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European small pelagic fish distribution under global change scenarios

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Abstract

The spectre of increasing impacts on exploited fish stocks in consequence of warmer climate conditions has become a major concern over the last decades. It is now imperative to improve the way we project the effects of future climate warming on fisheries. While estimating future climate-induced changes in fish distribution is an important contribution to sustainable resource management, the impacts on European small pelagic fish—representing over 50% of the landings in the Mediterranean and Black Sea between 2000 and 2013—are yet largely understudied. Here, we investigated potential changes in the spatial distribution of seven of the most harvested small pelagic fish species in Europe under several climate change scenarios over the 21st century. For each species, we considered eight Species Distribution Models (SDMs), five General Circulation Models (GCMs) and three emission scenarios (the IPCC Representative Concentration Pathways; RCPs). Under all scenarios, our results revealed that the environmental suitability for most of the seven species may strongly decrease in the Mediterranean and western North Sea while increasing in the Black and Baltic Seas. This potential northward range expansion of species is supported by a strong convergence among projections and a low variability between RCPs. Under the most pessimistic scenario (RCP8.5), climate-related local extinctions were expected in the south-eastern Mediterranean basin. Our results highlight that a multi-SDM, multi-GCM, multi-RCP approach is needed to produce more robust ecological scenarios of changes in exploited fish stocks in order to better anticipate the economic and social consequences of global climate change.

KEYWORDS

climate change, ecological niche, exclusive economic zone, range shift, species distribution models, uncertainties

Patrice Francour and Virginie Raybaud contributed equally to this work.

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1 | INTRODUCTION

European Small Pelagic Fish (SPF) species have a key economic and ecological role (Checkley et al., 2009; Fréon et al., 2005). SPFs are the main harvested fish group worldwide, representing between 20% and 30% of the global commercial landings, depending on yearly environmental fluctuations and fishing effort (FAO, 2011). These species accounted for 17% of the E.U. catches in 2015 (European Commission & DG-MARE, 2018) and up to 53% of the Mediterranean and Black Sea landings between 2000 and 2013, but most of them are significantly impacted by overfishing (FAO, 2016). They are also the main prey of most piscivorous fishes, cetacean and seabirds (Bachiller & Irigoien, 2015; Cury et al., 2011), transferring organic matter from the base of the food web to upper trophic levels (Cury, 2000). Abundantly found in upwelling ecosystems (Cury, 2000), SPFs cover a wide range of regions, therefore overlapping with a large range of environmental conditions (Checkley et al., 2009). European Seas, especially the Mediterranean Sea host a high diversity of SPFs, including both temperate-cold and temperate-warm water species (Ben Rais Lasram et al., 2010; Coll et al., 2010). In the context of climate change, a potential range shift of SPFs may induce (a) major economic and social consequences—especially for countries that rely on fisheries for protein supply (Tacon & Metian, 2009)—and (b) deep changes in ecosystem and food web functioning (e.g. Chaalali et al., 2016). Predicting climate-induced range shifts of these largely harvested species is therefore essential for sustainable resource management and food security (Cheung et al., 2013).

Contemporary fisheries management is mainly based on stock assessment models (e.g., Methot & Wetzel, 2013) that estimate populational parameters (e.g., recruitment, abundance and sustainable harvesting rate) for a given fish stock. Over the last decade, several modelling procedures were developed to include environmental variability in fish stock assessment by focusing on the environment–recruitment relationship (e.g., MacKenzie et al., 2008; Tommasi et al., 2017). Considering environmental uncertainty in stock recruitment is a preliminary step towards a possible integration of global climate change impacts on stock dynamics, however (Edgar et al., 2019; Lee et al., 2018; Punt et al., 2014). In the context of ecosystem-based fisheries management (EBFM), several modelling techniques have been developed to integrate trophic, environmental and societal factors (e.g., Romagnoni et al., 2015; Smith et al., 2015) in order to thoroughly evaluate the status of fish stocks (Forrest et al., 2015). One caveat is that robust stock assessment or EBFM requires data-intensive models (Hilborn, 2011; Pauly, 2000; Wetzel & Punt, 2011), an approach not yet applicable to routine use at large-scale and long-term (Edgar et al., 2019). There is therefore an urgent need for basin-scale long-term management plans that include the combined effects of fishing pressure and climate change, for effective conservation of SPFs and sustainable fisheries management (Faillietaz et al., 2019).

Over the last decades, species distribution modelling has been intensively used to project the effects of past and future climate change on the distribution of suitable habitat for species of conservation concern. (Beaugrand et al., 2019; Bellard et al., 2013; Cheung

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et al., 2009). Species Distribution Models (SDMs), statistical tools based on the niche-biotope duality (Colwell & Rangel, 2009; sensu Hutchinson, 1978) to conceptualize and investigate biogeographical patterns in relation to environmental conditions, are a popular way to assess which species will be under most threat in a near future and/or which regions will be the most impacted by a reorganization of communities (Sinclair et al., 2010). While stock assessments are based on parameters related to stock dynamics (e.g. spawning biomass, recruitment, growth, mortality), these techniques model the ecological niches of species using (a set of) environmental conditions where the species has been observed. The modelled niche can then be used to project potential distribution of species under different environmental conditions on a broad temporal and spatial scale (Colwell & Rangel, 2009), allowing the investigation of potential future range shifts. The capacity of SDMs to produce long-term, large-scale and comparable (i.e. between species, regions or management zones and periods) future projections is of major importance for species conservation and management (Hollowed et al., 2013). The main objective of SDM-based approaches is the production of robust scenarios of future species distribution for reliable management and conservation perspectives (Cheung, Frölicher, et al., 2016; Goberville et al., 2015; Stock et al., 2011) and best practices recommend multimodel ensemble projections (Buisson et al., 2010), that is the use of a large set of SDMs and climate models (e.g. General Circulation Model, GCM; Wilby & Dessai, 2010). Most SDM applications on European SPFs did not include long-term distributional range projections at the regional or European scales (Brown et al.,

2006; Maynou et al., 2020; Sabatés et al., 2006; Tsikliras, 2008), however, and a few studies addressed this challenge at the European scale (Lenoir et al., 2011; Raybaud et al., 2017) but only for a few SPFs.

Our study aims to address this gap in knowledge by examining (a) long-term and (b) large-scale distributional range projections under different climate change scenarios (IPCC Representative Concentration Pathways; RCP) for a set of seven largely harvested European Small Pelagic Fish (SPF) species of major ecological and economic importance (Checkley et al., 2009; Fréon et al., 2005): Atlantic horse mackerel (*Trachurus trachurus*, Carangidae), European pilchard (*Sardina pilchardus*, Clupeidae), European sprat (*Sprattus sprattus*, Clupeidae), European anchovy (*Engraulis encrasicolus*, Engraulidae), Mediterranean horse mackerel (*Trachurus mediterraneus*, Carangidae), round sardinella (*Sardinella aurita*, Clupeidae) and bogue (*Boops boops*, Sparidae). Based on the contemporary SPFs distribution retrieved from Schickele et al. (2020) and using a multi-SDM, multi-GCM and multi-RCP approach, we investigated future potential range shifts of these largely harvested species at the European scale. To evaluate expected changes at a manageable level (Zeller et al., 2016), we then aggregated our results per Exclusive Economic Zones (Flanders Marine Institute, 2019; EEZ; U.N. General Assembly, 1982; General Assembly, 1982) and discussed possible economic consequences of climate change on the allocation of fishing effort.

2 | MATERIAL AND METHODS

2.1 | Description of the modelling framework

We used the future Environmental Suitability Index (ESI; i.e. spatialized index ranging from 0 to 1, based on suitability estimated from

contemporary 1990–2017 conditions) of the seven SPFs, retrieved from Schickele et al. (2020). This recently developed modelling framework includes (a) a spatial and environmental sampling bias reduction, (b) the use of the convex hull method to generate pseudo-absence, (c) a numerical and ecological evaluation of model outputs and (d) the quantification of uncertainties associated to the selection of SDMs. Environmental parameters used to assess contemporary species distribution (Table 1), the calibration procedure and how we selected the most accurate models (Table 2) are therefore only briefly discussed in this section.

Contemporary (1990–2017) distributions of SPFs were obtained using an ensemble forecasting framework that select—among eight different statistical algorithms—the models that best reproduce the observed spatial distribution of each species (Araújo & New, 2007; Buisson et al., 2010; Pearson et al., 2006). To account for the source of uncertainty related to the choice of a given species distribution model, we considered seven algorithms computed from the Biomod2 package (Thuiller et al., 2009, 2016): (i) Generalized Linear Model (GLM), (ii) Generalized Additive Model (GAM), (iii) Generalized Boosting Model (GBM), (iv) Artificial Neural Network (ANN), (v) Flexible Discriminant Analysis (FDA), (vi) Multiple Adaptive Regression Splines (MARS) and (vii) Random Forest (RF), plus (viii) the Non-Parametric Probabilistic Ecological Niche (NPPEN) model from Beaugrand et al. (2011). We therefore considered a large range of modelling techniques (see details and references in Supplementary Material 1), including regression-based (i.e., GLM; GAM, MARS), machine learning (i.e., GBM, ANN, RF, FDA) and profile (i.e., NPPEN) methods.

To model each of the seven contemporary distribution, we first constructed an ecologically and statistically meaningful set of environmental parameters by calculating their respective explicative power using a bootstrap method (Leroy et al., 2014). The following environmental parameters were tested: (a) mean annual Sea Surface Temperature (SST), (b) annual SST range, (c) monthly SST variance, (d)

TABLE 1 Description of the environmental parameters considered in the ensemble model procedure and corresponding references

| Environmental parameter | Contemporary | Future |
|--|---|---|
| Bathymetry: spatial seafloor depth (m) | Global seafloor topography (Smith & Sandwell, 1997) | |
| Distance to coast: distance to the nearest coast (km) | NASA Goddard Space Flight Center (2009) (https://oceancolor.gsfc.nasa.gov/docs/distfromcoast/) | |
| SSS: sea surface salinity | Levitus' climatology (Levitus, 2011) completed with ICES data (http://www.ices.dk/) | |
| Log_PP: log-transformed sea surface primary production | IPSL (Dufresne et al., 2013; Hourdin et al., 2013), MPI (Giorgetta et al., 2013; Stevens et al., 2013), CNRM (Voldoire et al., 2013), HadGEM (Jones et al., 2011) and GISS (Schmidt et al., 2014) models. | |
| SST: mean annual sea surface temperature (°C) | AVHRR Very High Resolution Radiometer (Casey et al., 2010) | IPSL (Dufresne et al., 2013; Hourdin et al., 2013), MPI (Giorgetta et al., 2013; Stevens et al., 2013), CNRM (Voldoire et al., 2013), HadGEM (C. D. Jones et al., 2011) and GISS (Schmidt et al., 2014) models. |
| SSTr: mean annual sea surface temperature range (°C) | | |
| SSTvar: mean monthly sea surface temperature variance (°C) | | |

Note: Empty cells stands for parameters that we considered as constant over time in our simulations.

TABLE 2 Environmental parameters used to model each SPF species. Parameters are ranked according to their explanatory power.

| Species | Environmental parameters |
|------------------------------|--------------------------|
| Mediterranean horse mackerel | SST, SSTvar, log_PP |
| Atlantic horse mackerel | SST, SSTvar, log_PP |
| European pilchard | SST, SSTr, SSS |
| Round sardinella | SST, SSTr, log_PP |
| European sprat | SST, SSTr, log_PP |
| European anchovy | SST, SSTvar, SSS |
| Bogue | SST, SSTr |

Primary Production (PP), (e) mean annual Sea Surface Salinity (SSS), (f) bathymetry and (g) distance to coast. To reduce model over-parameterization, bathymetry and distance to coast were included by means of a hierarchical filtering approach (Hattab et al., 2014). Because SPFs are strictly planktonophagous species and depend on coastal ecosystems for their early lifestages, they are distributed in the epipelagic zone (i.e., bathymetrical area where photosynthesis takes place) and neritic areas only (Checkley et al., 2009). Geographical cells were therefore considered as suitable for SPF only if suitable environmental conditions were found in neritic areas (i.e., >50 km from the coast, independently of depth) or in low-bathymetric (i.e., between 0 and 300 m depth) oceanic regions (Schickele et al., 2020). To prevent from multicollinearity and unnecessary model complexity (Dormann et al., 2007), only one parameter from clusters of correlated parameters (Pearson's r correlation >0.7) was retained (Leroy et al., 2016).

For each species and combination of environmental parameters, the calibration data set was then filtered in an environmental space to reduce sampling bias as much as possible (Varela et al., 2014). Pseudo-absences were then generated in the same filtered environmental space outside the corresponding convex hull of observation (i.e. considered as a proxy of environmental suitable conditions; Cornwell et al., 2004; Getz & Wilmsers, 2006), excluding the 2.5 and 97.5 percentiles. Finally, we used the Continuous Boyce Index (CBI; Hirzel et al., 2006)—the appropriate evaluation metric for a presence/pseudo-absence calibration data set—to evaluate the robustness of model outputs (see discussion in Leroy et al., 2018): each model with a CBI value over 0.5 was retained (e.g., Faillettaz et al., 2019). Finally, we calculated the response curve of each environmental parameters by keeping other parameters at their mean values for modelled species, using the evaluation strip method (Elith et al., 2005). The ecological realism and relevance of the models were then corroborated by an expert-based inspection/validation of each response curve in order to discard spurious responses to environmental factors (e.g. bimodal response to temperature).

2.2 | Future scenarios and General Circulation Models (GCMs)

To project the future ESI of each species, we considered five GCMs retrieved from the 5th phase of the Coupled Model Intercomparison Project (CMIP5; Table 1). Future SST and PP were averaged for three different periods to cover: (i) short-to-medium (2030–2039), (ii) mid-century (2050–2059) and (iii) late-century (2090–2099) range time-scales. To cover the range of year-2100 radiative forcing values found in the literature, that is from 2.6 to 8.5 W/m², we used three RCPs scenarios: (a) the optimistic peak and decline (RCP2.6), the intermediate “stabilization” (RCP4.5) and the “business as usual” (RCP8.5) scenarios (Meinshausen et al., 2011; van Vuuren et al., 2011). We considered SSS as constant over time because its temporal variance is negligible in comparison with its spatial variance (Dickson et al., 1988; Faillettaz et al., 2019; Le Marchand et al., 2020). While the spatial variance of SSS allowed us to discriminate marine from brackish waters (e.g., from 35 to 15 between the west and the east of the Danish strait), its temporal variance is negligible: for the period 2016–2065, Lavoie et al. (2019) report expected salinity trends of +0.063 per decade at the maximum, a value comparable to the rise of SSS observed since 1950 (Durack et al., 2012).

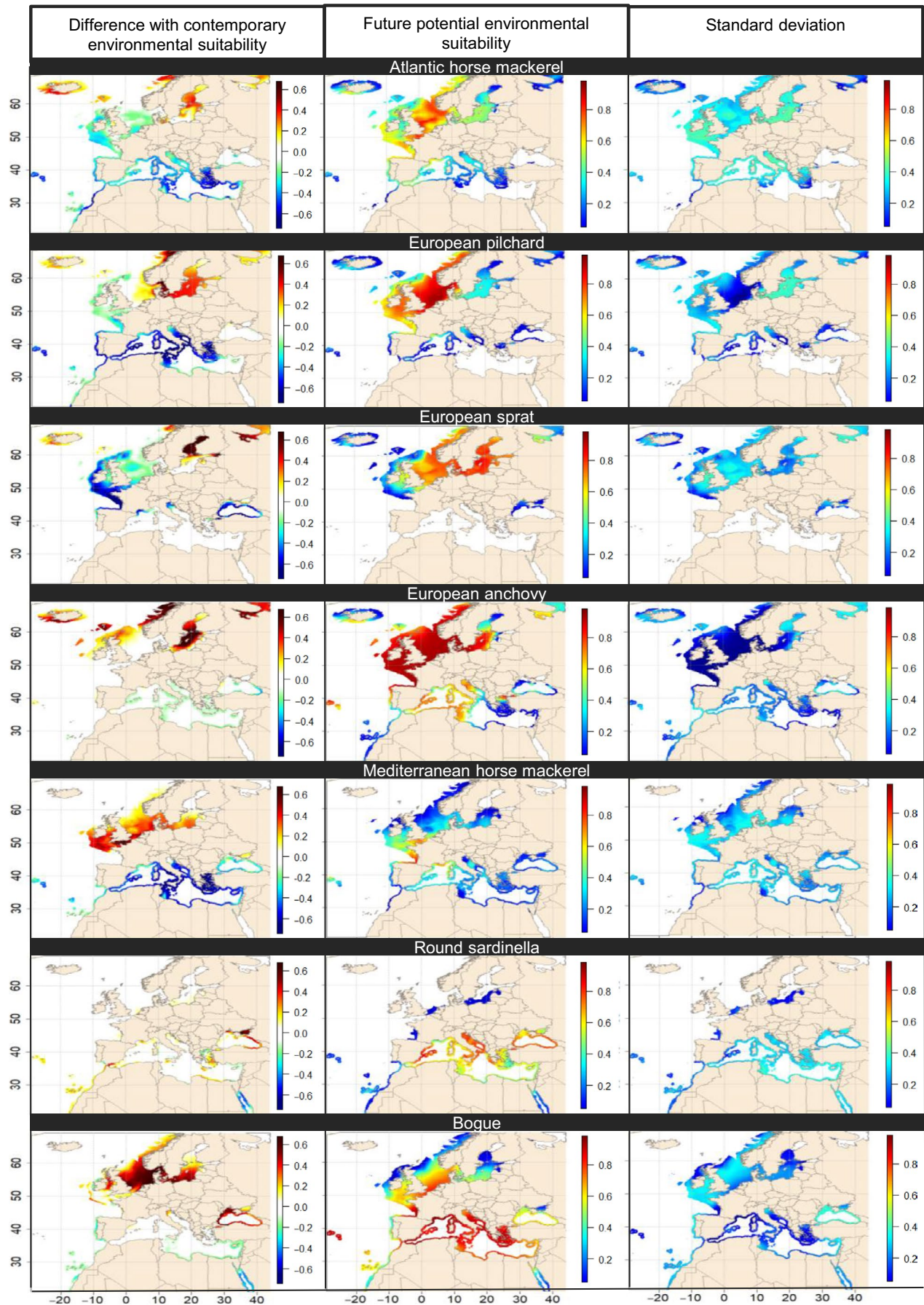
2.3 | Pre-treatment of future temperature data

Because temperature-related parameters (Table 1) were retrieved from both observation-based (i.e. for the contemporary period) and GCM-based data (i.e. for the three future periods), our projections may be altered. To assess possible bias, we performed Taylor diagrams (Taylor, 2001) using a common time period (i.e. 2006–2017) to estimate the consistency between current and future climate data (Supplementary Material 2): the correlation coefficient, the root-mean-square difference (RMSD) and the standard deviation (SD) difference were calculated for each temperature-related parameter (Table 1). For each GCMs, RCPs, and geographical cell, we therefore estimated the difference between the two datasets and corrected the model-based temperature data accordingly. This process, already applied by Péron et al. (2012) and Cristofari et al. (2018), ensured (a) a perfect correlation (Pearson coefficient $r = 1$), (b) no RMSD and (c) the same SD between the two data sets for a common period. Results from the correction procedure and corresponding anomalies are shown in Supplementary Material 3.

2.4 | Projection of future environmental suitability

Projections of ESI values were carried out at spatial resolutions suitable for either ecological analyses, that is on a 0.1° × 0.1° spatial grid obtained from a linear spatial interpolation (Goberville et al., 2015), or

FIGURE 1 Left panels: maps showing the differences in Environmental Suitability Index (ESI) values between 2090–2099 under scenario RCP8.5 (Representative Concentration Pathway) and 1990–2017. Middle panels: modelled ESI of the seven small pelagic fish species for the period 2090–2099 under scenario RCP8.5. Right panels: standard deviation based on 50 simulations per algorithm (i.e., 10 cross-validation runs × 5 general circulation models per algorithm). Note that the figure appears in colour in the online version only



policy application, that is in each Exclusive Economic Zone (Zeller et al., 2016). Among the existing fishery zones, we chose to focus on EEZs—area stretching from the coastline out to 200 nautical miles over which a country has special rights regarding the use of marine resources—as they are (a) basic units for fisheries management (e.g. attribution of maximum allowed catches by EEZs) and conservation perspectives (Allison et al., 2009; Cheung, Jones, et al., 2016; Zeller et al., 2016), (b) at a spatial resolution well-adapted for biogeographic research (Claus et al., 2014) and (c) commonly used in the literature to project the socioeconomics consequences of climate change on fisheries (Cheung, Jones, et al., 2016; Sumaila et al., 2011, 2015). The stock assessment areas considered for SPFs (<http://www.ices.dk/>) overlap with the EEZs of the European Seas (Flanders Marine Institute, 2019) as the European Atlantic façade and enclosed seas do not include high sea areas (i.e. outside EEZs). In 2014, 35% of the SPFs were captured by fishing fleet operating outside the EEZ of their respective countries (e.g. Denmark, Poland, Spain, Sweden; Supplementary Material 4), indicating the importance of international fishing agreements within the European Union (i.e. the latest available data; SAUP, 2020). Here, the mean ESI value was calculated by aggregating, within each EEZ, the $0.1^\circ \times 0.1^\circ$ geographical cells retained after application of the hierarchical filtering approach (see 2.1.).

2.5 | Uncertainties related to future projections

The selection of a GCM may greatly influence the projected distributions of a species (Goberville et al., 2015): GCMs may diverge for technical or parameterization reasons, may simulate ocean-atmosphere processes in different ways or may vary due to their initial spatial resolution (Beaumont et al., 2008; Goberville et al., 2015; Wiens et al., 2009). Because of their wide variety and complexity, and because we cannot identify a model that performs better than another (Martinez-Meyer, 2005), it is essential to consider a full range of GCMs to examine the full range of potential future species distributions (e.g. Friedlingstein et al., 2013; Shepherd, 2014). In our study, we adapted the ensemble modelling for future projections: for each set of environmental parameters and each statistical algorithm, five GCMs and three RCP scenarios were considered to project future environmental suitability. For a given period and for each RCP, we performed 10 cross-validation runs, leading to the production of 50 simulations ($5 \text{ GCM} \times 10 \text{ cross-validation runs}$) per statistical algorithm. We then computed the corresponding SD among SDMs (i.e. the variability related to the calculation of the ecological niche) and GCMs (i.e. the intrinsic variability linked to the climate system and expected climate conditions) to fully explore the uncertainty related to future environmental suitability projections (Goberville et al., 2015).

3 | RESULTS

3.1 | Future environmental suitability

Here, we present for each of the seven SPFs, the projected ESIs in the spatial domain ranging from 10 to 70°N and –30 to 45°E. Species

distributional range under RCP8.5 conditions for the late 21st century (2090–2099) are detailed in Figure 1 while other RCPs and periods are provided in Supplementary Material 5.

3.1.1 | Temperate-cold water species

Strong northward shifts in the distribution of ESI are expected for “temperate-cold” water species (Figure 1; i.e. Atlantic horse mackerel, European pilchard, European sprat and European anchovy). While ESI values increased along the Norwegian and Baltic seas between +0.2 and +0.6—especially for European anchovy (+0.6)—we forecasted a decrease in ESI values that ranged from –0.2 to –0.6 along the Mediterranean Sea, the Bay of Biscay and the English Channel, but to a lesser extent, except for European anchovy. We projected a potential local extinction (ESI values <0.05) in the south-western Mediterranean Sea for all temperate-cold water species, in particular for European sprat that may face unsuitable environmental conditions in the whole Mediterranean Sea. With ESI values above 0.4, the distributional centre of the four temperate-cold species may range from the North Sea to the southern Norwegian Sea by the end of the century. For all temperate-cold species, we projected the amplitude of the changes in ESI values to increase through time and when the intensity of the radiative forcing increases (Supplementary Material 5). The decrease in ESI value (maximum value of –0.6) in the Mediterranean Sea, that may potentially lead to local extinctions by the end of the century under RCP8.5 conditions, may be limited under scenario RCP2.6 with a reduction between –0.1 (2030–2039) and –0.4 (2090–2099). The potential range expansion of temperate-cold species in the Baltic and Norwegian seas is expected to increase by +0.4 for all RCPs and periods. The geographical expansion may decrease for scenario RCP2.6, however.

3.1.2 | Temperate-warm water species

Expected changes in ESI values for “temperate-warm” water species (Figure 1; i.e. Mediterranean horse mackerel, round sardinella and bogue) were variable with species-specific patterns. No major changes in ESI values were expected for round sardinella but we showed a potential increase in the Black Sea (between +0.4 to +0.6). For Mediterranean horse mackerel and bogue, we projected an important increase in ESI values (between +0.2 and +0.6) in northern regions (e.g. in the North Sea) and a moderate to high decrease in ESI values in the Mediterranean Sea for both species (ranging from –0.2 to –0.6 for the Mediterranean horse mackerel and about –0.2 for the bogue). We expect a range expansion towards the Norwegian Sea for both species. With ESI values ranging from 0.6 to 0.8, our models also projected a distributional shift of Mediterranean horse mackerel towards the Bay of Biscay. For all temperate-warm species, projected changes in ESI values may increase in amplitude over time, when the magnitude of the warming increases (Supplementary Material 5). If global warming is small (RCP2.6), the decrease in ESI

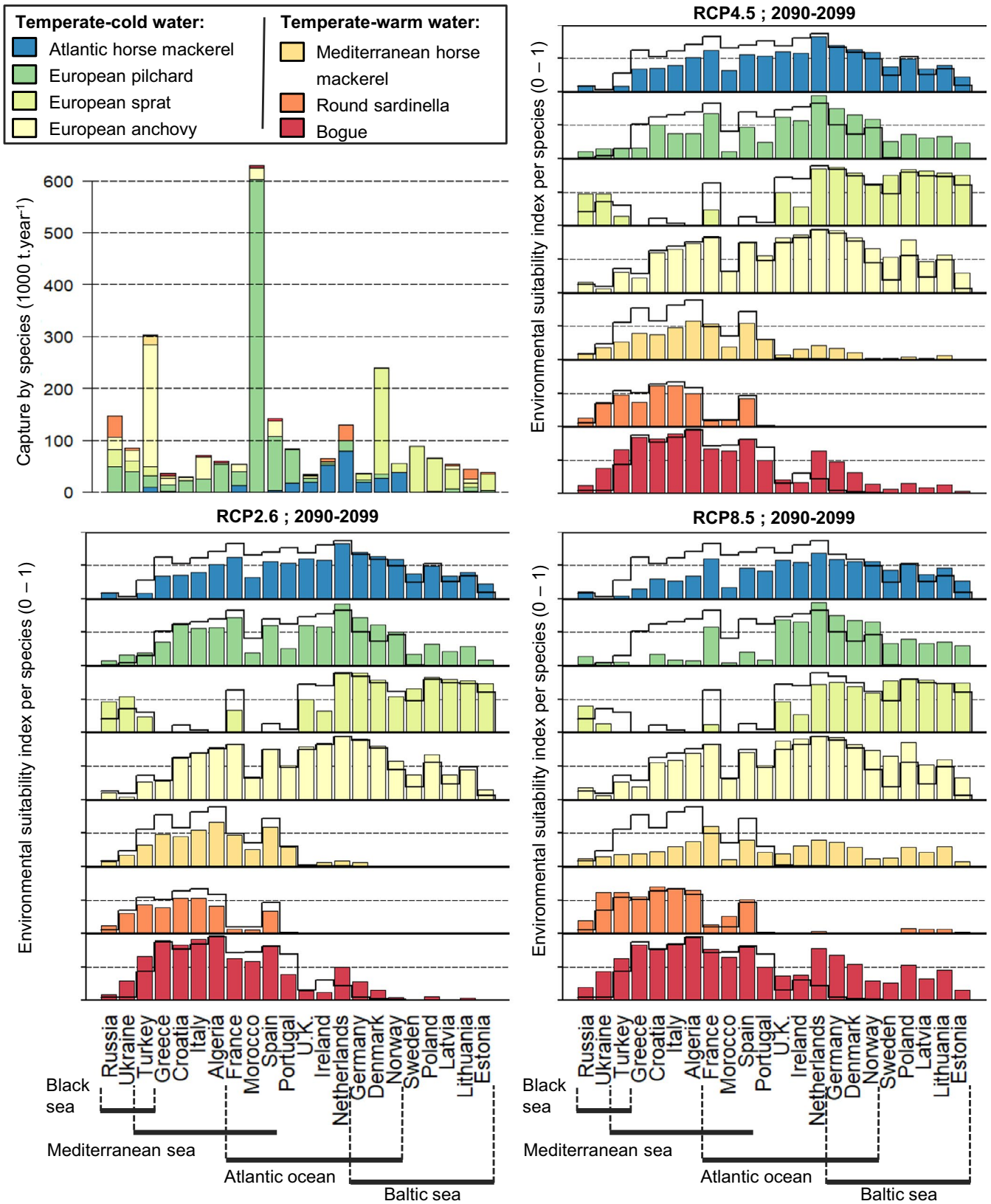


FIGURE 2 Changes in the Environmental Suitability Index (ESI) per Exclusive Economic Zone (EEZ) and species in comparison to their fish landings. From top to bottom and left to right: the averaged (1990–2017) landings per species and EEZ, the ESI values per EEZ for the decade 2090–2099 for Representative Concentration Pathways (RCPs) 2.6, 4.5 and 8.5. Bar plots for ESI are scaled from 0 to 1, the dashed lines correspond to an ESI value of 0.5 and the full line spectre corresponds to the ESI values per EEZ for the period 1990–2017. Countries with catches under 20,000 metric tons are not shown. Note that the figure appears in colour in the online version only

values may range between -0.3 (2030–2039) and -0.4 (2090–2099) for Mediterranean horse mackerel in the Mediterranean Sea. By limiting global warming to $+2^{\circ}\text{C}$ (i.e. RCP2.6), an expansion of Mediterranean horse mackerel and bogue may be negatively affected, despite a maximum increase in ESI value of about $+0.4$ for all RCPs and periods.

3.1.3 | Uncertainties in expected environmental suitability

For all SPFs, our projections showed only weak variations, with mean SD ranging from 0.1 to 0.4 (Figure 1). This demonstrates the spatial convergence of our simulations based on a multi-SDM and multi-GCM framework. For temperate-cold species, we projected low SD values (0.1 in average) in geographical cells where we projected low (<0.2) or high ESI values (>0.8). This indicates that our simulations converged towards either potential local extinctions (e.g. in the south-east Mediterranean) or shifts in the distribution centre of SPFs (e.g. European anchovy in the Norwegian or Baltic seas). Our models showed higher (about 0.4) SD values in geographical cells that correspond to intermediate ESI values, suggesting a lower confidence in moderate range expansion (e.g. in the Norwegian Sea). For all temperate-warm species, we projected similar results between SD and ESI values. Because the regions of low and high ESI values (<0.2 and >0.8 respectively) are less emphasized for temperate-warm species, our models showed less convergence in comparison with temperate-cold species, except for bogue in the Mediterranean Sea (SD values <0.2). The overall, low SD values (<0.4) expected for late-century projections, confirms that our models showed comparable estimates of future environmental suitability of SPFs, including projected local extinctions.

3.2 | Climatic range shifts between Exclusive Economic Zones

Here, we explored the consequences of potential distribution shifts at the scale of EEZs (Figure 2), manageable units commonly used for projecting the possible socioeconomic impacts of climate change on fish stocks (Cheung, Jones, et al., 2016). For each EEZ and SPF, we calculated the total value of landings for the period 1990–2017 (Figure 2, top-left panel) and confronted observed landings with potential changes in ESI by the end of the century for RCP2.6, RCP4.5 and RCP8.5 (Figure 2, bottom and right panels).

3.2.1 | Temperate-cold water species

The four temperate-cold water species are of major importance in European fisheries (FAO, 2020), especially along the Atlantic façade (c.a. 50,000 t/year per EEZ), except for European sprat that is largely harvested in the Baltic Sea (Figure 2). These species are currently

mostly captured in regions where we found high ESI values over the period 1990–2017 (Figure 2; Schickele et al., 2020). Our models projected a decrease in the ESI values in southern and western Europe (Figure 2). While the Mediterranean EEZs showed a decrease in mean ESI values from 0.48 (1990–2017) to 0.39 (RCP2.6) or 0.24 (RCP8.5), we projected an increase in the EEZs of the Baltic Sea from 0.43 (1990–2017) to 0.51 (RCP2.6) or 0.59 (RCP8.5; Figure 2). Our results highlight that a potential mismatch between current fisheries areas and changes in the species climatic range of temperate-cold water species could occur by the end of the century; a major decrease in ESI values was for example expected in Morocco and Turkey (Figure 2), that is where species are currently abundantly captured. In contrast, we projected that ESI values may remain steadily constant over the current century in Denmark, the main fishing area for European sprat (Figure 2). At the European scale, the absolute variation of ESI values (i.e. relative to 1990–2017) was expected to range from 22% (RCP2.6) to 33% (RCP8.5), suggesting a potential reallocation of temperate-cold water species population in fisheries management zones.

3.2.2 | Temperate-warm species

In European seas, the three temperate-warm water species are less harvested than temperate-cold water species (FAO, 2020) (Figure 2, top-left panel). For all species except round sardinella, we projected important late-century changes in the ESI values at the EEZs scale. While we forecasted a moderate decrease in ESI values—from 0.62 (1990–2017) to 0.54 (RCP2.6) and 0.53 (RCP 8.5)—in the EEZs of the Mediterranean Sea (RCP8.5; Figure 2), our simulations revealed a moderate to high increase in EEZs of the Atlantic façade, the Black Sea and the Baltic Sea. The Baltic Sea EEZs are likely to undergo an important expansion of temperate-warm species, with changes in ESI values from 0 (1990–2017) to 0.03 (RCP2.6) or 0.22 (RCP8.5), and so a major extension of the northern boundary of temperate-warm species (Figure 2). In contrast, we expect lower ESI values throughout their distributional ranges, especially for Mediterranean horse mackerel. At the European scale, the absolute variation in ESI (i.e. relative to 1990–2017) is predicted to range from 30% (RCP2.6) to 51% (RCP8.5). Our simulations therefore suggest a possible major reallocation of the suitable environment for temperate-warm species along European EEZs.

4 | DISCUSSION

4.1 | Ecological impact of climate change on Small Pelagic Fishes

For all climate scenarios and all SPFs—except round sardinella—we projected substantial climate-induced northward distributional range shifts (Figure 1, Supplementary Material 5; Dulvy et al., 2008; Jorda et al., 2020; Perry et al., 2005). The narrow aerobic tolerance of

species embryonic and reproduction lifestages—under direct influence of SST—is the main limiting factor of the physiological activity, growth, and survival of SPFs (Dahlke et al., 2020; Peck et al., 2013). The projected decrease in ESI value in the Mediterranean Sea, as a response of the expected increase in temperature, may be explained by a limitation of eco-physiological processes (Dahlke et al., 2020) that hinders the survival and/or development of SPFs (Lehodey et al., 2006; Perry et al., 2005; Torri et al., 2018). If warming continues in the Mediterranean Sea (Supplementary Material 3), SPFs may experience hypoxia during their reproduction stage (Dahlke et al., 2020), leading to lower egg production rates, with putative effects on recruitment, and a bottleneck effect towards northern regions of the Mediterranean Sea (Ben Rais Lasram et al., 2010). The combination of warmer annual and winter temperature in northern Europe and the Black Sea rather may allow SPFs to overcome thermal constraints during reproduction and development, with positive effects on egg quality (Dahlke et al., 2020). While sea water salinity may influence the specific gravity of marine pelagic fish eggs, that is their vertical distribution in the water column, egg size of SPFs—that has a fundamental impact on the capacity of young larvae to be active, grow, and survive—is under direct influence of SST (Huret et al., 2016; Peck et al., 2013; Torri et al., 2018). SPFs are planktonic feeders (Bachiller & Irigoien, 2015) which depend on high productive areas such as the gulf of Gabès or the eastern North Sea during early development (Rijnsdorp et al., 2009). Despite the projected warming in the Mediterranean Sea, temporal changes in primary production may remain negligible in comparison with its spatial variance: using a multimodel approach, Macias et al. (2015) report a slight increase in primary production of about 9.5 mmol N/m² over the period 2015–2095. This supports why primary production did not greatly influence our projections. At an ecosystem scale, SPFs have a pivotal role (Chaalali et al., 2016) in marine food webs, contributing to carbon fluxes from lower trophic level to top predators (Cury, 2000). Projected distributional range shifts—and potential ensuing changes in abundance patterns (Helaouet & Beaugrand, 2009; Kulhanek et al., 2011; VanDerWal et al., 2009)—may deeply modify the Mediterranean or Baltic seas ecosystems through trophic cascading effects on the upper trophic levels which feed on these species, including negative effects on their fisheries (Maynou et al., 2014). This climatic resilience-related issue may be assessed through the development and adaptation of ecosystem management and protection strategies (Giakoumi et al., 2017; e.g. McLeod et al., 2009), in regions or for species (e.g. SPFs) identified as sensitive to climate-induced changes (e.g. the Mediterranean Sea; Figure 2).

4.2 | Management and economic implications

While fishing has expanded into the high seas over the last decades as a result of an increasing demand for fish and the overexploitation of coastal waters (Sumaila et al., 2015), quantifying changes in the allocation of fisheries catches by maritime country and within EEZ waters allows to focus on a spatial scale that is politically and

economically viable (Cheung, Jones, et al., 2016; Zeller et al., 2016). Depending on the EEZ, SPFs may experience high fishing mortalities, especially in the Mediterranean Sea (i.e. twice the maximum sustainable yield; FAO, 2016), with putative negative impacts on species growth, reproduction and stock production (Brander, 2007; Fréon et al., 2005; Lehodey et al., 2006). In our study area, 65% of the SPFs were captured in 2014 by fishing fleets originating from the same EEZ (Supplementary Material 4), mostly low to medium size and coastal fishing vessels (FAO, 2016; SAUP, 2020). In comparison, European EEZs may experience a variation of suitable environmental conditions for SPFs up to 51% (Figure 2). These potential upcoming changes in fishing ground location and the magnitude of impacted vessels may lead to (a) a redefinition of the European distribution of SPF stocks, (b) allocate fishing effort (i.e. licenses, number of boats) in a way that explicitly incorporate the influence of climate change on SPF stocks and (c) design new international fishing agreements in order to allow fishing fleets to operate in areas outside their EEZs (Gaines et al., 2018; Link et al., 2011; e.g. based on historical fisheries; Perry et al., 2010). We argue that basing fisheries management strategies—such as a progressive and precautionary adaptation of fishing fleet (e.g. gear, target or quotas; Grafton 2010)—on an ensemble of long-term ecological scenarios that take into account projections of climate change effects at the scale of manageable units (i.e. EEZ), is a valuable information to mitigate the unsustainability of marine fisheries (Lotze et al., 2019). The vulnerability of marine countries depends on the state of their fishery (Barange et al., 2014; Sumaila et al., 2011): local fisheries (e.g. Morocco, Turkey) may be less resilient than long-range fisheries (e.g. Denmark; Supplementary Material 4) to a climate-induced range shift on their primary target (i.e. SPFs). Our projections at the scale of EEZs may therefore serve as a support for future socioeconomic research (e.g. Allison et al., 2009; Badjeck et al., 2013).

4.3 | Perspectives on modelling small pelagic fisheries

Despite their popularity, SDMs have inherent limitations—depending on their application context—such as the assumption of niche conservatism (Peterson & Soberón, 2012) and the failure to integrate species interactions or dispersal processes (Araújo & Guisan, 2006). While recent advances in species distribution modelling proposed to overcome such shortcomings (e.g. dispersal constrained SDM; Boulangeat et al., 2012; e.g. joint-SDMs; Harris, 2015), most of these ecological processes are mainly associated with local changes (Beaugrand & Kirby, 2018). These perspectives are at the cost of the amount of data needed to calibrate the models which can impede their broad scale-applicability, one of the main strength of SDM (Marmion et al., 2009). Based on our multi-GCM, multi-SDM and multi-RCP approach that integrated climate uncertainty (Friedlingstein et al., 2013; Goberville et al., 2015; Shepherd, 2014) and to contribute to increase the probability of success in fishery management strategies (Jones et al., 2012), we

encourage further research in the regions that we have identified as the most vulnerable, such as the Mediterranean Sea. The whole Mediterranean Sea ecosystem, including highly impacted regions (Bănară et al., 2013; Hattab et al., 2013; Piroddi et al., 2015), has been extensively studied over the last decades, and it is now well documented that changes in small pelagic populations—due to fishing or natural drivers—will strongly alter ecosystem structure and functioning (Palomera et al., 2007). Considering results from SDMs in combination with ecosystem models for fisheries management will help to better anticipate the consequences of climate-induced distributional shifts in small pelagic fish on the whole ecosystem (Chaalali et al., 2016). The need is urgent as many countries in the Mediterranean Sea are directly or indirectly dependant on activities that involve exploitation of marine fish resources (Selig et al., 2019).

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTION

VR and PF conceived and supervised the study. AS, VR and EG collected the data. BL provided the initial modelling framework. AS performed the numerical analysis. GB, BL, TH, EG and VR helped in the modelling process. AS wrote the first draft. All authors made substantial contributions to the successive versions of the manuscript.

DATA AVAILABILITY STATEMENT

These data were derived from the following resources available in the public domain: the Ocean Biogeographic Information System Mapper (OBIS, <http://www.iobis.org/mapper/>), the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/>) and Fishbase (<http://www.fishbase.org/>). Supplementary information on the data that support our findings is available in: Schickele et al. (2020). Modelling European small pelagic fish distribution: Methodological insights. Ecological Modelling 416: 108902

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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