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Fish distribution shifts due to climate change in the Northeast Atlantic: Using a hierarchical filtering approach on marine-estuarine opportunist species

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ABSTRACT

Marine-estuarine opportunist (MEO) species are fish that occur in the continental shelf and use estuaries and/or shallow coastal areas as nurseries. These commercially important resources are facing significant environmental modifications caused by direct and/or indirect anthropogenic climate change effects. In this study, we investigated the directionality and the magnitude of the distribution shifts (i.e., range size, gravity centroids, and margins) in marine environment suitability for six main MEO fish species within the Northeast Atlantic expected for the end of the 21st century. In the framework of this study, we have distinguished ‘sub-boreal’ from ‘sub-tropical’ species. The ‘hierarchical filters’ concept was adopted for modelling the potential species distributions and combined the predictions of i) a bioclimatic model with ii) a habitat model. The bioclimatic model is based on large-scale and time-variant variables while variables of the habitat model are fine-grained and time-invariant. Two Intergovernmental Panel on Climate Change (IPCC) scenarios are tested: an intermediate (SSP2-4.5) and a pessimistic one (SSP5-8.5). We applied this framework using international databases of biodiversity occurrences, ensemble forecasting producing consensual predictions, and innovative indices of distribution shifts. A visible north-westward shift was predicted for all six species in our study area. However, the northward expansion was greater for ‘sub-tropical’ than for ‘sub-boreal’ species due to faster gravity centroid displacement shifts and faster margins shifts. These range shifts may lead to major ecological impacts (e.g., changes in recruitment to estuarine and coastal nurseries, as well as changes in spawning grounds) that may alter populations’ connectivity.

Abbreviations: ANN, Artificial Neural Networks; AWA, Abundance-Weighted Average; COGDs, Centres Of Gravity of the Distributions; COGEs, Centres Of Gravity of leading edge Expansions; COGCs, Centres Of Gravity of trailing edge Contractions; CMIP6, Coupled Model Intercomparison Project Phase 6; CTA, Recursive Partitioning; DATRAS, Database of Trawl Surveys; EMODnet, European Marine Observation and Data Network; EUNIS, European Nature Information System; FDA, Flexible Discriminant Analysis; GAM, Generalized Additive Models; GBIF, Global Biodiversity Information Facility; GBM, Boosted Regression Trees; GLM, Generalized Linear Models; ICES, International Council for the Exploitation of the Sea; IFREMER, Institut Français de Recherche pour l’Exploitation de la Mer; IPCC, Intergovernmental Panel on Climate Change; MARS, Multivariate Adaptive Regression Splines; MaxEnt, Maximum Entropy formalism; MEO, Marine-Estuarine Opportunist; OBIS, Ocean Biodiversity Information System; PCA, Principal Component Analysis; RF, Random Forest; SDMs, Species Distribution Models; SSP, Shared Socioeconomic Pathways; SRC, Species Range Change; TSS, True Skill Statistic; VertNet, Vertebrate Biodiversity Data Networks.

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1. Introduction

Marine fish species are experiencing human-induced alterations in their ecophysiological and/or biological processes in response to climate change (Poloczanska et al., 2013). These alterations include changes in demography and phenology (e.g., a significant increase in the proportion of small-sized fish species – Perry et al., 2005; and 20–30% body mass reduction – Pauly and Cheung, 2018) as well as strategies of energy allocation (Poloczanska et al., 2013); seasonal shifts in life cycle (Daufresne et al., 2009); and alterations in sensory system resulting in swimming behaviour changes (Servili et al., 2022). All of these changes explain why climate change currently turned 45% of marine species to be at risk of extinction and caused a decrease in the amount of ‘sustainable’ fish stocks by up to 4% since 1930s (Poloczanska et al., 2013; Penn and Deutsch, 2022). However, marine fish species also adjust their spatial distributions to follow the movements of their ecological niche and/or prey at the same rate or not as projected climate change will strike (Poloczanska et al., 2013).

Tropicalization is a prevalent process explaining climate change induced shift in marine communities (McLean et al., 2021). It has been well documented in some temperate marine ecoregions as in the Northeast Atlantic Ocean (Costa et al., 2014). Northeast Atlantic is a biogeographic transition zone where fish species of different thermal affinity co-occur, and this area has been increasingly exposed to climate change particularly since the mid-20th century (Levitus et al., 2000; Rutterford et al., 2023). Consequently, observed northward species range shifts (Perry et al., 2005; Pinsky et al., 2013), and/or shifts of species’ distributional cores to deeper and more remote areas (Dulvy et al., 2008), and/or species range size changes (Thorson et al., 2016) correspond to large-scale marine habitat losses and/or gains (Morato et al., 2020; Ramos Martins et al., 2021). In terms of community, these have resulted in northern cold-water species’ declines due to their range contractions, and/or arrival of new or emerging southern warm-water species due to their range expansions leading to a tropicalization of fish communities (Le Marchand et al., 2020).

Among the most valuable marine fish species, the marine-estuarine opportunist (MEO) fish species constitute one fifth of the species richness of estuarine systems along the French and Iberian coasts of the Northeast Atlantic (Teichert et al., 2017). Indeed, MEO fish species are unique species distinguished by their complex life cycle involving dependence to estuarine or coastal environments (Potter et al., 2015; Cabral et al., 2022). Specifically, juveniles of MEO fish species regularly enter and use estuaries (or sometimes protected nearshore shallow coastal areas) as nurseries; while adults use deep coastal areas and the continental shelf as migratory, feeding, and/or spawning grounds giving rise to seasonal migration to and from estuaries (Potter et al., 2015; Whitfield et al., 2023). MEO fish species is an ecologically (e.g., they occur in high abundance in estuarine and coastal systems with a seasonal periodicity, consuming high quantities of benthic macro-invertebrates and other prey) and socio-economically (e.g., artisanal and commercial fisheries, recreational fisheries, and nutrition security) important group (Seitz et al., 2014). Their climate vulnerability was classified from moderate to high depending on the species considered (Cheung and Oyinlola, 2018). For some of these species, a significant change in their abundance in estuaries along the French Atlantic coast due to climate warming has already been documented (Hermant et al., 2010). Most studies have focused on the impact of climate change on larval dispersion on the continental shelf before the recruitment of larvae and juveniles in estuarine nurseries (e.g., Cabral et al., 2021), the suitability of estuarine habitats for juveniles (e.g., Vinagre et al., 2006) as well as their contribution to adult populations (e.g., Le Pape et al., 2003). However, the suitability of marine environment for adult populations on a scale covering their distribution ranges have been far less studied. Among the studies looking at shifts in environment suitability distribution, few have analyzed the directionality and the magnitude of different distributional characteristics (e.g., range size, gravity

centroids, and margins) (Morato et al., 2020; Soultan et al., 2022). In this context, there is a crucial need to understand the climate-induced shifts in marine environment suitability for populations of MEO fish species within the Northeast Atlantic, covering a large part of their ranges to anticipate the potential future impacts that these biological redistributions may have on ecosystem functioning and human well-being (Pecl et al., 2017).

Species Distribution Models (SDMs) represent valuable tools to simulate the environmental suitability for species settlement and survival. SDMs have been applied exponentially, notably in the Northeast Atlantic over the past fifteen years (Melo-Merino et al., 2020). They are mainly based on a correlative approach of the species-environment relationships relating species observations to environmental variables through statistically derived response curves (Guisan et al., 2017). Correlative models thus allow approximating the potential niche of the species (*sensu* Hutchinson (1957)). They have been the most widely used models due to their simplicity of data requirements and to constant technical progress (Peterson et al., 2015). This popularity is accompanied by numerous publications and the dissemination of data and tools in open access and provides relevant feedback on the most relevant approaches. Indeed, it appeared that these models perform better and are more realistic when they account for some important points such as the species vertical habitat dimension (Hattab et al., 2014; Ben Rais Lasram et al., 2020), and when they combine both habitat (e.g., sediments, depth) and bioclimatic (e.g., temperature, salinity) variables (Sohl, 2014). In most cases, the inclusion of habitat dimension requires the application of a hierarchical approach that allows respecting the appropriate spatial extent and resolution at which coarser scale bioclimatic and finer-scale habitat variables are expected to influence the underlying ecological processes particularly for highly mobile species (Guisan et al., 2017; Melo-Merino et al., 2020). Moreover, hierarchical filters avoid overfitting of a single model with too many environmental predictors (Randin et al., 2006). Finally, the application of an ensemble forecasting procedure for each hierarchical filter allows the variations in the accuracy of predictions produced from several statistical techniques to be considered and provides more accurate fitting for a set of training data (Hao et al., 2019).

The main purpose of this study was to investigate the effects of climate change on the environment suitability distribution for six benthic-demersal MEO fish species in the Northeast Atlantic Ocean. In the framework of this study, we have distinguished ‘sub-boreal’ (sea bass, *Dicentrarchus labrax*; flounder, *Platichthys flesus*; plaice, *Pleuronectes platessa*; and common sole, *Solea solea*) from ‘sub-tropical’ (meagre, *Argyrosomus regius*; and Senegalese sole, *Solea senegalensis*) species. These projected distributions were derived under present and late 21st century conditions based on the SSP2-4.5 (intermediate) and the SSP5-8.5 (pessimistic) possible emission scenarios proposed by the Intergovernmental Panel on Climate Change (IPCC – IPCC, 2021). These projections were made using the ‘hierarchical filters’ concept combining both bioclimatic (with large-scale and time-variant variables) and habitat (with fine grained and supposedly time-invariant variables) components of the potential species niche from consensual ensemble forecasting. Three main hypotheses were tested: (i) distribution shifts in environment suitability in response to ocean warming, i.e., northward range shifts, deeper water shift, and/or seaward shift; (ii) a range contraction for the four ‘sub-boreal’ species and a range expansion for the two ‘sub-tropical’ species; and (iii) stronger effects under the SSP5-8.5 scenario than under the SSP2-4.5 scenario. Methodological choices along this work used an existing framework of hierarchical modelling (Ben Rais Lasram et al., 2020 – <https://github.com/TarekHattab/SDM>) but incorporated improvements and/or adaptations to fit with the MEO species ecology and the ecology of climate change in terms of shifting distributions.

2. Material and methods

2.1. Data acquisition and processing, and exploratory data analyses

2.1.1. MEO fish occurrence data

For bioclimatic suitability distribution modelling, presence-only records for the six MEO fish species were downloaded from four international open-access datasets of biodiversity occurrences based on participative science projects: (i) the Global Biodiversity Information Facility (GBIF - <https://www.gbif.org/>), (ii) the Ocean Biodiversity Information System (OBIS - <https://obis.org/>), (iii) the Vertebrate Biodiversity Data Networks (VertNet - <http://www.vertnet.org/index.html>), and (iv) the INaturalist (<https://www.inaturalist.org/>) via the *rgbif*, *robis*, *rvernet* and *rinat* packages in R (R Core Team, 2021). For habitat suitability distribution modelling, presence-only occurrences were retrieved from research samplings and/or monitoring of professional fisheries from two datasets: (i) the MigrenMer database (Elliott et al., 2023) regrouping the open-access fisheries-independent Database of Trawl Surveys (DATRAS) maintained by the International Council for the Exploration of the Sea (ICES - <https://www.ices.dk/data/d/ata-portals/Pages/DATRAS.aspx>), the fisheries-independent French scientific surveys collected by the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER) and the fisheries-dependent data belonging to the ObsMer program available upon request from the French Ministry of Fisheries and Aquaculture especially for European flounder; and (ii) the online DATRAS for data that were not included in the MigrenMer database via the R *icesDATRAS* package (R Core Team, 2021). For both hierarchical filters, a careful data pre-processing was applied for each species (see Text S1 for more details).

2.1.2. Environmental variables

The bioclimatic component of the potential niche was predicted from three hydrodynamic and/or biogeochemical variables: (i) the bottom seawater temperature (*thetao*), (ii) the bottom dissolved dioxygen concentration (*o2*), and (iii) the log-transformed surface chlorophyll-a level (*log chl*) as a proxy for resource availability. Since the species studied are all euryhaline (see for instance Able et al., 2022; Whitfield et al., 2022 for a recent update on ecology of MEO fish species), we decided not to consider salinity as a predictive variable. The avoidance of multicollinearity issues was checked (i.e., thresholds of Pearson correlation coefficients $r < 0.7$ – Green (1979), and Variance Inflation Factor estimates < 5 – Dormann et al. (2013)). *Log chl*, *o2*, and *thetao* were retrieved from bias-adjusted, statistically downscaled, high-resolution climate ensemble projections (Kristiansen et al., 2024). The ensemble projections were derived by averaging a set of eight individually downscaled CMIP6 models including: (i) IPSL-CM6A-LR (Institut Pierre-Simon Laplace), (ii) MPI-ESM1-2-LR (Max Planck Institute for Meteorology), (iii) CanESM5-CanOE (Canadian Centre for Climate Modelling and Analysis), (iv) UKESM1-0-LL (Met Office Hadley Centre), (v) GFDL-ESM4 (NOAA/OAR Geophysical Fluid Dynamics Laboratory), (vi) CMCC-ESM2 (Fondazione Centro Euro-Mediterraneo sui Cambiamenti Climatici), (vii) CMCC-CM2-SR5 (Fondazione Centro Euro-Mediterraneo sui Cambiamenti Climatici), and (viii) MIROC-ES2L (Research Institute for Global Change). Monthly values annually averaged were used for both historical (1993–2014) and future (2015–2099) periods under different possible emission scenarios at 1/12th degree (~6–7 kms) grid resolution for the desired spatial extent ($n = 53,431$ $0.08^\circ \times 0.08^\circ$ cells – Kristiansen et al., 2024) (Fig. A.4). Bioclimatic models were monthly predicted for the present (2001–2020) and future (2080–2099) periods. Two of the last IPCC future emission scenarios (IPCC et al., 2021) were used here: the SSP2-4.5 ‘intermediate’ scenario and the SSP5-8.5 ‘pessimistic’ scenario.

The habitat component of the potential niche was modelled from (i) the bathymetry, and (ii) the seabed type. These two variables were considered representative of use conditions of the bottom habitat supposedly time-invariant for the six MEO fish species. The bathymetry was

downloaded from the European Marine Observation and Data Network (EMODnet) Bathymetry (<https://www.emodnet-bathymetry.eu/>) at ~1/1000th degree grid resolution, and upsampled by bilinear resampling to 1/100th degree (~750–800 m) grid resolution. The seabed type was extracted from the EMODnet Geology (<https://www.emodnet-geology.eu/>) at 1:1,000,000 scale, rasterized by means of the R *terra* package (R Core Team, 2021), and resampled to the same spatial resolution as the bathymetry grid. Seven EUNIS substrate classes were represented: (i) mud, (ii) sandy mud, (iii) muddy sand, (iv) sand, (v) coarse-grained sediment, (vi) mixed sediment, and (vii) rock and boulders. The two habitat grids were then cropped to the desired spatial extent ($n = 0.01^\circ \times 0.01^\circ$ 1,647,760 cells – Fig. A.1). Due to the potential existence of multicollinearity between the two habitat variables and convergence issues of some statistical techniques from mixed variable types, a mixed Principal Component Analysis (PCA) following the ordination method of Hill and Smith (1976) was therefore performed via the R *ade4* package (R Core Team, 2021). This method allowed defining the habitat components to use in the modelling approach (Ben Rais Lasram et al., 2020; Le Marchand et al., 2020).

2.2. Bioclimatic and habitat suitability distribution modelling

2.2.1. Filtrations and pseudo-absence data generation

Bioclimatic and habitat filters were based on Hutchinson's ‘niche-biotope duality’ (Colwell and Rangel, 2009). This procedure reduces the under- or over-representation of some environmental conditions in models by assigning equal weight to over- and under-sampled areas (Ben Rais Lasram et al., 2020). The bioclimatic component of the potential niche was estimated by a restricted convex hull excluding the extreme bioclimatic conditions experienced by the species from the 2.5% and 97.5% percentiles of each bioclimatic variable (Cornwell et al., 2006; Schickele et al., 2020). The following resolutions were selected: 0.5-log $\text{mg}\cdot\text{m}^{-3}$ for *log chl*, 0.5 $\text{mL}\cdot\text{L}^{-1}$ for *o2* and 0.5 $^\circ\text{C}$ for *thetao*. The spatial extent of bioclimatic models' calibration was restricted to the coastal waters of the European seas (i.e., Baltic Sea, North Sea, English Channel, Celtic Sea, Irish Sea, Bay of Biscay, Cantabrian Sea, Portuguese Sea, and Mediterranean Sea) and using the application of a precautionary threshold (less than 50 km from the coast or less than 300 m deep) (Table A.2).

The habitat component of the potential niche was approximated in the same way but with a restricted surface range envelope (i.e., rectangular hypervolume excluding the 2.5% and 97.5% percentiles of each PCA axis retained) from the spatialisation of scores of the seven main PCA axes retained (Ben Rais Lasram et al., 2020). The spatial extent of habitat models' calibration was restricted to species-specific areas with occurrence data available across all the coastal waters of the Northeast Atlantic (i.e., the North Sea, English Channel, Celtic Sea, Irish Sea, Bay of Biscay, Cantabrian Sea, and Portuguese Sea) and using the same precautionary threshold used in bioclimatic modelling.

As regression techniques based on presence and absence data have been showed to work better than presence-only techniques, stratified pseudo-absence data (i.e., background data) were generated (Brotons et al., 2004). These were randomly selected within the bioclimatic and habitat space outside the restricted convex hull and restricted surface range envelope, respectively (Barbet-Massin et al., 2012). This selection followed the ‘D-designs’ theory (Montgomery, 2017): as many pseudo-absence data were generated as filtered presence data for each species except if too little presence data (i.e., 1000 pseudo-absences generated if < 1000 presence data) in order to avoid biases due to unbalanced prevalence and/or low sample size (Guisan et al., 2017). Because the recommendation to have more than 20 data was reached, all six MEO fish species could be studied although there were much fewer presence data for the two ‘sub-tropical’ species (Guisan et al., 2017 – Table A.2).

2.2.2. Validation and outputs of final suitability ensemble forecasting

As recommended in the literature, ensemble forecasting was used instead of strict selection of a single statistical technique was used for each of the species-specific bioclimatic and habitat suitability distribution models (Marmion et al., 2009; Hao et al., 2019). Ensemble forecasting were built with a slightly adapted code from the R package *biomod2* (Thuiller et al., 2009) from nine statistical techniques belonging to four statistical approaches: (i) regression-based approaches (Generalized Linear Models – GLM; Generalized Additive Models – GAM; Multivariate Adaptive Regression Splines – MARS), (ii) machine-learning approaches (Recursive Partitioning – CTA; Flexible Discriminant Analysis – FDA; Artificial Neural Networks – ANN), (iii) boosting and basting approaches (Random Forest – RF, Boosted Regression Trees – GBM), and (iv) Maximum Entropy formalism (Max-Ent). Default settings were used. The predictive accuracy of models was tested using the commonly three-fold cross-validation. In this approach, the dataset was split into three partitions (here, with a prevalence of 0.5). Each of the three runs was performed on two of the three partitions (i.e., training data), and evaluated on the third remaining partition (i.e., evaluation data), each partition used only once for test, for each statistical technique (Breiman, 2017).

The prevalence-independent metric, i.e., True Skill Statistic (TSS – Allouche et al., 2006), was used as mean predictive accuracy metric for each of the three runs of the nine statistical techniques. Only the statistical techniques considered having a high predictive power, i.e., three-run TSS average > 0.7, were selected in ensemble forecasting. Consensual predictions were obtained by weighting the sum of probability values of each run of all the selected statistical techniques by the predictive accuracy of its prediction (Marmion et al., 2009). The relative importance and response curves of these variables and estimates of the uncertainty between the different cross-validation runs retained were provided (Guisan et al., 2017). Final projections were obtained by taking the arithmetic mean of the 240 (i.e., 20 years × 12 months) model output projections. The thresholding method optimizing both sensitivity (i.e., percentage of presences correctly predicted) and specificity (i.e., percentage of absences correctly predicted) was chosen to transform probabilistic estimates into binary bioclimatic or habitat suitability prediction maps classifying areas as suitable or unsuitable (Guisan et al., 2017 – Table A.6).

2.3. Environment suitability distribution combining both the bioclimatic and habitat components of the potential species niche

The environment suitability distribution was obtained by combining the bioclimatic and habitat suitability distribution models in the form of probabilistic forecasting as well as in the form of binary maps ($n = 0.01^\circ \times 0.01^\circ$, 1,644,121 cells – Hattab et al., 2014; Fournier et al., 2017). To this end, the bioclimatic suitability distribution grids were downsampled by bilinear resampling to the same spatial resolution and cropped to the same spatial extent as habitat suitability distribution grids. Finally, environment suitability distribution arose from the multiplication of resampled and cropped bioclimatic and habitat suitability grids.

2.4. Indicators of environment suitability distribution shifts

2.4.1. From binary environment suitability maps

Two indicators of distribution shifts resulting from binary environment suitability maps comparisons between the present (2001–2020) and future (2080–2099) periods were estimated under each of the two future emission scenarios for each species studied. First, the Species Range Change (SRC expressed in %) representing change in size of suitable range was calculated as the difference between the relative proportion of range expansion and that of range contraction given the size of the present suitable range using the R package *biomod2* (Thuiller et al., 2009; Soultan et al., 2022). Second, a relative latitudinal shift of range margins (*Margins shift* expressed in %) was computed,

representing displacements of southern margins of ‘sub-boreal’ species or northern margins of ‘sub-tropical’ species (Ordonez and Williams, 2013). They were estimated as the This comment has been taken into account. we.

relative proportion of the linear distance separating the range margins for the present period and that of the future period (Perry et al., 2005) given the height of the suitable range (see Table A.8 for definition of margins, and height).

It was considered that: (i) positive and negative *Margins shift* estimates corresponded to a northward and southward shift, respectively; (ii) positively correlated SRC and *Margins shift* estimates for ‘sub-tropical’ species accompanied by a northward shift of northern margins would describe a gain in suitable areas at higher latitudes; and (iii) negatively correlated SRC and *Margins shift* estimates for ‘sub-boreal’ species accompanied by a northward shift of southern margins would correspond to a loss of suitable areas at lower latitudes (Soultan et al., 2022). Rates of margins displacement were calculated by dividing displacement shift distances separating the range margins between future and present periods by the number of decades (expressed in $\text{km} \cdot \text{decade}^{-1}$).

2.4.2. From probabilistic environment suitability maps

Distribution shifts were usually referred to north-south displacements but had also an east-west component (Hiddink et al., 2015). As such, an alternative was to study shifts in resulting probabilistic environment suitability predictions using three range centroids: (i) the centres of gravity of the distributions (COGDs), (ii) the centres of leading edge expansions (COGEs), and (iii) the centres of trailing edge contractions (COGCs) (Thorson et al., 2016; Pinsky et al., 2020; Soultan et al., 2022). COGD is the most commonly used metric to assess shifts in the spatial core of species predicted distributions (Soultan et al., 2022). COGEs and COGCs have been much less studied than COGDs. They represent part of the distribution ranges where bioclimatic conditions necessary to the species settlement and survival will be respectively gained (i.e., successful colonisations) and lost (i.e., local extirpations) between future and present periods (Hiddink et al., 2015).

Four indicators of distribution shifts were computed from the COGDs, COGEs, and COGCs. First, the actual direction of distribution shifts was given by the direction for the expansion (i.e., from COGDs to COGEs) and the opposite direction for the contraction (i.e., from COGCs to COGDs) (Hiddink et al., 2015) using geographical coordinates. Second, the absolute (expressed in km) and relative (expressed in %, relatively to width/height of the suitable range) displacement shift distances along the longitudinal/latitudinal axis were calculated using the COGD for the present distribution as origin (see Table A.8 for definition of width and height). Third, spatial variables such as bathymetry and distance to the nearest coast were estimated to highlight possible deepening and seawardness in distribution shifts, respectively. Finally, bioclimatic variables were also estimated to better understand the potential direct (i.e., *thetao*) and indirect (i.e., *log chl* and *o2*) effects of climate change in the directionality and the magnitude of distribution shifts.

The geographic coordinates of the COGDs were here calculated as the average values over all study area cells weighted by the values of probabilistic environment suitability predictions (Thorson et al., 2016). This method was shown to be more robust than the conventional methods (e.g., the abundance-weighted average – AWA) that were limited due to biases introduced in preferential sampling distribution or its changes over time (Pinsky et al., 2013; Hiddink et al., 2015). The calculation of the coordinates of COGEs and COGCs, usually calculated from binary maps as in Hiddink et al. (2015), were thus readapted in the same way as COGDs but from areas where the absolute variations in probabilistic environment suitability predictions between the future and present periods were positive and negative, respectively. Rates of COGDs displacement were calculated by dividing displacement shift distances separating the COGDs between future and present periods by

the number of decades (expressed in $\text{km}\cdot\text{decade}^{-1}$) or the temperature difference them separating (expressed in $\text{km}\cdot^{\circ}\text{C}^{-1}$). Unlike COGDs, displacement shift distances for the leading (i.e., COGEs) and trailing (i.e., COGCs) edges were not appropriate to be interpreted as actual rates but rather as index of the extent of distribution shifts (Hiddink et al., 2015).

3. Results

3.1. Changes in bioclimatic variables under possible emission scenarios

There were significant differences in bioclimatic variables' mean values between the present and future periods at the scale of the coastal waters of the Northeast Atlantic: \log_{chl} decreased by 33% and 38%, o_2

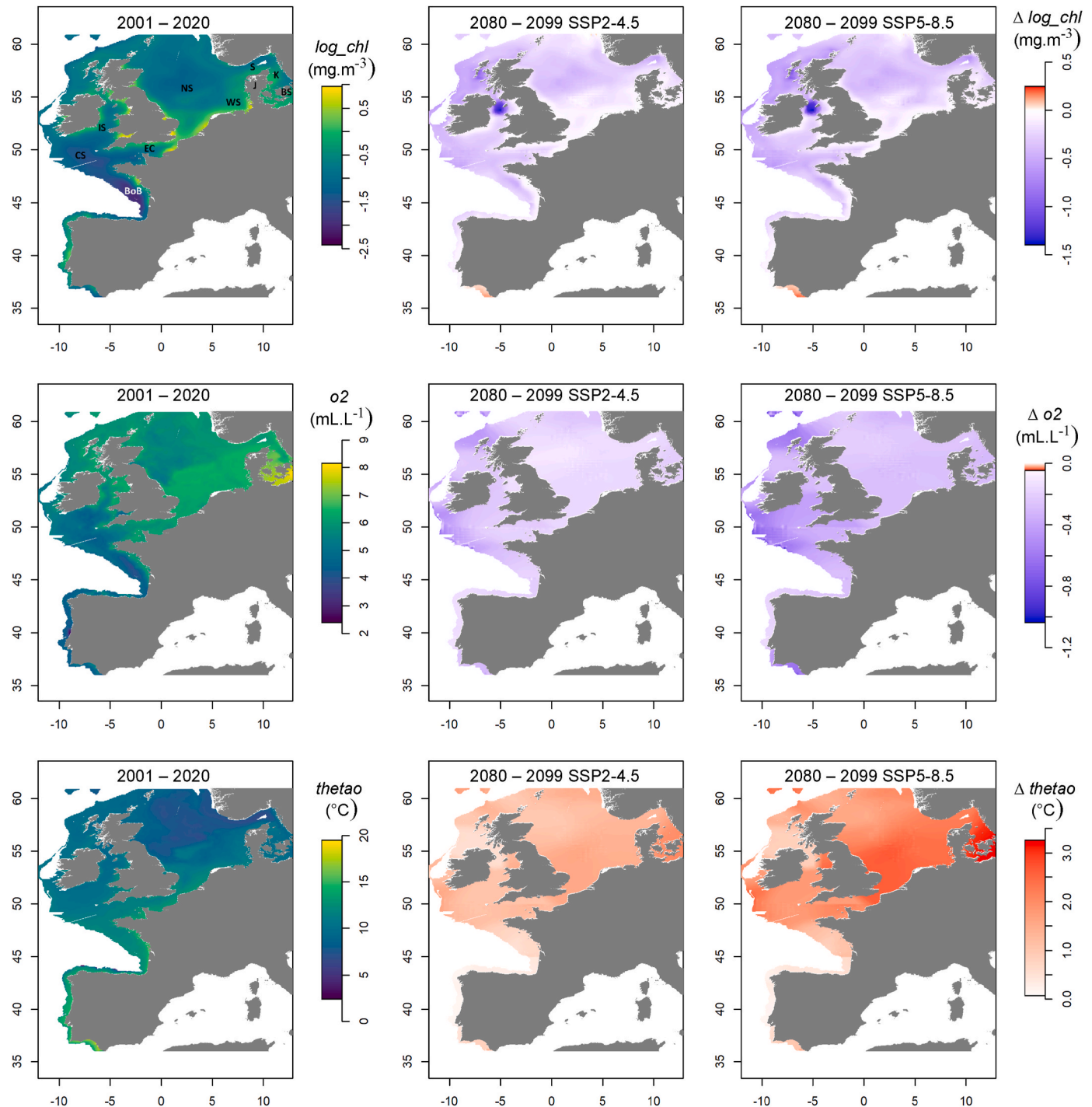


Fig. 1. Mapping of bioclimatic variables monthly values averaged (arithmetic mean of the 240 = 20 years \times 12 months projections) over the whole study area: \log -transformed surface chlorophyll-a (\log_{chl} expressed in $\text{mg}\cdot\text{m}^{-3}$ – first row), bottom dissolved oxygen (o_2 expressed in $\text{mL}\cdot\text{L}^{-1}$ – second row), and bottom temperature (thetao expressed in $^{\circ}\text{C}$ – third row) for the present (2001–2020 – first column); and their absolute variations to the future period (2080–2099) under the SSP2-4.5 (intermediate – second column) and SSP5-8.5 (pessimistic – third column) scenarios (see Fig. A2 and Table A.1 for more details). The main areas mentioned in the text: Bay of Biscay – BoB, Celtic Sea – CS, Irish Sea – IS, English Channel – EC, North Sea – NS, Wadden Sea – WS, Jutland – J, Skagerrak – S, Kattegat – K, and Belt Sea – BS.

decreased by 4% and 6%, and *thetao* increased by 12% and 19% under the SSP2-4.5 and SSP5-8.5 scenarios, respectively (Fig. A.2; Table A.1). Almost the whole study area and, particularly the northern Irish Sea, was affected by a decrease in *log chl* levels, except a few well-defined areas where levels always remained constant (i.e., the Wadden Sea, eastern British coasts, southern North Sea, coasts around the English Channel and the Irish Sea, Bay of Biscay coastal waters, and Portuguese coasts especially near the Mondego catchment) or increased (i.e., the southernmost Portuguese and Spanish coasts). The whole study area was affected by a decrease in *o2* (i.e., particularly in the northern British coasts, Irish Sea, Celtic Sea, western English Channel, and the southernmost Portuguese and Spanish coasts) and an increase in *thetao* (i.e., particularly in the Belt Sea, Kattegat, Skagerrak, west coast of Jutland, Wadden Sea, North Sea, English Channel, Irish Sea, and Celtic Sea) levels (Fig. 1).

3.2. Validation of final bioclimatic and habitat suitability ensemble forecasting

For final bioclimatic suitability ensemble forecasting, almost all the statistical techniques except the GLM were retained, and the three-run averages of TSS varied among species between 0.71 and 0.99 (Table A.3). Uncertainties between techniques (i.e., inter-technique standard deviation) were generally low over the whole study area since standard-deviations varied among species between 0.12 ± 0.07 and 0.17 ± 0.06 on average (Fig. A.4, A.5, A.6, A.7, A.8 and A.9). The contribution estimates of the three bioclimatic variables varied between

0.23 ± 0.04 and 0.63 ± 0.12 depending on variables and species. However, the variable with the greatest contribution tended to differ according to the species affinity: *log chl* (except for sea bass) and *o2* for the four 'sub-boreal' species; *o2* and *thetao* for the two 'sub-tropical' species (Table A.4).

For final habitat suitability ensemble forecasting, all the statistical techniques except GAM and MARS for some species were retained, and TSS averages were comprised between 0.70 and 0.94 (Table A.5). Uncertainties between techniques were also very low with standard deviation averages comprised between 0.13 ± 0.08 and 0.15 ± 0.13 (Fig. A.4, A.5, A.6, A.7, A.8 and A.9).

3.3. Present (2001–2020) predicted MEO fish species distributions

Three groups of species have similar present predicted distributions (when using probabilities >0.7): (i) sea bass and flounder (i.e., British coasts especially those around the Irish Sea, west coast of Jutland, Wadden Sea, southern North Sea, English Channel, Bay of Biscay coastal waters, Portuguese coasts, and southern Spanish coasts, but also the Kattegat and Belt Sea for flounder); (ii) plaice and common sole (i.e., almost everywhere except the south-western Celtic Sea, and the Norwegian, Cantabrian, Galician, Portuguese and Spanish trenches); and (iii) the two 'sub-tropical' species (i.e., the southern Bay of Biscay coastal waters, south-western and southern Portuguese coasts, and southern Spanish coasts) (Figs. 2–7).

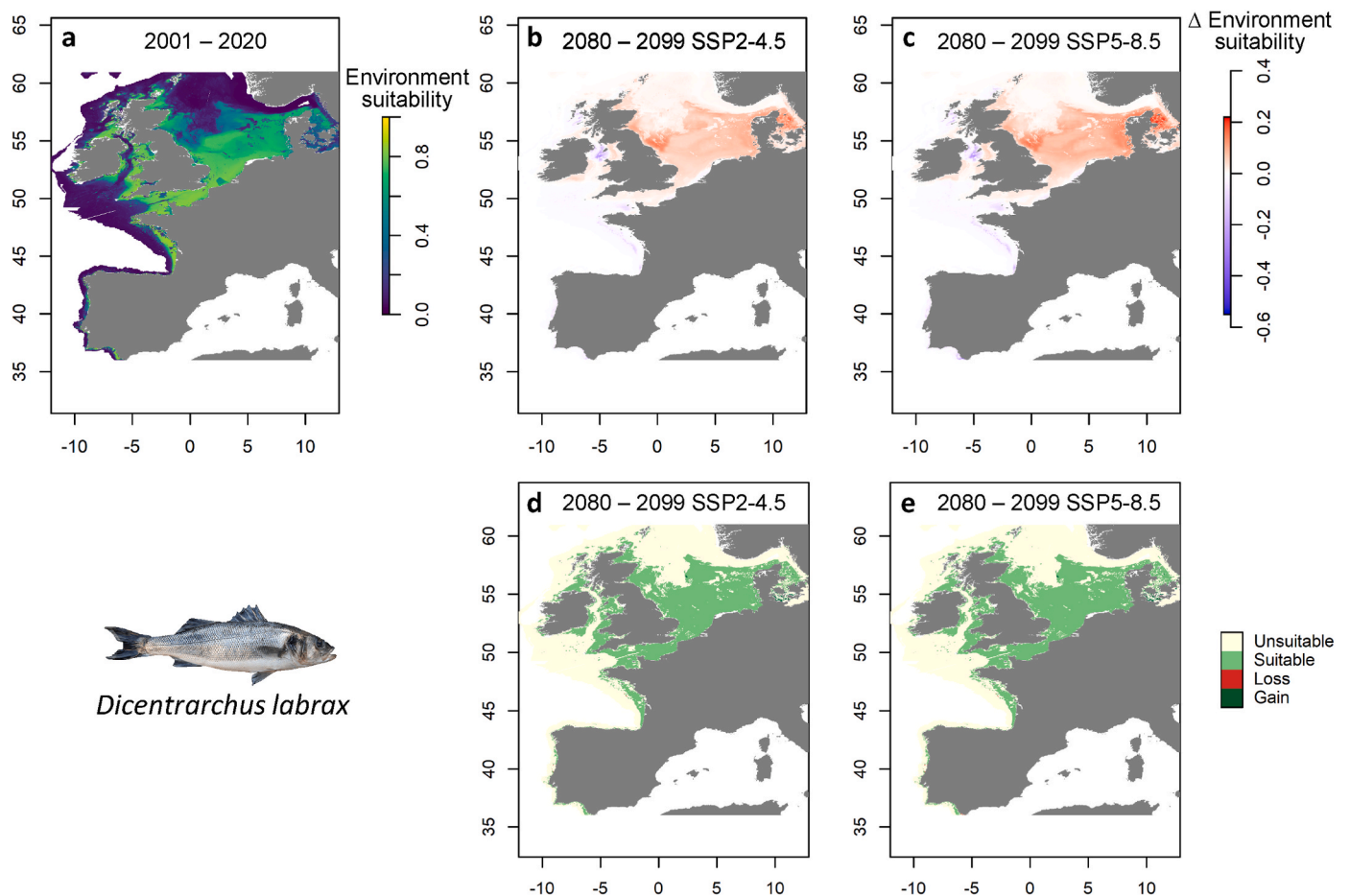


Fig. 2. Sea bass, *Dicentrarchus labrax* environment suitability geographic projections resulting from the combination of bioclimatic and habitat suitability predictions weighted by a chosen predictive accuracy metric (e.g., TSS scores of statistical techniques retained in respective final ensemble forecasting): probabilistic environment suitability predictions for the present period (2001–2020 – a); their absolute variations to the future period (2080–2099) under the SSP2-4.5 (intermediate – b) and SSP5-8.5 (pessimistic – c) scenarios; and the resulting species range change under the SSP2-4.5 (d) and SSP5-8.5 (e) scenarios after binarisation.

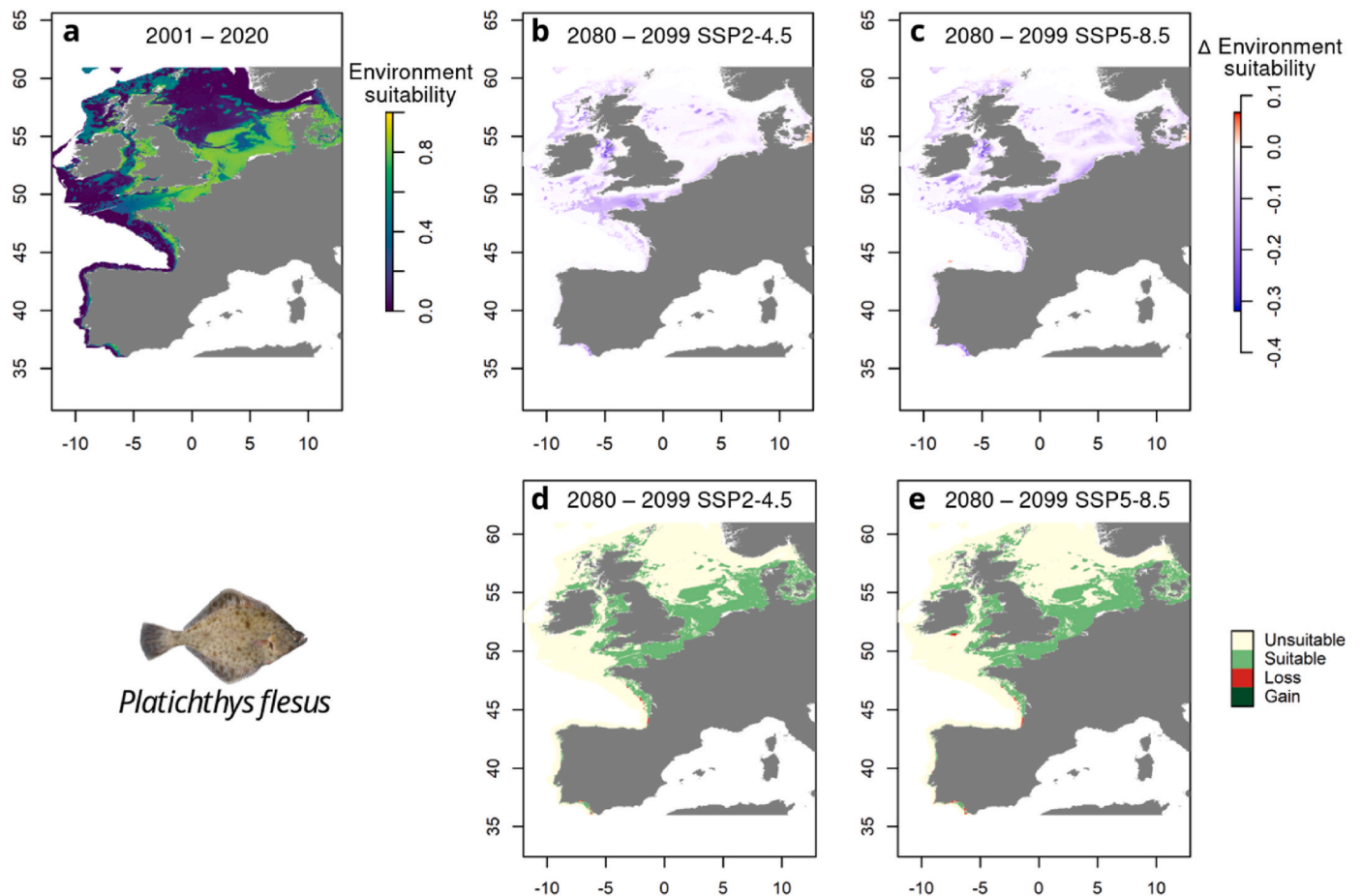


Fig. 3. Flounder, *Platichthys flesus* environment suitability geographic projections resulting from the combination of bioclimatic and habitat suitability predictions weighted by a chosen predictive accuracy metric (e.g., TSS scores of statistical techniques retained in respective final ensemble forecasting): probabilistic environment suitability predictions for the present period (2001–2020 – a); their absolute variations to the future period (2080–2099) under the SSP2-4.5 (intermediate – b) and SSP5-8.5 (pessimistic – c) scenarios; and the resulting species range change under the SSP2-4.5 (d) and SSP5-8.5 (e) scenarios after binarisation.

3.4. Future (2080–2099) predicted MEO fish species distributions under the two emission scenarios

SRC and northward *Margins shift* were positively correlated for the two ‘sub-tropical’ species under both possible emission scenarios reflecting an increase in the number of suitable areas at northern boundaries (Figs. 6 and 7 and A.10). Conversely, SRC and northward *Margins shift* were negatively correlated for two ‘sub-boreal’ species (i.e., flounder and plaice) highlighting a decrease in the number of suitable areas at southern boundaries (Figs. 3 and 4, and A.10). However, ‘sub-tropical’ species, and more specifically meagre, showed significant SRC expansion and northward *Margins shift* under the SSP2-4.5 scenario and even more pronounced under the SSP5-8.5 scenario (Fig. A.10; Tables A.7, A.8 and A.9). Moreover, margins displacement were faster for ‘sub-tropical’ species ($\sim 79\text{--}97\text{ km decade}^{-1}$) than for ‘sub-boreal’ species ($\sim 0\text{--}3\text{ km. decade}^{-1}$) (Table A.9).

There were significant increases in probabilistic environment suitability predictions’ mean values from the present to future periods and even more pronounced under the SSP5-8.5 scenario for ‘sub-tropical’ species. Conversely, there were significant decreases in probabilistic environment suitability predictions’ mean values for ‘sub-boreal’ species (except for sea bass) (Fig. A.11; Table A.10). We identified three groups of species with similar distribution of absolute variations of their future environment suitability probabilities under both possible emission scenarios. First, sea bass and common sole exhibited similar trends. They especially increased on the eastern British coasts, Kattegat, west coast of Jutland, Wadden Sea, southern North Sea, and coasts around the

north-eastern Irish Sea, but also the south-western Irish coasts and southern English coasts for sea bass. But they decreased in the northern Irish Sea, Western English Channel, Bay of Biscay continental shelf, and Portuguese and Spanish coasts, but also in the Celtic Sea and central North Sea for common sole. Second, flounder and plaice exhibited a global decrease in all areas especially in the northern Irish Sea, Celtic Sea, Western English Channel, Bay of Biscay continental shelf, and the southernmost Portuguese and Spanish coasts, but also the southern Wadden Sea for flounder. And finally, the two ‘sub-tropical’ species increased almost everywhere especially in the Kattegat, west coast of Jutland, Wadden Sea, southern North Sea, eastern English Channel, the coasts around the English Channel, British coasts especially those around the Irish Sea, and Bay of Biscay coastal waters. However, they decreased highly localized in the ‘Basque’ Bay of Biscay coastal waters, but also south-western Portuguese coasts for meagre or the southernmost Portuguese and Spanish coasts for Senegalese sole (Figs. 2–7).

A global and visible north-westward shift of increases in probabilistic environment suitability predictions was highlighted under the SSP2-4.5 scenario and even more pronounced under the SSP5-8.5 scenario for the six MEO fish species (Fig. 8). This shift, mostly northward (69–75%) rather than westward (25–28%), was towards shallower areas closer to the coasts for ‘sub-boreal’ species (except for sea bass) and towards areas further from the coasts for ‘sub-tropical’ species (Fig. A.13; Table 1). COGDs tended to shift towards areas with lower $\log chl$ and o_2 levels and higher θ_{tao} level under the SSP2-4.5 scenario and even more pronounced the SSP5-8.5 scenario for the six MEO fish species (Fig. A.13). However, displacement shifts of COGDs were greater and even more

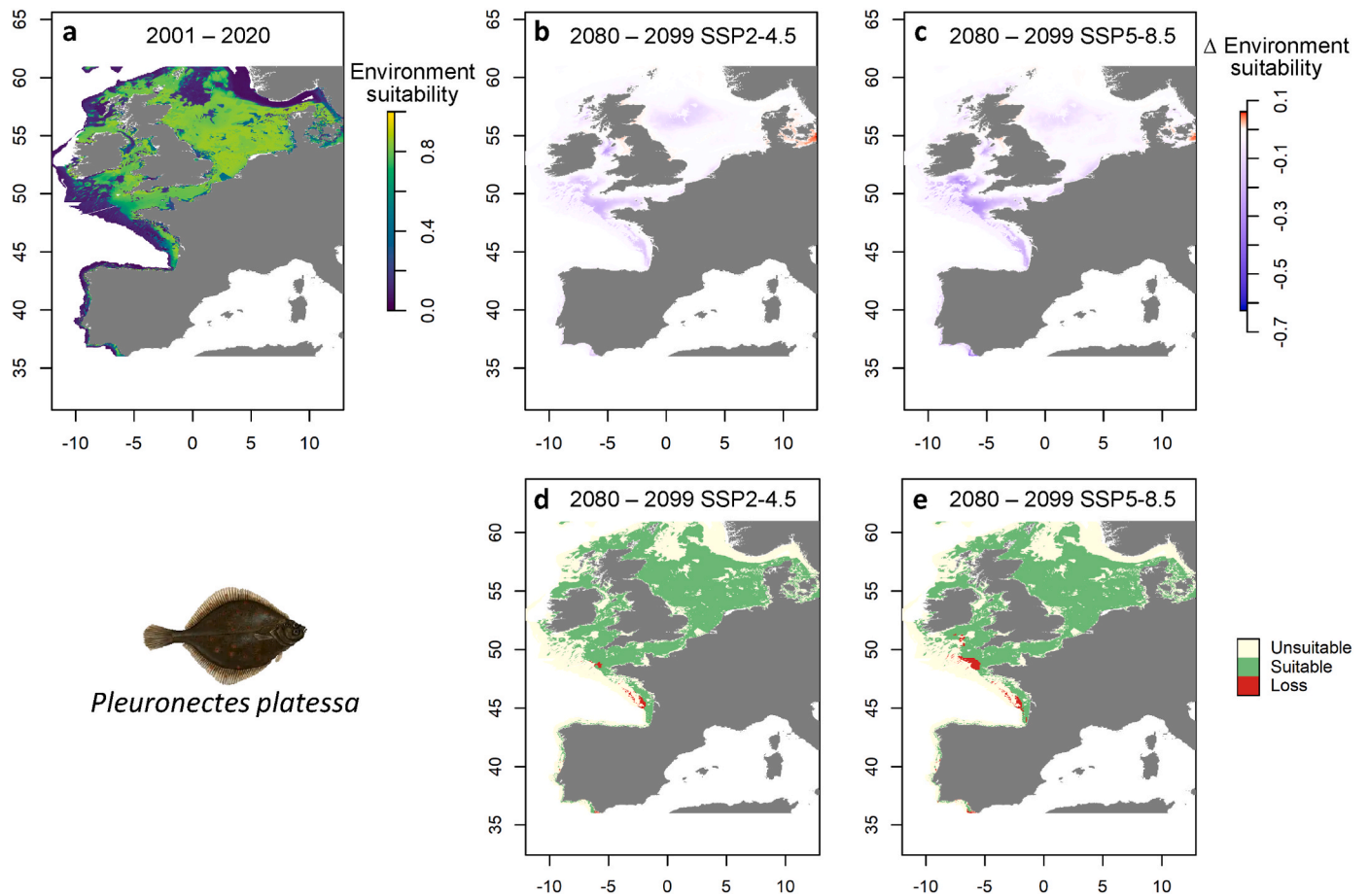


Fig. 4. Plaice, *Pleuronectes platessa* environment suitability geographic projections resulting from the combination of bioclimatic and habitat suitability predictions weighted by a chosen predictive accuracy metric (e.g., TSS scores of statistical techniques retained in respective final ensemble forecasting): probabilistic environment suitability predictions for the present period (2001–2020 – a); their absolute variations to the future period (2080–2099) under the SSP2-4.5 (intermediate – b) and SSP5-8.5 (pessimistic – c) scenarios; and the resulting species range change under the SSP2-4.5 (d) and SSP5-8.5 (e) scenarios after binarisation.

pronounced under the SSP5-8.5 scenario for the two ‘sub-tropical’ (73–81 km/ \sim 10 km.decade $^{-1}$ / \sim 43 km $^{\circ}$ C $^{-1}$ to north or 3–4% relative northward shift; and 45–50 km/ \sim 6 km.decade $^{-1}$ / \sim 27 km $^{\circ}$ C $^{-1}$ to west or 4–6% relative westward shift) than for the four ‘sub-boreal’ (8–24 km/ \sim 1–3 km.decade $^{-1}$ / \sim 4–12 km $^{\circ}$ C $^{-1}$ to north or 0–1% relative northward shift; and 5–14 km/ \sim 1–2 km.decade $^{-1}$ / \sim 2–7 km $^{\circ}$ C $^{-1}$ to west or 0–1% relative westward shift) species (Fig. A.12; Table 1). Displacement shifts were nevertheless much greater for COGCs (particularly much more importantly for the two ‘sub-tropical’ species) and COGEs than for COGDs under the SSP2-4.5 scenario and even more pronounced under the SSP5-8.5 scenario for the six MEO fish species (Fig. A.12; Table 1). ‘Sub-boreal’ species tented to contract from areas with lower *log chl* and *o2* levels and ‘sub-tropical’ species from areas with lower *o2* level and higher *theta0* level under the SSP2-4.5 scenario and even more pronounced under the SSP5-8.5 scenario (Fig. A.13).

4. Discussion

This study re-adapted the ‘hierarchical filters’ method employed in Hattab et al. (2014), Fournier et al. (2017), Ben Rais Lasram et al. (2020), and Schickele et al. (2020) in focusing on a relevant and consistent match between the particular case of MEO species ecology and distribution and the time-space frame of climate. Anthropogenic climate change was predicted to induce a global and visible north-westward, more to the north than to the west, distribution shift for six of the main benthic-demersal MEO fish species contributing to coastal fisheries and seafood production within the Northeast Atlantic. A

greater northward range expansion was also observed in our results especially for ‘sub-tropical’ species contrary to ‘sub-boreal’ species. Decreases in chlorophyll-a and dissolved dioxygen levels seemed to be the main drivers in the loss of environment suitability especially for ‘sub-boreal’ species while increase in temperature led the gain of environment suitability for ‘sub-tropical’ species. Finally, all of these modelling conclusions were globally and unsurprisingly even greater under the SSP5-8.5 scenario than the SSP2-4.5 scenario at the horizon of the 21st century end.

4.1. Relevance and accuracy of the data, method and models

Application of ensemble forecasting to build consensual environment suitability predictions is now recognized to provide the most reliable and robust correlative models’ outputs (Hao et al., 2019) while the ‘hierarchical filters’ concept aimed to both improve models’ predictive accuracy and limit sampling bias (Hattab et al., 2014; Fournier et al., 2017; Ben Rais Lasram et al., 2020; Schickele et al., 2020). In addition, two main aspects of the original Ben Rais Lasram et al. (2020) framework were changed. First, finer temporal resolution (i.e., a monthly scale instead of a decadal-scale) and larger temporal extent (i.e., over twenty years instead of one decade) were chosen for the present and future projections of species distribution. These different choices allowed to capture a more robust estimation of the trend in the impacts of climate change on the spatial distribution and obtain more accurate final projections (Castillo-Escrivà et al., 2020). Second, the spatial extent of bioclimatic models’ calibration was not on a global scale but limited

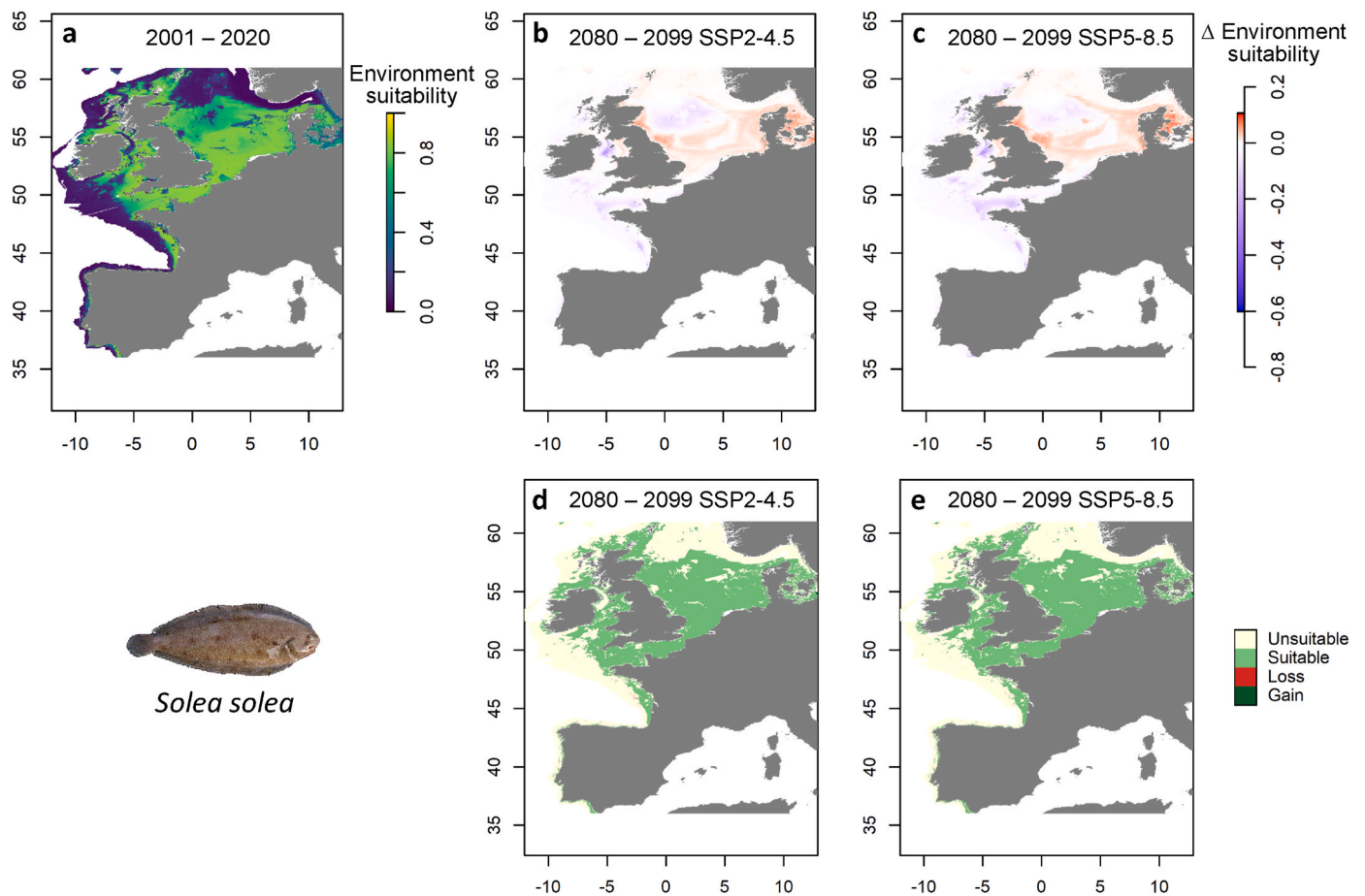


Fig. 5. Common sole, *Solea solea* environment suitability geographic projections resulting from the combination of bioclimatic and habitat suitability predictions weighted by a chosen predictive accuracy metric (e.g., TSS scores of statistical techniques retained in respective final ensemble forecasting): probabilistic environment suitability predictions for the present period (2001–2020 – a); their absolute variations to the future period (2080–2099) under the SSP2-4.5 (intermediate – b) and SSP5-8.5 (pessimistic – c) scenarios; and the resulting species range change under the SSP2-4.5 (d) and SSP5-8.5 (e) scenarios after binarisation.

to the coastal waters of the European seas and using the application of a precautionary threshold. The spatial extent of habitat models' calibration was species-specific: it was delineated to areas with occurrence data available across all the coastal waters of the Northeast Atlantic and using the same precautionary threshold used in bioclimatic modelling. These choices allowed to take into account biogeographic history and/or dispersal ability of the six MEO fish species or avoid over-predictions of the species range due to presence and pseudo-absence data conflicts (Hanberry et al., 2012). Nevertheless, some limitations regarding the quantity and quality of occurrence data should be pointed out. The data used in our analysis are coming from international voluntary databases, although these data are largely derived from scientific monitoring. These data are limited for the two 'sub-tropical' species (e.g., in the database that was used in our analyses only 113 and 63 observations were available for meagre and for the Senegalese sole, respectively – Table A.2), particularly in the south of the study area for some 'sub-boreal' species. In addition to the limited data availability, there may be taxonomic confusion between some species (e.g., sea bass and spotted bass, or common sole and Senegalese sole – Muus et al., 1988; Quéro and Vayne, 1997). These potential problems highlight the need to improve species identification skills and increase participatory reporting in all sampled and/or exploited areas, which is one of the main challenges for sustainable biomonitoring scientists in the 21st century (Ferreira et al., 2021).

At the same time, this study provided interpretable present distributions of environment suitability for species settlement and survival as many methodological choices were made in agreement with the species

ecology. On the one hand, these predictions were obtained from the combination of the bioclimatic and habitat components of the potential species niche that were judged to be accurate during models' evaluation process, and finally resulted from consensual predictions by at least seven statistical techniques over the nine proposed by *Biomod2* (Tables A.3 and A.5). On the other hand, the resulting response curves of each bioclimatic variable were carefully controlled and considered plausible since smoothed unimodal physiological responses reflecting more realistic ellipse-like niche visualisations were the most frequently encountered in natural systems (Fig. A.3 – Guisan et al., 2017). Moreover, the optimal temperature ranges obtained from these response curves were in the similar range to those found in the literature (e.g., Baensch and Riehl, 1997; Quéro and Vayne, 1997). Finally, present distributions of environmentally highly suitable areas were consistent with knowledge on the species essential habitats in the present situation. Indeed, for instance, the main identified spawning and/or feeding grounds in the Northeast Atlantic coastal zone part are included in the present predicted distribution of highly suitable areas (Muus et al., 1988; Quéro and Vayne, 1997). All these suggest that we can be reasonably confident in the models' transferability and thus predictions for the end of the 21st century (Randin et al., 2006).

4.2. Distribution shift directionality and magnitude

One of the main trends highlighted by our results was the north-westward shift in distribution for the six MEO fish species studied in the Northeast Atlantic. Though not focusing on the same species,

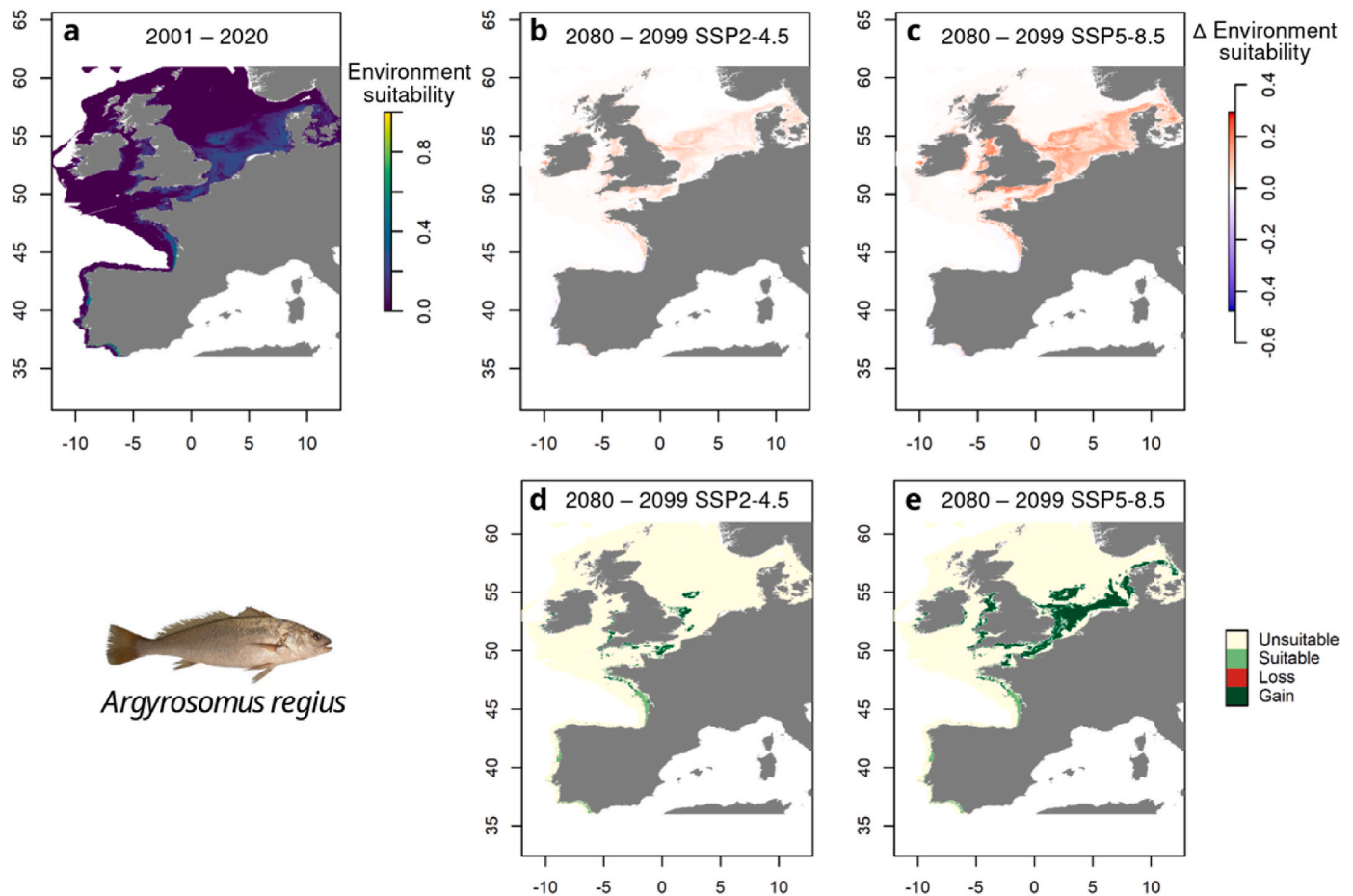


Fig. 6. Meagre, *Argyrosomus regius* environment suitability geographic projections resulting from the combination of bioclimatic and habitat suitability predictions weighted by a chosen predictive accuracy metric (e.g., TSS scores of statistical techniques retained in respective final ensemble forecasting): probabilistic environment suitability predictions for the present period (2001–2020 – a); their absolute variations to the future period (2080–2099) under the SSP2-4.5 (intermediate – b) and SSP5-8.5 (pessimistic – c) scenarios; and the resulting species range change under the SSP2-4.5 (d) and SSP5-8.5 (e) scenarios after binarisation.

ensemble climate projections, current and future periods (observed or predicted), modelling methodologies and/or spatial extent used in this study, several previous studies also highlighted a similar pattern for other fish species in the Northeast Atlantic. For cod *Gadus morhua*, the marine environment suitability would decrease in the southern area of the North Sea but increased in the remaining North Sea (Núñez-Riboni et al., 2019). For mackerel *Scomber scombrus*, the centre of gravity in the summer feeding area would have shifted from the Norwegian Sea core to Svalbard in the north and west to Greenland during the last decade (Boyd et al., 2020). This northward shift pattern was also observed in other taxa of the Northeast Atlantic from zooplankton (e.g., copepods species – Chust et al., 2014b) to top predators (e.g., Balearic shearwater *Puffinus mauretanicus* – Wynn et al., 2007), including also marine plants (e.g., temperate seaweed species – Neiva et al., 2016). This pattern has been shown also in other northern temperate regions (e.g., marine species on the U.S. Northeast continental shelf – Fredston et al., 2021).

This study put forward a greater northward expansion for ‘sub-tropical’ species than for ‘sub-boreal’ species in relation with a faster northward shift of COGDs (i.e., $\sim 10 \text{ km.decade}^{-1}$ or $43 \text{ km}^{\circ}\text{C}^{-1}$ versus $\sim 1\text{--}3 \text{ km.decade}^{-1}$ or $4\text{--}12 \text{ km}^{\circ}\text{C}^{-1}$) and faster northward margins shifts (i.e., $\sim 79\text{--}97 \text{ km.decade}^{-1}$ versus $0\text{--}3 \text{ km.decade}^{-1}$). However, interpretations concerning the differences in northward expansion rates between ‘sub-boreal’ and ‘sub-tropical’ species should be taken with a grain of salt since the entire distribution area of species and in particular that of the two ‘sub-tropical’ species were not fully captured in the models’ calibration. Nevertheless, these differences were also observed in other cases, and for instance regarding the predicted future spawning

distribution of other Northeast Atlantic ‘sub-boreal’ (e.g., mackerel, COGD shift of $16 \text{ km.decade}^{-1}$ or $25 \text{ km}^{\circ}\text{C}^{-1}$ – Bruge et al., 2016), and ‘sub-tropical’ (e.g., albacore *Thunnus alalunga*, northward margins shifts of $74 \text{ km.decade}^{-1}$ – Chust et al., 2019) fish species. More fluctuating dynamics at the range margins may explain the much faster shift rates than at the range core, with intermittent suitable conditions fostering rapid colonisation events (Hastings et al., 2018). Moreover, the fact that ‘sub-tropical’ species are probably still not in equilibrium with their environment and are still adjusting with the environmental conditions in present days may explain the observed patterns (Guisan et al., 2017). An observation that has already highlighted in the Bay of Biscay where the abundances of cold-water flatfish species decreased, and that of warm-water ones increased (Hermant et al., 2010). Thus, globally, transient dynamics are characterised by rapid colonisation of warm-water species and slower extirpation of cold-water species in response to climate change (Pinsky et al., 2020). This can be related with the potential difference in the influence of climate change components. Indeed, indirect effects (i.e., decreases in chlorophyll-a and dissolved dioxygen levels) seemed to influence the loss of environment suitability especially for ‘sub-boreal’ species, while direct effects (i.e., increases in temperature) were more related to gains of environment suitability in particular for ‘sub-tropical’ species.

4.3. Comparison of climate change impact between regions or across the studied area

The main areas where the environment suitability decreased were

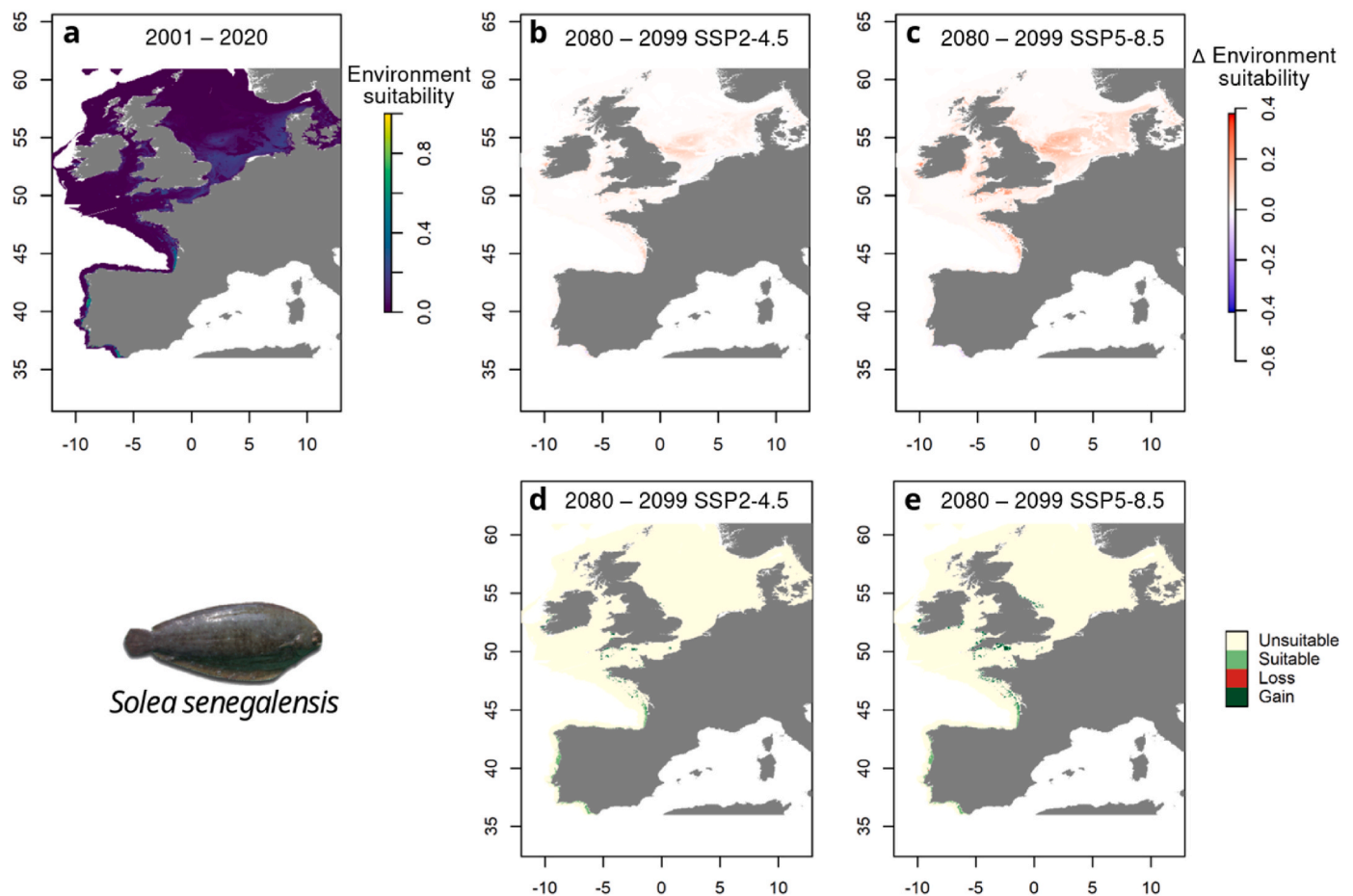


Fig. 7. Senegalese sole, *Solea senegalensis* environment suitability geographic projections resulting from the combination of bioclimatic and habitat suitability predictions weighted by a chosen predictive accuracy metric (e.g., TSS scores of statistical techniques retained in respective final ensemble forecasting): probabilistic environment suitability predictions for the present period (2001–2020 – a); their absolute variations to the future period (2080–2099) under the SSP2-4.5 (intermediate – b) and SSP5-8.5 (pessimistic – c) scenarios; and the resulting species range change under the SSP2-4.5 (d) and SSP5-8.5 (e) scenarios after binarisation.

the central and northern Irish Sea, Celtic Sea, Western English Channel, and Bay of Biscay continental shelf for ‘sub-boreal’ species, but also the southern Wadden Sea for flounder or along the southernmost Portuguese and Spanish coasts for the six MEO fish species. This should be put in relation with low present levels of chlorophyll-*a* and dissolved oxygen levels becoming limiting in the future (Fig. 1 and A.3). This interpretation is consistent with the negative trophic amplification, i.e., the decrease in primary production and zooplankton biomass in response to increase in ocean stratification that has been demonstrated in these areas (Chust et al., 2014a). However, this negative trophic amplification could likely be worse than expected if the Atlantic Meridional Overturning Circulation (AMOC) weakens over the 21st century (Collins et al., 2019). The contraction effect of chlorophyll-*a* and dissolved oxygen in these areas but also within the central North Sea would lead to an increase in potential species occupancy in areas where chlorophyll-*a* and dissolved oxygen levels would remain unchanged over time and still be sufficient for species settlement and survival (Fig. A.3). These areas would include the eastern British coasts, Kattegat, west of Jutland, Wadden Sea, southern North Sea, and coasts around the north-eastern Irish Sea for sea bass, common sole and the two ‘sub-tropical’ species; but also the remaining North Sea for seabass or the remaining coasts around the Irish Sea and English Channel, and the Bay of Biscay coastal waters for ‘sub-tropical’ species. In addition, the northward range expansion being greater for ‘sub-tropical’ than for ‘sub-boreal’ species was mainly explained by the fact that areas were currently calculated as unsuitable but would become suitable largely due to increasing temperatures (Fig. A.3). All these elements combined could explain distribution shifts

towards shallower areas closer to the coast for flounder, plaice and common sole or areas more far from the coast for seabass and ‘sub-tropical’ species. However, this difference in future use of the seabed between ‘sub-boreal’ and ‘sub-tropical’ species may probably be biased and due to the topology of the continental shelf in the Bay of Biscay. Indeed, as sub-tropical species move northward, the continental shelf becomes larger and their distribution can expand further from the coast.

Finally, the existence of three groups of species in our results with similar future distribution of suitable thermal habitats may be explained by finer thermal affinity differences. Flounder and plaice are the most cold-water ‘sub-boreal’ species and will not gain suitable areas due to their lower tolerance to warmer temperatures (>20 °C – Fig. A.3). Sea bass and common sole would gain suitable habitats in some places but to a lesser extent than the two warm-water species (i.e., meagre and Senegalese sole). This pattern of lower gains in suitable habitats is also highlighted for other highly cold-water (e.g., Acadian redfish *Sebastes fasciatus*, American plaice *Hippoglossoides platessoides*, Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, and thorny skate *Amblyraja radiata*), cool-water (e.g., spiny dogfish *Squalus acanthias*, and American lobster *Homarus americanus*), and warm-water (e.g., striped bass *Morone saxatilis*, summer flounder *Paralichthys dentatus*, and Atlantic croaker *Micropogonias undulatus*) species on the U.S. Northeast continental shelf (Kleisner et al., 2017). A relevant addition to this present work would be to expand the spatial extent of projected future distributions beyond the North Sea (e.g., the Norwegian Sea, Baltic Sea, Barents Sea, White Sea, or even the Irminger Sea, Denmark Strait, and

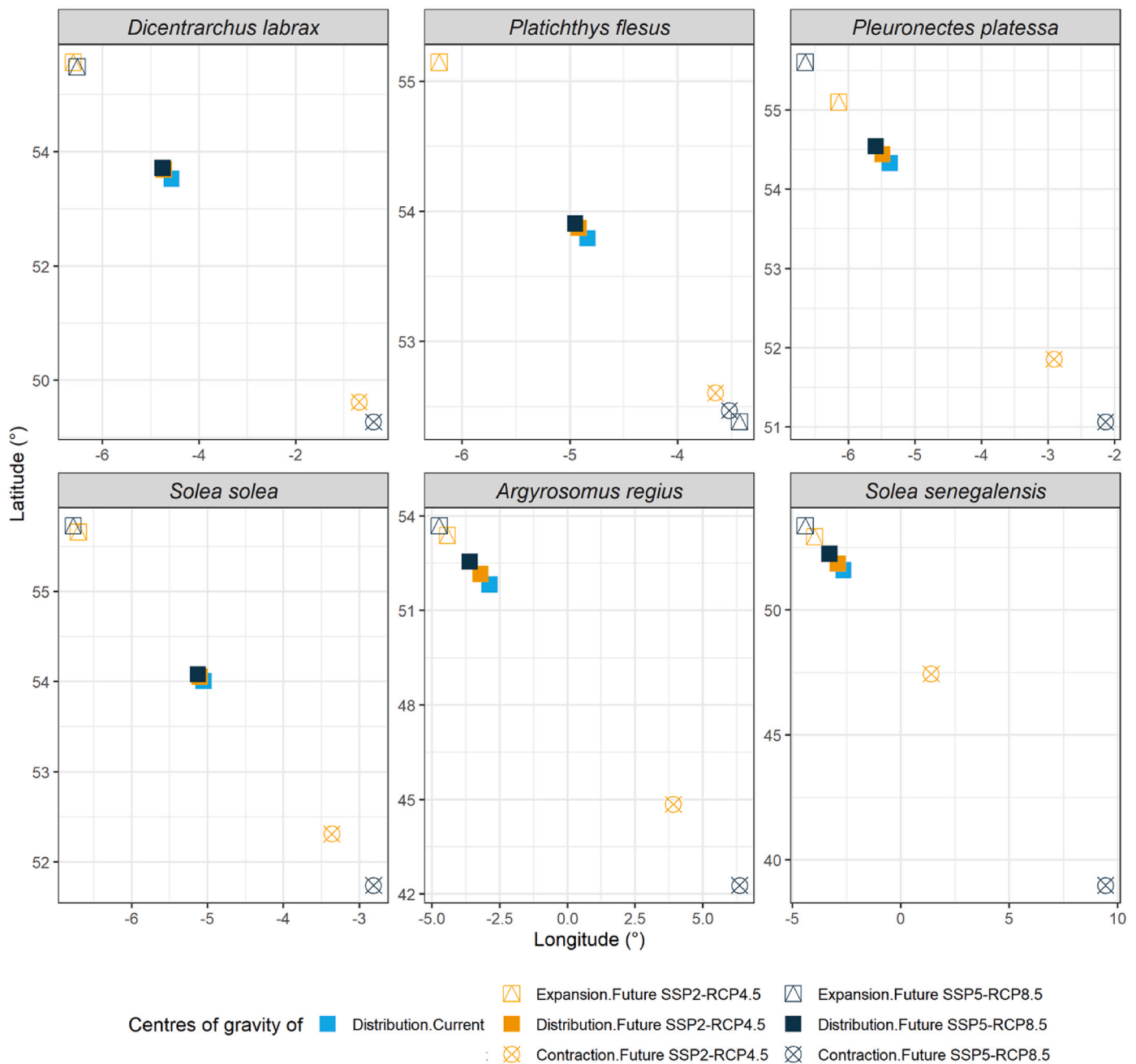


Fig. 8. Indicators of distribution shifts based on probabilistic environment suitability predictions – the centres of gravity of the distributions (COGDs – filled squares), the centres of leading edge expansions (COGEs – squares with a triangle inside), and the centres of trailing edge contractions (COGCs – circles with a cross inside) of geographic coordinates for the present (2001–2020 – blue) and future (2080–2099) periods under the SSP2-4.5 (intermediate – orange) and SSP5-8.5 (pessimistic – dark) scenarios. The specific case of *Platichthys flesus* COGE under the SSP5-8.5 scenario was due to a too low number of cells very localised within the Cantabrian trench where the absolute variations in probabilistic environment suitability predictions between the future and present periods were positive (see Fig. 3c). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Greenland Sea) where a positive trophic amplification would be reached in these areas in response to ocean stratification (Chust et al., 2014a).

4.4. Future research

To go further and notably to better understand transient dynamics and fine-scale organisms-environment relationships, future research should take into account a number of key-processes that are not included in this study such as population growth and dispersal dynamics, as well as stochasticity in demographic processes (Singer et al., 2018). In addition, to better discriminate potential and realized niches, it could be

relevant to use joint species distribution models such as the Hierarchical Modelling of Species Communities, in order to include the influence of biotic and random processes, species-specific life-history traits and inter-species phylogenetic relationships in addition to the environmental influence (Tikhonov et al., 2017).

Regarding the specific case of MEO, next step would be to consider connectivity between the marine habitats of adults and the estuarine habitat of juveniles (Gillanders et al., 2003; Whitfield et al., 2023). Hence, a relevant perspective could be to consider several functioning habitat types through ontogenetic life-history stages of MEO fish species (i.e., growth, feeding, spawning grounds, and migration corridors –

Table 1

Indicators of distribution shifts based on probabilistic environment suitability predictions – the centres of gravity of the distributions (COGDs), the centres of leading edge expansions (COGEs), and the centres of trailing edge contractions (COGCs) of the actual displacement shift distance (north-westward displacement shift expressed in km) and components of this distance along the longitudinal (westward component displacement shift expressed in km) or the latitudinal (northward component displacement shift expressed in km) axis for the present (2001–2020) and future (2080–2099) periods under the SSP2-4.5 (intermediate) and SSP5-8.5 (pessimistic) scenarios. The percentages in brackets represented the relative contribution of the longitudinal or latitudinal displacement shift to the actual displacement shift.

Species	Thermal affinity	North-westward displacement shift (km)		Westward component displacement shift (km)		Northward component displacement shift (km)	
		SSP2-4.5	SSP5-8.5	SSP2-4.5	SSP5-8.5	SSP2-4.5	SSP5-8.5
COGDs							
<i>Dicentrarchus labrax</i>	Sub-boreal	20.97	24.67	10.72 (26%)	12.58 (26%)	18.03 (74%)	21.23 (74%)
<i>Platichthys flesus</i>	Sub-boreal	10.48	14.91	5.34 (26%)	7.57 (26%)	9.02 (74%)	12.84 (74%)
<i>Pleuronectes platessa</i>	Sub-boreal	14.46	27.31	7.27 (25%)	13.70 (25%)	12.50 (75%)	23.64 (75%)
<i>Solea solea</i>	Sub-boreal	6.45	9.76	3.27 (26%)	4.92 (25%)	5.56 (74%)	8.43 (75%)
<i>Argyrosomus regius</i>	Sub-tropical	43.14	94.74	22.61 (27%)	49.80 (27%)	36.79 (73%)	80.84 (73%)
<i>Solea senegalensis</i>	Sub-tropical	34.04	85.38	17.93 (28%)	44.99 (28%)	28.96 (72%)	72.77 (72%)
COGEs							
<i>Dicentrarchus labrax</i>	Sub-boreal	262.40	251.87	135.04 (26%)	129.58 (26%)	226.94 (74%)	217.78 (74%)
<i>Platichthys flesus</i>	Sub-boreal	175.06	183.06	90.61 (26%)	92.94 (26%)	150.65 (74%)	156.79 (73%)
<i>Pleuronectes platessa</i>	Sub-boreal	98.55	163.33	49.71 (25%)	82.60 (25%)	85.36 (75%)	141.65 (75%)
<i>Solea solea</i>	Sub-boreal	212.17	221.05	108.11 (25%)	112.66 (25%)	183.84 (75%)	191.57 (75%)
<i>Argyrosomus regius</i>	Sub-tropical	202.27	241.96	106.76 (27%)	127.89 (27%)	172.95 (73%)	207.05 (73%)
<i>Solea senegalensis</i>	Sub-tropical	174.03	230.55	92.10 (28%)	122.09 (28%)	148.51 (72%)	197.06 (73%)
COGCs							
<i>Dicentrarchus labrax</i>	Sub-boreal	510.40	554.54	257.28 (25%)	276.98 (25%)	433.98 (72%)	472.68 (73%)
<i>Platichthys flesus</i>	Sub-boreal	154.07	171.41	78.16 (26%)	86.70 (26%)	132.12 (74%)	147.08 (74%)
<i>Pleuronectes platessa</i>	Sub-boreal	321.03	424.17	160.22 (25%)	210.63 (25%)	275.43 (74%)	363.44 (73%)
<i>Solea solea</i>	Sub-boreal	219.78	293.66	110.66 (25%)	146.67 (25%)	188.58 (74%)	252.12 (74%)
<i>Argyrosomus regius</i>	Sub-tropical	924.34	1270.65	467.79 (26%)	636.03 (25%)	776.41 (71%)	1062.15 (70%)
<i>Solea senegalensis</i>	Sub-tropical	546.43	1686.88	280.18 (26%)	835.98 (25%)	461.59 (71%)	1401.54 (69%)

Levin and Stunz, 2005) as proposed in multi-state distribution models (Frans et al., 2018). The next step would be to collect a biological database with estuarine occurrences but also, more importantly, to obtain environmental variables and their projections in estuaries. This would be a great challenge for the European Union, which is investing in this subject of reducing observation gaps in the land-sea continuum through satellite imagery. Nonetheless, more process-driven modelling approaches require more data and are time-consuming. Therefore, the degree of biological realism chosen in modelling approaches should be analyzed in the light of the work objectives.

CRedit authorship contribution statement

Anaïs Janc: Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Chloé Dambrine:** Writing – review & editing, Validation. **Patrick Lambert:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Géraldine Lassalle:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Mario Lepage:** Writing – review & editing, Validation. **Jérémy Lobry:** Writing – review & editing, Validation. **Maud Pierre:** Writing – review & editing, Validation. **Trond Kristiansen:** Writing – review & editing, Validation, Resources. **Momme Butenschön:** Writing – review & editing, Validation, Resources. **Henrique N. Cabral:** Writing – review & editing, Validation, Project administration, Funding acquisition.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2024.109013>.

Data availability

Data will be made available on request.

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