% | AIC | D% | AIC | D% | AIC | D% | AIC |
| SP ~ s(SST) + s(SSS) + s(CVEL, DIST) | 96 | 8693.4 | 95.7 | 9259.8 | 96.1 | 8478.2 | 95.8 | 9259.8 | 95.8 | 9021.7 | 96.1 | 8552.9 | 96.1 | 8469.4 |
| SP ~ s(SST) + s(SSS) + s(CVEL) + s(DIST) | 96 | 9468.5 | 85.9 | 12,161.4 | 88.6 | 8972.6 | 89.9 | 9976.3 | 90 | 11,151.4 | 89 | 8796.5 | 95 | 8968.5 |
| SP ~ s(SST) + s(SSS) + s(CVEL) | 80.3 | 13,151.4 | 66.5 | 13,177.5 | 93.4 | 9333.7 | 60.7 | 9564.9 | 88.6 | 11,127.7 | 88.9 | 8679.2 | 94.6 | 12,751.7 |
| SP ~ s(SST) + s(SSS) + s(DIST) | 73.4 | 13,189.5 | 70.6 | 222,045.7 | 70.2 | 8651.1 | 88.4 | 9348.8 | 89.4 | 9478.2 | 92.6 | 8622.5 | 78.8 | 12,766.4 |
| SP ~ s(SST) + s(CVEL, DIST) | 77.6 | 13,177.1 | 90.2 | 9376.3 | 70.3 | 87,225.7 | 60.8 | 11,141.5 | 94 | 9376.3 | 93 | 86,383.3 | 60.7 | 12,799.1 |
| SP ~ s(SST, SSS) + s(CVEL, DIST) | 95.7 | 8874.5 | 95.2 | 9964.9 | 95.9 | 9036.4 | 95 | 9268.8 | 95.2 | 9367.4 | 95.8 | 8667.7 | 96 | 9876.6 |
| SP ~ s(SST, CVEL) + s(SSS, DIST) | 60.7 | 9003.6 | 59.8 | 9873.8 | 90.3 | 8776.4 | 78.4 | 9769.6 | 90 | 9200.9 | 93 | 9041.5 | 90 | 8976.8 |
| SP ~ s(SST, SSS) + s(CVEL) + s(DIST) | 60.4 | 8701.7 | 91.6 | 10,771.8 | 58.6 | 12,131.3 | 77 | 17,883.3 | 70.8 | 88,773.1 | 78.8 | 21,754.6 | 89.7 | 8701.7 |
| SP ~ s(SST) + s(SSS) | 60.8 | 87,535.4 | 64.8 | 87,535.4 | 62.3 | 12,179.6 | 59.2 | 13,177.6 | 89.2 | 98,511.5 | 80.4 | 23,756.4 | 94 | 86,585.3 |
| SP ~ s(SST, SSS) + s(DIST) | 95.3 | 214,045.9 | 93.1 | 13,359.2 | 60.4 | 12,157.8 | 79 | 263,046.3 | 94.8 | 14,456.8 | 69 | 27,766.4 | 96 | 227,645.9 |
| SP ~ s(SST, by = SSS) + DIST:CVEL | 90.2 | 233,750.6 | 90 | 104,163.2 | 90.1 | 97,466.1 | 88.6 | 111,811.1 | 69.5 | 100,230.7 | 58.3 | 106,965.7 | 70.7 | 103,758.3 |
| SP ~ s(SST) + CVEL:SSS | 89.6 | 87,535.4 | 79.8 | 112,875.6 | 83.7 | 82,455.3 | 70.7 | 163,376.2 | 66 | 277,945.3 | 77 | 97,586.8 | 90.3 | 88,935.4 |

maximum trend of 1 m (Vousdoukas et al., 2017) and shoreline retreat driven by SLR is predicted to be less than 97 m on average by 2100 under RCP 8.5 (Athanasίου et al., 2020). Thus, given that the species is often found within 100 km offshore (Tous et al., 2015), we considered the gain of less than 1 km over the next 79 years as negligible in terms of habitat expansions in relation to present-day shoreline positions.

2.4. Data analysis and spatial mapping

GAMs were applied in a presence/pseudo-absence approach to forecast the habitat suitability of the European sardine for the present-day condition, by 2050 and by 2100 under RCP's 2.6, 4.5 and 8.5. As response variable (y_i), we used the presence/pseudo-absence of the European sardine. As explanatory variables (x_i), we examined those variables selected by the bootstrap method [i.e. SST, SSS, CVEL and DIST (Fig. S1)]. We followed Barbet-Massin et al. (2012) to select pseudo-absences that best perform with GAMs. It was used a large number of pseudo-absences data, with equal weighting for presences. The binomial error distribution with the logit link function was used (Hastie and Tibshirani, 1990). Twelve GAMs were set a priori (Table 2). For each case, a model was built by testing all variables that were considered meaningful; and the best models were determined by fitting across the full set of possible models. The MGCV package in the R statistical software was used to select the GAM smoothing predictors and the natural cubic spline smoother was applied for GAM fitting (Wood, 2019). To help in the identification of important features, a double penalty was applied to the penalized regression of each model, allowing variables to be solved out of the model (Marra and Wood, 2011). The degree of smoothing was chosen based on the restricted maximum likelihood method (REML), which outperforms the generalized cross validation (GCV) smoothing parameter selection (Marra and Wood, 2011). To avoid overfitting, the number allowed to the smoothing functions were limited to 5 for single terms and 20 for two-interaction terms (5% level of significance) (Wood, 2006).

The goodness-of-fit of the models was also assessed using Akaike's Information Criterion (AIC) (Hastie and Tibshirani, 1990) and by the percentage (%) of explained deviance. To validate the selected models, the normal probability QQ-plots of the residual components of the deviance vs. quantiles, as well as the Receiver Operating Characteristic curve (ROC; Hanley and McNail, 1982; Guisan and Zimmermann, 2000) and the AUC metric (the area under the ROC) were evaluated to check model performance and misspecification (Franklin, 2009) (Fig. S2). To further assess the quality of our models, we applied a cross-validation test using 75% of the dataset as training data and 25% as test dataset.

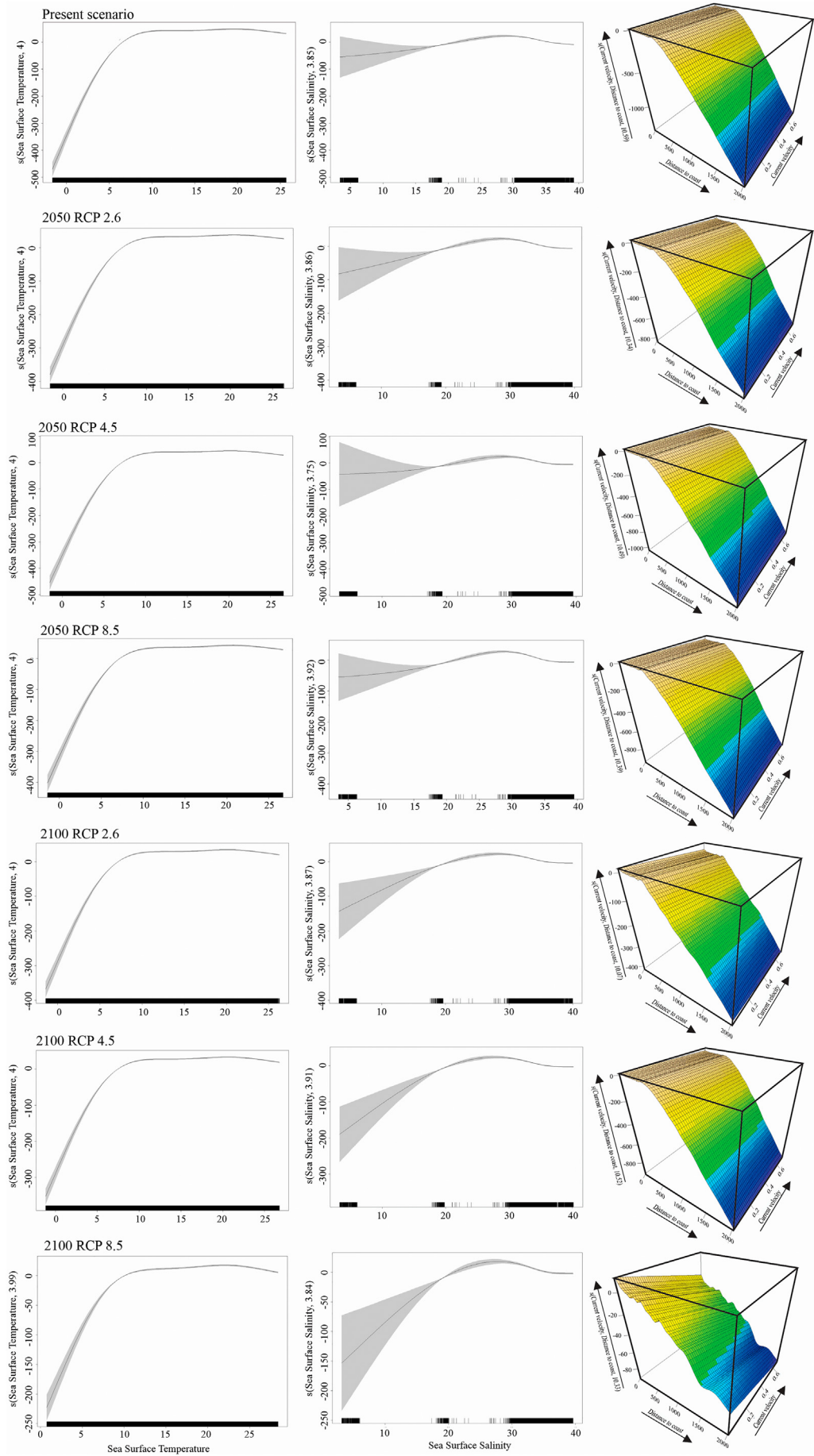
Then, we obtained a confusion matrix with a threshold at 0.5 to identify the proportion of observed positives that are correctly predicted (or sensitivity) and the proportion of observed negatives that are correctly predicted (or specificity) as a measure of model evaluation (Lobo et al., 2008). The Cohen's kappa was used to check model power [poor $K < 0.4$; good $0.4 < K < 0.8$, and excellent $K > 0.8$] (Manel et al., 2001). The output of the final selected GAM is presented as plots of the best-fitting smooths where single and interaction effects are shown as perspective and 3-D plots, respectively (Fig. 2). Based on validation results, the selected model was applied in a predictive mode to provide response estimates of suitability (0 to 1) over a wider grid of a largescale map at a GIS resolution of 0.083°, covering the northeast Atlantic Ocean, the Mediterranean and the Black Sea. As we have few occurrence data for the Mediterranean Sea, we checked whether predictions inside this basin is biased by the greater number of occurrences available for the northeast Atlantic by applying the same modelling procedures to each region separately (Fig. S3). The potential shifts in the habitat suitability of the European sardine were investigated by evaluating the differences between climatic scenarios under each RCPs (Fig. S4). Finally, we created binary HSMs to calculate the percentage of change in suitable area in square kilometres between present-day and future maps in order to detect range expansion and contraction using spatial analyst tools in ArcGis 10.4.1 (<https://www.esri.com/>). The binary HSMs followed the threshold established by Ahmad et al. (2019), which considered probabilities <0.25 as unsuitable habitats ($=0$) and >0.25 –1 as potential areas ($=1$) of species' occurrence, namely "overall suitability".

3. Results

3.1. Habitat suitability modelling

The explanatory powers of the selected environmental variables were 31.14% for SST, 28.68% for DIST, 21.32% for SSS and 18.86% for CVEL for the present-day condition (Table S3). Therefore, the final GAMs for the pooled dataset concerning the present-day condition and future scenarios included as main effects: SST, SSS and the interaction of CVEL with DIST [European sardine (presence/pseudo-absence) ~ s(SST) + s(SSS) + s(CVEL, DIST)] based in the lowest AIC and higher deviance explained (Table 2). The GAMs exhibited high capacity to accurately predict species presence or absences since sensitivity and specificity were always at a rate of >0.9 . AUC and K values were also >0.9 and >0.8 , respectively, validating the quality and the predictive accuracy of the models (Fig. S2).

Fig. 2. Relative importance of the selected environmental variables for the present-day and future scenarios. First and second column: Single variable effect plot for the single smooth terms [s(SST) and s(SSS)]. Third column: 3-D interaction plots. The x and y-axis of the interaction plots reflects the relative importance of each variable in the model and the interaction effect is presented on the z-axis. The dashes on the x-axis of single terms, the so-called 'rug', indicate the density of points for the different variable values. The solid black line indicates the GAM coefficients, and the shadowed gray area represents the 95% point-wise confidence bands at $p = 0.05$. GAM: *Sardina pilchardus* ~ s(SST) + s(SSS) + s(CVEL, DIST).



Sardine's suitable temperatures ranged from 9.6 °C to 26.4 °C (on average) (Table 3). The response curves showing the relative importance of SST indicated that habitat suitability for the European sardine was low below in waters ≤ 10 °C, high and nearly constant between 11 °C and 22 °C and declined at > 23 °C (Fig. 2). Regarding SSS, a range between 17.3 (PSU) and 39.6 (PSU) on average was detected (Table 3). Despite this, habitat suitability is low below ~ 18 (PSU), and high and nearly constant > 20 (PSU) (Fig. 2). However, a more pronounced decrease in suitability when the SSS is below ~ 20 (PSU) is expected to occur by 2100 under all RCPs when compared to the previous scenarios. Moreover, according to the interaction terms, suitability is higher in the neritic zone (< 250 km from the nearest coast) regardless current velocities. An exception is predicted by 2100 under RCP 8.5, when suitability will be higher in calmer waters ($CVEL < 0.1 \text{ m s}^{-1}$) closer to the coast (< 50 km from the nearest coast) (Fig. 2).

3.2. Suitability mapping and predictive shifts based on IPCC climatic scenarios

The suitability maps showed that suitable areas for the European sardine were dominated by areas characterized by higher probability (> 0.6 to 1) of occurrence closer to the coasts. A higher variability in the probability of occurrence was observed as suitability gradually decreases towards the break of continental shelves, thus, represented by occasional (probability > 0.25 – 0.6) and rare habitats (probability < 0.25) (Fig. 3). The species inhabit areas closer to the coast (< 50 km from the nearest coast) around the Azores, Madeira and Canary archipelagos, in the Atlantic coast of Morocco, Spain and Portugal, in the northwestern Mediterranean, Adriatic Sea, Tyrrhenian Sea, the Mediterranean coast of Africa and in the southeast coasts of the Mediterranean and Black Seas (Fig. 3). The GAMs predicted that suitable habitats were more distant from the shore (< 250 km from the nearest coast) in the Bay of Biscay, the Atlantic coast of France and English Channel, around Ireland and U.K., in the entire North Sea and the southern Norwegian Sea and entire Aegean Sea. Moreover, the southwest coast of Iceland was also predicted to be suitable habitat for the species, while the Baltic Sea is unsuitable (Fig. 3).

The projections from the present-day to 2100 suggested that the species will experience slight changes in environmental variability along most part of its distribution range (Fig. S4). Concomitantly, in all scenarios, a strong and gradual poleward shift in the distribution of the species was projected due to increased suitability of habitats along the coast of Norway (eastern Norwegian Sea). It was projected that the strongest northward shift will be observed by 2100 under RCP 8.5. At this scenario, habitat suitability increases along the entire coast of Norway up to the White Sea. On the other hand, suitability in the southwest coast of Iceland decreases over time, potentially leading to local extirpation by 2100 under RCP 8.5.

According to the maps of predictive shifts, the more prominent shifts were predicted for occasional and rare habitats far from the coasts (Fig. 4). It was projected that, by 2100 under RCP4.5 and RCP 8.5, habitat suitability will increase between $+0.1$ to $+0.5$ in most part of the north and eastern Mediterranean, eastern Black sea, eastern Azores, around

Madeira and Canary archipelagos, in Galicia and Bay of Biscay and central North Sea. Losses between -0.1 and -0.6 will be observed in the Atlantic coast of Morocco and Portugal, along the coast of Algeria and Tunisia, Central Aegean Sea, North Adriatic Sea, in the western and northern Ireland, in the northern North Sea and western Azores (Fig. 4). This pattern was nearly similar across scenarios, except for the fact that in the coast of Portugal it was predicted gains up to $+0.5$ under RCP 4.5 and gains up to $+1$ in the Mediterranean coast of France and eastern Black Sea, and between $+0.1$ and $+0.5$ in the central North Sea under RCP 8.5. In the southwest coast of Iceland, suitability reduced up to -1 by 2100 possibly indicating local extirpation, independently of climatic scenarios. Along the coast of Norway, suitability gains might reach $+1$ in specific sites regardless scenario (Fig. 4). However, the more prominent gains ranging between $+0.4$ and $+1$ were projected to occur along the entire coast of Norway and within the White Sea by 2100 under RCP 8.5.

Our results indicated that total suitable area will increase towards the end of the century regardless of the climatic scenario (Table 4). The highest gain was observed by 2100 under RCP 8.5, with an increase of 9.57% in suitable habitats when compared to the present-day condition ($2,477,791 \text{ km}^2$ vs. $2,715,051 \text{ km}^2$). When considering specific geographic regions, range expansions were observed in the entire Mediterranean Sea, with gains of up to 21% in the Eastern Mediterranean ($366,421 \text{ km}^2$ vs. $443,026 \text{ km}^2$); as well as in the Iberia Peninsula, with gains of up to 11% ($242,638 \text{ km}^2$ vs. $269,371 \text{ km}^2$), both by 2100 under RCP 8.5 (Table 4). Slight range contractions were observed in Western U.K. coast, around Ireland, in the English Channel and North Sea. Range contractions were more prominent in the Atlantic African Coast, with losses of up to 19.31% ($236,663 \text{ km}^2$ vs. $190,970 \text{ km}^2$) by 2050 under RCP 4.5 (Table 4).

4. Discussion

4.1. Environmental drivers for the spatial distribution of the European sardine

It is critical to make robust projections of how important living marine resources will respond to climate change, a particularly important task for small pelagic fish. These species support populations of site-based predators such as marine birds and are important for protein security and cultural identities of human communities (Peck et al., 2021). For all climatic scenarios considered in our study (present-day vs. 2050 and 2100 under RCPs 2.6, 4.5 and 8.5 scenarios) we projected that potential "hot-spot" areas for the European sardine are located along the neritic zone (< 250 km from the nearest coast) comprising the entire distribution range of the species (eastern Atlantic, Mediterranean and Black Seas). These areas of increased probability of sardine occurrence exhibit low variability among scenarios because they meet species-specific environmental optima, which are predicted to be in areas under the influence of ocean currents $< 0.4 \text{ m s}^{-1}$, where SST ranges between > 10 °C and 22 °C and SSS > 20 (PSU) on average. Above or below this environmental interactive range, habitat suitability decreases significantly originating occasional and rare habitats.

Table 3

Environmental conditions for each climatic scenario (annual averages from monthly-means) based on the occurrence dataset.

| Climatic scenarios | Sea surface temperature | | | Sea surface salinity | | | Current velocity | | | Distance to the nearest coast | | |
|--------------------|-------------------------|-------|--------------------|----------------------|-------|--------------------|------------------|-------|--------------------|-------------------------------|-----|--------------------|
| | Min | Max | Average \pm S.D. | Min | Max | Average \pm S.D. | Min | Max | Average \pm S.D. | Min | Max | Average \pm S.D. |
| Present-day | 9.64 | 23.08 | 17.93 \pm 3.51 | 18.89 | 38.84 | 35.71 \pm 1.31 | 0.025 | 0.438 | 0.102 \pm 0.032 | 0 | 460 | 16.70 \pm 22.28 |
| 2050 RCP 2.6 | 10.21 | 24.03 | 18.78 \pm 3.47 | 18.70 | 39.26 | 35.65 \pm 1.33 | 0.027 | 0.441 | 0.104 \pm 0.033 | | | |
| 2050 RCP 4.5 | 10.42 | 24.18 | 18.81 \pm 3.36 | 18.98 | 39.21 | 35.71 \pm 1.28 | 0.026 | 0.441 | 0.104 \pm 0.033 | | | |
| 2050 RCP 8.5 | 10.40 | 24.41 | 18.97 \pm 3.42 | 18.71 | 39.05 | 35.58 \pm 1.40 | 0.026 | 0.442 | 0.105 \pm 0.033 | | | |
| 2100 RCP 2.6 | 10.19 | 23.94 | 18.51 \pm 3.42 | 18.49 | 39.56 | 35.48 \pm 1.44 | 0.024 | 0.441 | 0.103 \pm 0.033 | | | |
| 2100 RCP 4.5 | 10.33 | 24.51 | 18.96 \pm 3.51 | 18.30 | 39.62 | 35.43 \pm 1.52 | 0.024 | 0.441 | 0.101 \pm 0.034 | | | |
| 2100 RCP 8.5 | 12.02 | 26.43 | 20.70 \pm 3.33 | 17.34 | 39.08 | 35.14 \pm 1.64 | 0.025 | 0.439 | 0.101 \pm 0.034 | | | |

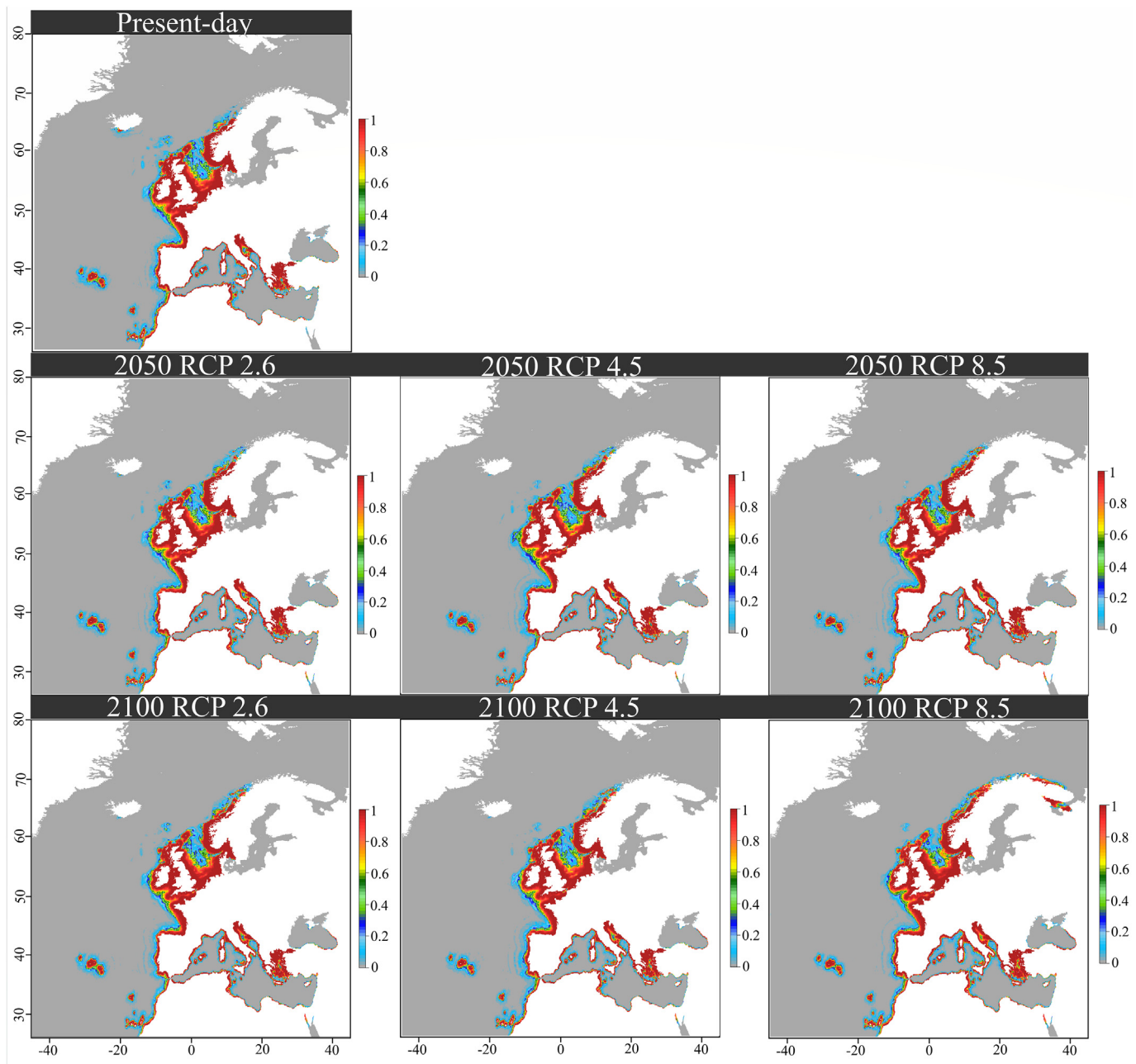


Fig. 3. Maps of suitability indicating the variability in the probability of occurrence of *Sardina pilchardus* (from 0 to 1) as predicted by the selected binomial model $Sardina\ pilchardus \sim s(SST) + s(SSS) + s(CVEL, DIST)$ according to the present-day and future scenarios. Geographic coordinate system: WGS 1984.

The present study investigated a wider range of possible explanatory variables when compared to other studies on the distribution of SPF (Giannoulaki et al., 2011; Raybaud et al., 2017; Pennino et al., 2020; Schickele et al., 2021). Here, we confirmed that, at least for largescale approaches, the most important predictors for the present-day condition can be used into future projections of sardine distribution. SST, SSS, CVEL and DIST are the factors that better explained largescale patterns of habitat suitability and produced models with the best goodness-of-fit regardless climatic scenario. The selection of the same model for all scenarios is possibly a result of the proportional rate at which mean environmental variability will change towards the end of 21st century and the low variability between RCPs according to IPCC models. Additionally, HSMs deal with species' environmental optima to predict probabilities of occurrence across distribution ranges based on presence/absence (or pseudo-absence) datasets. For this reason,

caution needs to be taken into account to avoid the gathering of biased occurrence datasets due to differences in sample size, weight of point data and the use of opportunistic surveys. In some cases, the use of joint likelihoods (the product of individual likelihoods for each data source) might be needed to improve predictions (Fletcher et al., 2019). In addition, these HSMs have no ability to predict how and whether sardines would be viable in new locations where they will need to compete with other species or the impact of migration of sub-tropical species to current habitats due to climate change. Moreover, variability in abundance, biomass and phenology, among other factors still needs to be investigated to provide a holistic view of the impacts of climate change on ecologically relevant factors affecting the productivity and distribution of small pelagic fish such as the European sardine; high habitat suitability does not necessarily imply population viability. Another limitation is that HSMs normally ignore seasonal

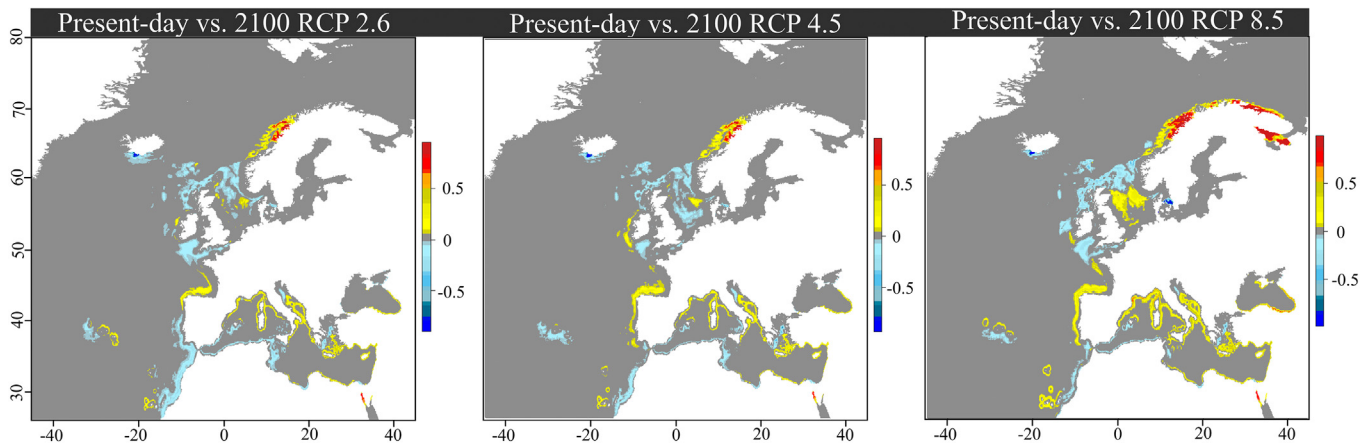


Fig. 4. Maps of suitability shifts due to climate change indicating gains and losses in the probability of occurrence of *Sardina pilchardus* as revealed by the differences between the present-day and 2100 scenarios under each RCP. Geographic coordinate system: WGS 1984.

differences in key abiotic factors which, at mid- and high-latitudes, can be important drivers of population persistence due to physiological constraints (Peck et al., 2012; Petitgas et al., 2013). However, datasets containing model projections of future changes in marine physical, chemical and biological factors are also limited or are still not accurate to permit an adequate use in small-scale modelling, especially for surface water masses.

The European sardine is an eurythermal clupeoid that can tolerate variable oceanographic conditions characteristics of temperate shelf seas and sub-tropical upwelling zones such as temperatures ranging from $>8^{\circ}\text{C}$ to 26°C (Coombs et al., 2006; Zwolinski et al., 2010; Garrido et al., 2016, 2017). According to its relative importance, SST was a direct predictor of present-day habitats (those between $>10^{\circ}\text{C}$ and 22°C). Our models also predicted that sardines might occasionally or rarely, inhabit regions where temperatures are below 9.6°C on average under present-day conditions, such as observed in the North Sea and in the south coast of Norway (Zwolinski et al., 2010). However, a gradual poleward expansion of the suitability for the European sardine was expected across the three RCP scenarios. This expansion was more pronounced by 2100 under RCP 8.5 and sardines are predicted to inhabit the entire coast of Norway and the White Sea, when these regions warm up and SST reaches values within the optimum for the species ($>10^{\circ}\text{C}$).

Climate change is acknowledged as being responsible for the shift to higher latitudes of European sardine and anchovy (*Engraulis encrasicolus*) stocks after mid-1990s due to the loss of cold winters (favouring survival) and warming to better support spawning (Petitgas et al., 2012; Giannoulaki et al., 2014). In the case of European anchovy, local population productivity increased creating an apparent

movement to higher latitudes (Petitgas et al., 2012). However, behaviourally mediated movement to track isotherms has been acknowledged to influence historical changes in the distribution of many species of SPF (e.g. *Engraulis encrasicolus*, *Clupea harengus* and *Sardinella longiceps*), allowing them to track their optimal thermal physiological conditions during extreme climatic shifts, especially by migrating polewards (Silva et al., 2014; Han et al., 2020; Sebastian et al., 2020). Once SPF move to new areas, genetic markers have revealed adaptive changes which may favour population persistence and/or key physiological factors shaping their life history. For example, a seascape genetic approach using targeted sequencing of mitochondrial genes directly involved in metabolic pathways revealed a temperature- and O_2 -dependent distribution of haplotype frequencies as signatures of selection of European sardines to cold temperatures and low-oxygen levels (Baltazar-Soares et al., 2021).

In contrast to SST, the average SSS changed more towards the end of this century in areas far from the coastline, especially along the north-east Atlantic. The largest projected changes in SSS [declines from ~ 35 to ~ 32 (PSU)] were observed in the Bay of Biscay, in the centre of the North Sea and along the entire coast of Norway. As habitat suitability was predicted to slightly decrease above 30 (PSU) in the GAMs, most projected shifts in habitat suitability (gains and losses) among future scenarios occurred in present-day areas considered to be occasional and rare habitats. On the other hand, nearshore habitat suitability changed little across the different scenarios. Nearshore SSS along the distribution range of sardines varied between >17 (PSU) and 39 (PSU), on average, regardless of the climatic scenario. This range was considered suitable for the European sardines in our study as our models included occurrence data in the Skagerrak Strait and in the

Table 4

Area in square kilometres (km^2) showing suitable habitats under present-day conditions and future climatic scenarios (2050 and 2100) considering overall suitability between 0.25 and 1. Parenthesis indicates the % of gains or losses in area when compared to the contemporary condition.

| Geographic area | Present-day | RCP 2.6 | | RCP 4.5 | | RCP 8.5 | |
|--------------------------------|-------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| | | 2050 | 2100 | 2050 | 2100 | 2050 | 2100 |
| Total area | 2,477,791 | 2,522,353 (1.79%) | 2,541,090 (2.55%) | 2,528,369 (2.04%) | 2,546,007 (2.75%) | 2,539,435 (2.48%) | 2,715,051 (9.57%) |
| Iberian Peninsula | 242,638 | 258,581 (6.57%) | 246,099 (1.42%) | 243,856 (0.50%) | 265,172 (9.28%) | 250,007 (3.037%) | 269,372 (11%) |
| Eastern Mediterranean | 366,421 | 404,949 (10.51%) | 416,999 (13.80%) | 409,625 (11.79%) | 405,309 (10.61%) | 422,369 (15.26%) | 443,026 (21%) |
| Western Mediterranean | 463,781 | 472,497 (1.88%) | 482,664 (4.07%) | 475,883 (2.61%) | 483,089 (4.16%) | 484,156 (4.39%) | 521,263 (12.39%) |
| North Mediterranean | 630,194 | 652,472 (3.53%) | 679,524 (7.82%) | 668,842 (6.13%) | 671,769 (6.59%) | 673,295 (6.84%) | 727,524 (15.44%) |
| South Mediterranean | 209,858 | 237,188 (13.02%) | 232,251 (10.67%) | 228,216 (8.75%) | 226,105 (7.74%) | 244,771 (16.63%) | 250,183 (19.21%) |
| Norwegian Coast and White Sea | 92,087 | 106,975 (16.17%) | 124,851 (35.58%) | 115,400 (25.32%) | 124,923 (35.66%) | 124,916 (35.64%) | 209,521 (127.52%) |
| Atlantic African Coast | 236,663 | 214,480 (−9.37%) | 207,154 (−12.47%) | 190,970 (−19.31%) | 220,224 (−6.95%) | 210,829 (−10.91%) | 237,308 (0.27%) |
| Western U.K. coast and Ireland | 442,719 | 446,667 (0.89%) | 438,260 (−1%) | 466,277 (5.32%) | 441,388 (−0.3%) | 436,673 (−1.36%) | 419,862 (−5.16%) |
| English Channel and North Sea | 564,092 | 559,126 (−0.88%) | 556,867 (−1.28%) | 559,301 (−0.84%) | 550,245 (−2.45%) | 553,627 (−1.85%) | 553,695 (−1.84%) |

Kattegat Bay, where salinity varied between 17 and 20 (PSU) (regardless scenarios). The inclusion of these records was important to shape the relative importance of SSS along the entire distribution range of the species, possibly indicating a wider SSS range for sardines, when compared to other studies with regional approaches (Giannoulaki et al., 2005; Palomera et al., 2007).

The effect of salinity on the ecology of European sardine is still not well understood (Fernández-Corredor et al., 2021). A positive relationship is observed between salinity and landings in the northwest Mediterranean (Quattrocchi and Maynou, 2017), suggesting that less saline waters are not suitable for adult sardines, while a negative relationship with abundance and biomass are reported in the Spanish coast, in the Gulf of Lion, in the southern Alboran Sea and in the northern Tyrrhenian Sea (Bonanno et al., 2016; Jghab et al., 2019; Pennino et al., 2020). Salinity is not expected to directly influence adult distribution (Jghab et al., 2019). However, our models emphasized that SSS may also be a climate-driven factor inducing shifts in environmental optima when the whole distribution range of the species is considered.

The interaction of current velocity and distance to the nearest coast was an important proxy for casual factors due to its high capacity to distinguish the preference of sardines for highly productive areas close to the coast from those beyond the neritic zone, where the absence of the species is naturally expected (Giannoulaki et al., 2014). Thus, it is possible to detect that occasional and rare habitats are mainly located close to the break of continental shelves and in the centre of the North Sea. Although the average current velocity had little spatial variability across the distribution range projected for the species among different scenarios, and hardly ever overpassed 0.4 m s^{-1} this velocity coincided with those found in upwelling systems (Xie et al., 2017; Cordeiro et al., 2018). Furthermore, our projections suggested a stronger dependency of sardines on coastal habitats by 2100 under RCP 8.5, where suitability will be higher in calm waters ($\text{CVEL} < 0.1 \text{ m s}^{-1}$) closer to the coast ($< 50 \text{ km}$ from the nearest coast).

The importance of coastal waters has been widely reported as one of the most significant drivers of sardine (and European anchovy) spatial distribution (Bellido et al., 2008; Giannoulaki et al., 2008; Falco et al., 2010; Carpi et al., 2015; Bonanno et al., 2016). Sardines have higher probability to be found nearshore during summer months and expand their distribution to deeper waters during autumn and winter (Tugores et al., 2011). The European sardine is known to profit from upwelling zones/nutrient-rich waters and areas of high river discharge, especially by using these regions as feeding and breeding grounds (Lloret et al., 2004; Guisande et al., 2004; Giannoulaki et al., 2011; Checkley et al., 2017; Schickele et al., 2021).

4.2. Regional impacts of climate change on the distribution range of European sardines

Our projections showed that in areas of high suitability, the probability of occurrence of the species is maintained the same over the scenarios, while most variability in the probability of occurrence is observed in habitats of moderate to low suitability. Areas with the highest suitability are observed over the continental shelf up to 250 km from the nearest coast, what is consistently noticed in areas of high productivity, such as the coast of Portugal, Bay of Biscay, around Ireland and U.K., in the North Sea and in the southern Norwegian Sea (Giannoulaki et al., 2011; Checkley et al., 2017). Here, we predicted that the total range of the species within suitable areas (> 0.25 – 1) might change from $2,477,791 \text{ km}^2$ at the present-day condition to $2,715,051 \text{ km}^2$ by 2100 under RCP 8.5, leading to a total expansion of 9.57% towards the end of this century. Expansions of suitable areas are observed in the Mediterranean, Iberian Peninsula, Norwegian coast and the White Sea. Contraction of suitable areas is observed in the Atlantic African coast, the western U.K. coast, around Ireland, in the English Channel and in the North Sea. These results emphasize that spatial variability within species' environmental optima due to climate change have a great influence

on habitat expansion and contraction of European sardines with a strong dependence on regional scales. In addition, this is the first study to propose gains and losses in sardines' suitable areas (km^2) towards the future and may provide a basis to define new fishing areas or to expand existing ones if fisheries viability is consistently monitored and to better manage those areas were habitat contractions and climatic refuges are predicted to occur.

4.2.1. Northern distribution: Iceland, British Isles, North Sea, Norwegian Coast and White Sea

According to our study, the spatial variability of SST across most parts of the species' distribution range was projected to change very little across most IPCC climatic scenarios. However, a gradual warming in the region of the North Atlantic and the Norwegian currents is observed towards the end of the century. This gradual warming of the northern Atlantic will produce physical forcings influencing the tidal-mixing, river plumes upwelling zones and shelf break fronts, changing productivity and altering the food web in the region, likely affecting the distribution and/or abundance of sardines through bottom-up control (Peck et al., 2021). The most distinguishable climatic shifts are projected to occur by 2100 under the most pessimistic greenhouse gas scenario, in which we observed an ocean warming between $+2^\circ\text{C}$ and $+4^\circ\text{C}$ across the entire species' distribution range with a sharp increase in the average SST from -6°C to -12°C along the entire coast of Norway and in the White Sea. Therefore, our models indicate a gradual poleward shift in the distribution of the European sardine, the magnitude of which increases as one moves from RCP2.6, to 4.5 to 8.5 with a stronger poleward-eastward expansion by 2100 under RCP 8.5 along entire coast of Norway. This leads up to the White Sea, with a predicted range expansion of $+117,434 \text{ km}^2$ ($+127.52\%$) relative to the present-day condition. Controversially, the sea south of Iceland gradually cools (from -11°C to -6°C), and for this region, we projected a decrease of -0.7 in habitat suitability, suggesting local extirpation for the species by 2100 under RCP 8.5. These results coincide with a recent ensemble forecasts for temperate-cold water SPF [e.g. European sardine, European sprat (*Sprattus sprattus*) and European anchovy], corroborating that northward migration is ruled by the warming of the Norwegian Sea by 2100 under the pessimistic scenario (Schickele et al., 2021). Moreover, this study also predicted low habitat suitability around Iceland, but local extirpation was not detected by the end of this century (Schickele et al., 2021).

In the sea west of U.K and around Ireland, a range contraction of $-22,893 \text{ km}^2$ (-5.16%) was predicted by 2100 under RCP 8.5. As well, across the English Channel and North Sea, we predicted slight range contractions among scenarios, with the greater loss of $-13,847 \text{ km}^2$ (-2.45%) by 2100 under RCP 4.5. Although we predicted suitability losses between -0.2 and -1 in these regions towards the future, present-day studies have ascertained that the European sardine, as well as other SPF (e.g. the European anchovy *Engraulis encrasicolus*), have expanded their distribution towards the north. In the North Sea, for example, the abundance of sardines has increased since the mid-1990s and the species even use this region as spawning ground (Beare et al., 2004; Fréon et al., 2009; Alheit et al., 2012). This long-term rise in sardine abundance at higher latitudes was attributed to climate change and probably reflects the sudden warming noticed by 1985, when SST in the northern North Sea increased from 6.5°C to 8.5°C on average associated to the strengthening of the North Atlantic Oscillation (Beare et al., 2004; Alheit et al., 2012).

4.2.2. Iberian Peninsula and Atlantic African Coast

The distribution range of the species within suitable areas around the Iberian Peninsula was predicted to change from $242,638 \text{ km}^2$ at the present-day condition to $269,372 \text{ km}^2$ by 2100 under RCP 8.5, leading to a regional expansion of 11% towards the end of this century. In the Atlantic African Coast, the most prominent contractions of $-45,693 \text{ km}^2$ (-19.31%) and $-29,509 \text{ km}^2$ (-12.47%) are both

observed by 2100 under RCP 2.6 and by 2050 under RCP 4.5, respectively. These results differ from the ensemble forecasts proposed by Schickele et al. (2021), in which sardines exhibit signs of extirpation around the Iberian Peninsula, but coincided with the slight suitability loss (-0.2) in the African Coast by 2100 under the pessimistic scenario. The ensemble forecast differs from our model by not considering the distance to the nearest coast and current velocities, which might project different outcomes (Schickele et al., 2021).

Different projections of the same species are important to provide a deeper understanding of climate change impacts, especially because the influence of future abiotic environment on SPF distribution still needs further investigation. For example, coastal upwelling zones are highly suitable for sardines. Upwelling intensity has increased in the western Iberian Peninsula and decreased in the north-west African coast due to rising temperatures (Wang et al., 2015; Sousa et al., 2017). However, upwelling of oxygen-depleted waters had also intensified since 1950 and many coastal sites along the Northeast Atlantic have been reported to be in hypoxic condition (oxygen concentrations ≤ 2 mg liter $^{-1}$) due to global warming and nutrient enrichment (Breitburg et al., 2018). Since the middle of the 20th century, the oxygen content of the ocean has declined by $\sim 2\%$ (Claireaux and Chabot, 2019) and is expected to fall on an average of 3–4% by 2100 as warmer waters have decreased potential to dissolve O_2 (Schmidtke et al., 2017). Furthermore, oxygen minimum zones are expanding in world oceans as a result of climate change and reducing suitable habitats vertically (Checkley et al., 2009).

In our study, dissolved oxygen was also a good predictor explaining sardines' distribution but presented a high, negative correlation with SST independent of climatic scenario (> -0.9) and never had explicative power higher than those of SST, when different sets of environmental predictors were compared. Therefore, dissolved oxygen was not selected for modelling purposes. In addition, a recent study suggested that low levels of dissolved oxygen may be an important variable structuring the genetic diversity of the European sardine around the Iberian Peninsula (Baltazar-Soares et al., 2021).

4.2.3. Mediterranean and Black Sea

The distribution range of the species within suitable areas of the Mediterranean Sea was predicted to expand regardless the region. The most prominent expansion of $+76,605$ km 2 ($+21\%$) is observed in the eastern Mediterranean, followed by the southern Mediterranean with gains of $+40,325$ km 2 ($+19.21\%$), both by 2100 under RCP 8.5. In the Mediterranean and Black Seas, salinity does not change much among scenarios and environmental optima is mainly ruled by the spatial variability in SST. The influence of SST as a good predictor for most variability in the habitat suitability of the European sardine was already described for the Mediterranean (Tugores et al., 2011; Jghab et al., 2019) and the Black seas (Schickele et al., 2021). The entire Mediterranean and Black seas will become warmer, where SST may increase $+4$ °C on average by 2100 under RCP 8.5. The average SST never overpasses 23 °C in the northern Mediterranean and in the Black Sea, while SST might reach up to 26 °C along the coasts of northern Africa, Israel, Lebanon, Syria and Turkey. Suitability increases between $+0.2$ and $+1$ by 2100 under RCP 8.5 along most part of the Mediterranean coasts, with the highest suitability gains being predicted to occur in the Gulf of Lion and Ligurian Sea, and in the eastern Black Sea. Northward shifts have also been reported for other SPF (e.g. *Sardinella aurita*) in the Mediterranean Sea with unknown effects on sardine populations (Giannoulaki et al., 2014). Moreover, Pennino et al. (2020) also detected that waters next to the Gulf of Lion will probably become future climate refuges for the European sardine and anchovy with probability of occurrence >0.7 by the end of this century. Moreover, although oligotrophic, the northern Mediterranean also exhibited coastal expanded suitable areas, such as in the Adriatic and Aegean Seas. Similar pattern of high suitability was also observed in the shallow waters of the eastern

Mediterranean due to river outflow and the input of Black Sea waters into the Aegean Sea, and by the association of the Adriatic Sea with the Po River Delta region (Tugores et al., 2011).

In the southern Mediterranean, habitat suitability was projected to decline between -0.1 to -0.6 along the southeast coast of Spain and in waters off northern Morocco, Algeria and Tunisia, as habitat suitability decreases above 23 °C and the species may not withstand temperatures warmer than 26 °C. This pattern is also compatible with the ensemble forecast for European SPF, where climate-related local extirpations are expected under the most pessimistic scenario in the south-western Mediterranean coasts (Schickele et al., 2021). However, although warmer, slight gains in suitability (between $+0.1$ and $+0.8$) along the coasts of Israel, Lebanon, Syria and Turkey are also predicted by the end of this century. The Mediterranean is one of the most basin vulnerable to climate change as it experiences fast warming, accelerated records of invasive species, unknown risk of competition with other SPF and intense exploitation that might disrupt habitat suitability in the future.

4.3. The effects of climate variability and climate change on SPF

Fluctuations on sardine populations have been mainly controlled by bottom-up processes, such as climate variability, and secondarily by top-down processes, such as natural and fishing mortality (Checkley et al., 2017). Making robust projections of changes in bottom-up forcing is critical because of the economic, ecological and cultural importance of SPF worldwide. Rising ocean temperatures due to global changes is an example of bottom-up factors induced by climate change, which, in turn, lead to changes in other processes that influence the environmental optima of sardines (Peck et al., 2018). The magnitude at which climate change alter the match-mismatch of sensitive species within their environmental optima has been challenging to forecast (Petitgas et al., 2013; Evans et al., 2015). In the marine environment each species exhibits specific responses to ocean warming, acidification and/or O_2 depletion by improving physiological performance to adapt, shifting dispersal range limits to preserve climatic niche, or even may face local extirpation (Lima et al., 2019; Jutfelt, 2020). A particular attention has been given to populations of organisms that are currently exploited because overfishing has threatened stocks that are already heavily affected by variability and change in climate. Fishing hotspots for the European sardine (and the European anchovy) coincide with marine fishing areas already affected by climate change. Thus, to maintain the species resiliency within a "safe operating space", it is suggested the redistribution or reduction of fishing intensity along these fishing areas (Ramírez et al., 2021).

Climate change is acknowledged to reshape the geographical distribution of prey, predators, and/or competitors of the European sardine with complex trophodynamic consequences including negative effects on fisheries (Maynou et al., 2014). Although productivity and plankton availability are unlikely to pose limitation to the spatial expansion of sardine in the future, changes in top predators' abundance (e.g. larger fish, marine mammals and birds) might affect sardine populations (Checkley et al., 2017). For example, in regions where projections revealed increased habitat suitability by the end of the century (e.g. Iberian Peninsula, the Norwegian, the White Sea and the Mediterranean Seas), range expansion might be counterbalanced by a higher abundance of predators or competitors and the lack of adequate prey, leading to decreased sardine populations (Fréon et al., 2009).

The European sardine is widely distributed and share their habitats in northeast Atlantic, Mediterranean and Black Seas with many other SPF of high ecological and economic importance [e.g. Atlantic horse mackerel (*Trachurus trachurus*), European sprat (*Sprattus sprattus*), European anchovy (*E. encrasicolus*), Mediterranean horse mackerel (*Trachurus mediterraneus*), round sardinella (*Sardinella aurita*) and bogue (*Boops boops*) among others] (Schickele et al., 2021). As these species have different environmental optima, the dominance of other SPF that co-occur with the European sardine could also be modified by

changeable environmental conditions (Guisande et al., 2004). By comparing our results with other projections, it is possible to conclude that the higher degree of overlapping between the European sardine and the European anchovy along continental shelves will be maintained towards the end of this century (Raybaud et al., 2017; Schickele et al., 2021). Adult sardines are morphologically better suited to capture smaller prey items than anchovies, and their diet generally does not overlap completely when inhabiting the same areas (Garrido and van der Lingen, 2014). Such pattern is confirmed by carbon and nitrogen isotopic signatures that suggest that prey and trophic position between these two species changes at regional and spatio-temporal scales (Chouvelon et al., 2014). However, projections show that larger-sized phytoplankton will experience more severe declines, leading to variation in resources availability and in the prey choice of a species, which may enhance competition between these two species in the future (Marinov et al., 2010; Bacha et al., 2017).

Global warming also promotes intensification of alongshore winds on the ocean surface and may lead to acceleration and intensification of coastal upwelling (Xiu et al., 2018). Upwelled or mixed water is rich in nutrients but also enriched in CO₂ and depleted in O₂. Thus, ocean acidification and oxygen depletion are expected to be highly dependent on changes in upwelling intensity (Xiu et al., 2018). Consequences of these processes include decreased biodiversity, decreasing biomass, shifts in species distributions, displacement or local extirpation. Sardines may also experience long and lasting hypoxic episodes during the reproduction stage, leading to the decreasing of eggs production and putative effects on recruitment (Dahlke et al., 2020). Most of these alterations are also expected to intensify in the future, leading to changes in primary and secondary productivity and forcing sardines to respond differently to the use of coastal habitats and different diets (Garrido et al., 2015). Likewise, the predatory pressure on sardines has changed and may continue to change markedly towards the future as new communities emerge due to latitudinal migration, leading to shifts in the top-down regulation of sardine stocks.

Global warming also induces alterations of hydrological cycles/river discharges, winds, ocean currents, stratification and acidification, affecting pelagic habitats and species distributions (often poleward), but SPF may have different constraints in their ability to respond to these shifts. However, the phenology of sardine spawning and primary/secondary production may evolve differently under climate change, potentially leading to seasonal mismatches, affecting mortality and recruitment (Fréon et al., 2009; Checkley et al., 2017). Eco-physiological limitations may also be pronounced if warming continues in the Mediterranean Sea, pushing sardines to “climatic refugees” likely to occur in the northern regions (Ben Rais Lasram et al., 2010), confirming the projections of our study. On the other hand, along the northeast Atlantic and Black Sea, the combination of warmer annual patterns and winter temperatures may allow sardines to overcome thermal constraints during spawning and recruitment (Dahlke et al., 2020).

Species' acclimation is expected to guarantee resilience and greater survival when climate change has little effect in environmental optima. When such conditions go beyond sardine's environmental optima range, acclimation may become weak to promote resilience (Anderson et al., 2013). Approximately 80 generations of sardine will occur between now and 2100 (Claireaux and Chabot, 2019). However, this number is relatively low, leading to uncertainties concerning whether sardines will adapt to these fast-changing climatic scenarios.

5. Conclusion and recommendations

A poleward shift in the centre of the distribution range of the European sardine is projected to gradually occur towards the end of this century along the coast of Norway, with a latitudinal expansion more prominent by 2100 under RCP 8.5, a pattern widely reported for other SPF. The environmental variables with highest explanatory power were sea surface temperature, distance to the nearest coast, sea

surface salinity and current velocity. The higher habitat suitability occurs especially in calmer waters (CVEL < 0.1 m s⁻¹) closer to the coast (<250 km from the nearest coast) where temperatures ranges between 11 °C and 22 °C, salinity between 17.3 (PSU) and 39.6 (PSU). It is calculated an expansion of 9.57% in the total distribution range of the European sardine by 2100 under RCP 8.5, while a prominent contraction of 19.31% is calculated in the Atlantic African Coast by 2050 under RCP 4.5. The responses of sardines to climate change scenarios seem to be mainly associated with shifts in environmental optima, likely influencing the suitability of spawning, recruitment and feeding habitats at regional scales. However, the effects of climate change on regional scales are often overlooked or misunderstood, leading to challenges in proper conclusions. Most species' distribution range will continue to exhibit high suitability between consecutive climatic scenarios, but local climatic variability [e.g. NAO, Atlantic Multidecadal Oscillation (AMO)] and fisheries (e.g. spatially-unbalanced fishing effort and density dependent processes) will continue to act in synergy with climate change putting pressure in sardine stocks and affecting the spatial dynamics of sardines towards the future. In this sense, the evaluation of historical datasets on the abundance/biomass of SPF landings and maximum sustainable yields, as well as the employment of fisheries and mass balance models under different climate change scenarios would be extremely important to fulfil some knowledge gaps regarding the future of population sizes. The availability of free access data of fisheries institutes is increasingly a necessity to the improvement in the quality and quantity of model projections of future environmental parameters to support a more sustainable management of these resources.

The combined effects of rising temperatures, O₂ depletion and acidification are expected to induce putative changes in metabolism and growth, energetic reserves, swimming ability and oxidative stress/damage. Additionally, unravelling signatures of selection in the context of changeable environments will help to understand more precisely whether SPF will be able to follow environmental optima and expand their distribution in the future or maintain viable populations in the impacted areas. Information about organismal putative responses to new climate conditions is needed to improve our capacity to predict climate impacts on sardines and other SPF. Therefore, the use of mechanistic SDMs is urged by the scientific community in order to consider the full range of processes shaping species distribution because individuals' occurrences will be conditional to the species' adaptive responses to climate change.

CRedit authorship contribution statement

André R.A. Lima: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Investigation. **Miguel Baltazar-Soares:** Conceptualization, Visualization, Writing – review & editing. **Susana Garrido:** Project administration, Funding acquisition, Writing – review & editing, Investigation, Validation, Data curation. **Isabel Riveiro:** Writing – review & editing, Data curation. **Pablo Carrera:** Data curation. **A. Miguel Piecho-Santos:** Writing – review & editing, Data curation. **Myron A. Peck:** Writing – review & editing, Investigation, Validation, Visualization. **Gonçalo Silva:** Project administration, Funding acquisition, Investigation, Supervision, Conceptualization, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.150167>.

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