Biologically meaningful distribution models highlight the benefits of the Paris Agreement for demersal fishing targets in the North Atlantic Ocean

Running Head: Future of demersal fish in differing scenarios

Abstract

Aim: With climate change challenging marine biodiversity and resource management, it is crucial to anticipate future latitudinal and depth shifts under contrasting global change scenarios to support policy-relevant biodiversity impact assessments (e.g., Intergovernmental Panel on Climate Change; IPCC). We aim to demonstrate the benefits of complying to the Paris Agreement (UN Framework Convention on Climate Change) and limiting environmental changes, by assessing future distributional shifts of 10 commercially important demersal fish species.

Location: Northern Atlantic Ocean

Time period: Distributional shift analyses compared near present-day conditions (2000-2017) with two Representative Concentration Pathway (RCP) scenarios of future climate changes (2090-2100). One following the Paris Agreement climate forcing (RCP2.6) and another without stringent mitigation measures (RCP8.5).

Major taxa studied: Demersal fish

Methods: We use machine learning distribution models coupled with biologically meaningful predictors to project future latitudinal and depth shifts. Structuring projections with information beyond temperature-based predictors allowed us to better encompass species physiological limitations.

Results: Our models highlighted the additional role of temperature, primary productivity, and dissolved oxygen to shape fish distributions (average relative contribution to the models of 32.12±10.24%, 15.6±7.5% and 12.1±6.1%, respectively). We anticipated a generalized trend of poleward shifts in both future scenarios, with aggravated changes in suitable area with RCP8.5 (average area loss with RCP2.6= 13.3±4.1%; RCP8.5= 40.9±13.3%). Shifts to deeper waters were also predicted to be of greater magnitude with RCP8.5 (average depth gain= 25.4±21.5m) than with RCP2.6 (average depth gain= 10.4±7.9m). Habitat losses were mostly projected in the Mediterranean, Celtic and Irish Seas, the southern areas of the North Sea and along the NE coast of North America.

Main conclusions: Including biologically meaningful predictors beyond temperature in species distribution modelling can improve predictive performances. Limiting future climate changes by complying with the Paris Agreement can translate into reduced distributional shifts, supporting biodiversity conservation and resource management.

Keywords: Biologically meaningful predictors, Climate change, Demersal fish, North Atlantic fisheries, Paris Agreement, Species Distribution Modelling

Introduction

Empirical evidence shows climate-driven changes producing poleward and depth shifts across marine taxa (Pinsky et al., 2020). Future changes in physical (e.g. temperature), chemical (e.g. oxygen content) and biological (e.g. primary productivity) ocean components, linked to greenhouse gas emissions, are expected to further shift the distribution of species and ecosystems (Champion et al., 2018; Cheung et al., 2010), with severe implications for marine biodiversity and fisheries (Poloczanska, 2013; Sumaila et al., 2011; Weatherdon et al., 2016). On one side, local population extinctions at low latitude distributional margins might produce negative cascading effects and reduce global genetic pools (Cheung et al., 2013). On the other side, expansions to higher latitudes might change biological interactions (e.g., competition) and restructure the composition of biological communities (Pecl et al., 2017).

To timely address potential changes, the Paris Agreement was developed to provide a roadmap limiting global warming below 2°C above pre-industrial levels while striving to contain the increase to 1.5°C (United Nations Framework Convention on Climate Change, 2015). This initiative considered climate change impact assessments on biodiversity (e.g., Intergovernmental Panel on Climate Change; IPCC) based on policy-relevant research (Geden, 2016). Such assessments are mostly performed with Species Distribution Modelling (SDM) contrasting near present-day distributions with projections derived from atmosphere-ocean general circulation models (AOGCMs), which estimate climate conditions under different concentrations of greenhouse gases and mitigation strategies (Handorf & Dethloff, 2012; Melo-Merino et al., 2020). SDM has the advantage of allowing ecological applications across taxa and systems, however, models not incorporating the broad complexity of environmental conditions driving geographic distributions could yield misleading impact assessments (McHenry et al., 2019; Spence & Tingley, 2020). For instance, marine SDM generally miss important drivers beyond thermal conditions, even though the distribution of organisms is influenced by additional drivers like dissolved oxygen, salinity, primary productivity, nutrients, among others (Duncan et al., 2020; Pörtner & Farrell, 2008; Pörtner & Knust, 2007; Sunday et al., 2012).

Here we produce a policy-relevant biodiversity impact assessment anticipating future distributional shifts of 10 demersal fish species with high commercial value in the intensively exploited northern Atlantic Ocean (EU, 2018; FAO Fisheries Department, 2011). In this broad area, climate conditions are changing significantly (Cheung et al., 2010; Free et al., 2019) and producing distributional shifts for demersal fish, both latitudinally and in depth (Mills et al., 2013; Perry et al., 2005). For instance, exposure to oxygen minimum zones (OMZ) is escalating in the northern Atlantic, with most of the worlds' anoxic regions (Breitburg et al., 2018) expanding to coastal areas where fishing targets reside (Diaz & Rosenberg, 2008). In the same way, the expected changes in primary productivity and nutrient availability might further produce a challenging environment for fish to thrive (Cheung et al., 2010). Accordingly, fisheries management might be less effective in the face of environmental changes (Baudron et al., 2020), with conflicts over catch allocation as fishing targets shift across management boundaries which can lead to the discard of high fished volumes due to poor allocation of fish stocks based on outdated species distribution information (Bell et al., 2015; Miller & Munro, 2004).

Previous studies striving to anticipate future distributions of fish species in the northern Atlantic Ocean have mostly been focused on single species and largely neglected additional predictors such as oxygen availability or productivity changes (Kleisner et al., 2017; Rutterford et al., 2015). We use machine learning SDM fitting a comprehensive dataset of species' occurrence records with biologically meaningful predictors (i.e. predictors that are known to directly impact species physiology, and therefore potentially structure distributional limits; Rödder & Lötters, 2010) tailored for demersal conditions. Near present-day distributional patterns are compared with two scenarios of future climate change: the Representative Concentration Pathway 2.6 (van Vuuren et al., 2011), following the Paris Agreement expectations of global warming levels below 2 °C (Wang et al., 2018), and the Representative Concentration Pathway 8.5 (Riahi et al., 2011), with minimal mitigation measures and greater climatic changes. By comparing contrasting future scenarios we aim to provide key information for IPCC impact assessments, for the fulfilment of the Sustainable Development Goals of the 2030 Agenda (United Nations General Assembly, 2015) and for better-informed conservation and management. We hypothesize that (i) additional drivers beyond thermal conditions are key to model the distribution of demersal fish and that (ii) latitudinal and depth shifts are positively correlated with anthropogenic greenhouse gas emissions, so that there is a substantial benefit to comply with the Paris Agreement (as inferred for terrestrial climate; Warren et al., 2018), limiting global changes and consequently biodiversity losses.

Methods

Focal species and study area

We modelled near present-day and future distributions of 10 demersal fish species (Table 1) throughout the northern Atlantic Ocean and adjacent Seas (i.e., the Mediterranean Sea, the Black Sea and the Barents Sea; study area extending from 120°E to 120°W and from 30°N to 90°N). In this region, fishing gears targeting demersal species (demersal purse seiners and trawlers) are more prominently present in the North-East (Fig. 1b). For this reason, we focused our study on species that are geographically concentrated on the eastern side of the ocean while still having high commercial value on the whole Atlantic (EU, 2018; FAO Fisheries Department, 2011). Focal species have different depth ranges, which were considered while modelling distributions (Table 1), and are exclusively demersal, with the exceptions of *Clupea harengus* and *Micromesistius poutassou*. The former is a demersal spawner (Stratoudakis et al., 1998) and the latter performs diel vertical migrations and spends a large portion of the daytime near the bottom (Johnsen & Godø, 2007). Both species are frequently caught by fishing gears targeting demersal fish assemblages (Afzali et al., 2021; Sousa et al., 2005).

Data sources

Occurrence records for each species were obtained from GBIF (https://www.gbif.org/) and OBIS (https://www.obis.org/; Refer to Appendix S1 for all downloaded dataset citations). These were pruned to ensure that those included in the modelling framework matched each species known distribution and also the time span of predictors (2000 and 2017; please refer to Appendix S2). Predictors were obtained from Bio-ORACLE, a dataset providing layers at 5 arcmin resolution (data processing detailed by Assis et al., 2018; Tyberghein et al., 2012). These included long-term maximum and minimum temperatures (MaxTemp and MinTemp; ^{o}C), long-term minimum salinity (Salinity; PSS), mean dissolved oxygen concentration (Oxygen; mol.m^{-3}) and mean primary productivity (Productivity; g.m^{-3}.day^{-1}). Predictors focused on the benthic realm (i.e., along the bottom) for near present-day conditions (long-term climatologies between 2000 and 2017) and the two contrasting scenarios of global change RCP2.6 and RCP8.5. From the 3 benthic layers available per predictor in Bio-ORACLE, we choose to model species' distributions with the average depth layer. The RCP layers are provided as the ensemble of distinct models from the Coupled Model Intercomparison Project, namely, CCSM4, GFDL-ESM2G, HadGEM2-ES, IPSL-CM5A-LR and MIROC-ESM for temperatures and salinity, GFDL-ESM2G, HadGEM2-ES, IPSL-CM5A-LR for dissolved oxygen concentration and GFDL-ESM2G, IPSL-CM5A-LR, MIROC-ESM for primary productivity. Prior to modelling, Pearson's correlation coefficient was determined for all pairs of predictors, as well as the Variance Inflation Factor (VIF).

Gridded data of fishing effort from 2012-2016 (average hours per cell) was obtained from the Global Fishing Watch (Kroodsma et al., 2018) and filtered to only include fishing gear relevant to our focal species (demersal purse seiners and trawlers). These data were resampled using nearest neighbour method (Hofstra et al., 2008) to match the resolution and spatial extent of predictors.

Species Distribution Modelling

The distribution of species was modelled by ensembling (Araújo & New, 2007) the response of Boosted Regression Trees (BRT) and Adaptive Boosting (AdaBoost), two machine learning algorithms with high predictive performances in SDM (Assis, Araújo, et al., 2018; Krause-Jensen et al., 2020) that automatically fit complex interactions between predictor variables and non-linear relationships, while reducing overfitting by optimal parametrization and monotonicity responses (Elith et al., 2008; Hofner et al., 2011). The algorithms fitted occurrence records per species (presences and pseudo-absences) against the predictor variables. Pseudo-absences were randomly generated in a 1:1 ratio with each species presence records, in locations where no presences were recorded (Barbet-Massin et al., 2012) and geographically limited to the biogeographic provinces (Spalding et al., 2007) where the species occur and their neighbouring provinces. This kept pseudo-absences in areas where dispersal might potentially occur, a crucial step to accurately produce SDM (Barve et al., 2011). To eliminate excessive information, the correlation between predictors within the range of occurrence records was assessed as a function of geographic distance (Boavida et al., 2016). This was accomplished by building a correlogram to identify the shortest distance between occurrence records, at which predictors were not spatially correlated. Records were then thinned by randomly selecting one record from the groups falling within correlated distances.

A cross-validation (CV) framework with 10-fold latitudinal bands was implemented to find the optimal hyperparameter combination reducing overfitting and improving the potential for model's transferability (Assis, Araújo, et al., 2018; Krause-Jensen et al., 2020; Vignali et al., 2020). The "grid search" method was used to test all possible hyperparameter combinations of number of trees (50 to 1000, step 50), tree complexity (1 to 6) and learning rate (0.01, 0.005 and 0.001) for BRT, and number of interactions (50–250, step 50), shrinkage (0.25–1, step 0.25) and degrees of freedom (1–12) for AdaBoost (Fragkopoulou et al., 2021; Krause-Jensen et al., 2020). Models trained interactively the different hyperparameters by fitting occurrence records with one withheld latitudinal band at a time, where performance was tested with the area under the curve (AUC) of the receiver operating characteristic curve (Fragkopoulou et al., 2021; Vignali et al., 2020). The optimal hyperparameter combination was found as the one producing models with higher AUC in CV (Fragkopoulou et al., 2021; Krause-Jensen et al., 2020; Vignali et al., 2020). Overfitting was further controlled by forcing predictors to fit monotonic responses based on the biological effect (positive or negative) expected on species' probability of occurrence (Hofner et al., 2011). MaxTemp fitted negative monotonic responses, while MinTemp, Salinity, Oxygen and Productivity fitted positive monotonic responses. Species' depth range, predictor choice and monotonic responses were set based on literature (Appendix S1). The cross-validation framework further allowed estimating the performance and potential transferability of the models in independent data, by reporting the average AUC obtained in CV when modelling with the optimal hyperparameters (e.g., Assis, Araújo, et al., 2018; Boavida et al., 2016; Fragkopoulou et al., 2021; Krause-Jensen et al., 2020).

Final predictive BRT and AdaBoost models were trained with the full occurrence dataset, the predictor variables and the optimal hyperparameters found in cross-validation (Assis, Araújo, et al., 2018; Vignali et al., 2020). Predictive performance was also assessed with AUC and sensitivity (both metrics vary between 0 and 1) with models with AUC > 0.8 considered excellent performing models and sensitivity describing the proportion of accurately predicted occurrences (Allouche et al., 2006; Hosmer & Lemeshow, 2000). The relative contribution of predictors to the models was assessed by computing the increase in AUC when each predictor was added to its alternative full model (i.e., model including all predictors except that being tested). Wilcoxon Rank tests inferred the significant increase of each predictor contribution when compared to its alternative full model.

Distribution maps representing habitat suitability per species were produced for near present-day conditions and the two global change scenarios with BRT and AdaBoost. These maps were further reclassified to binomial presence-absence surfaces using a threshold maximizing both sensitivity and specificity (i.e. true negative rate; Assis, Araújo, et al., 2018; Jiménez-Valverde & Lobo, 2007). Climatic physiological limitations to species' distributions, i.e., tipping points from which the models predict absence, were inferred by producing individual response functions for each predictor, while accounting for the average effect produced by all alternative predictors (Assis et al., 2017; Elith et al., 2008). Along each individual response function, tipping points were captured by extracting the extreme climatic values (maximum or minimum depending on the predictor) setting the transition between suitable and unsuitable habitat conditions, while considering the reclassified binomial predictive surface (Boavida et al., 2016).

Latitudinal and depth distributional shifts

Latitudinal and depth distributional shifts were inferred by ensembling (mean function; Araújo & New, 2007) the maps produced with BRT and AdaBoost for near present-day conditions and each of the RCP scenarios. The ensembles followed the previously detailed reclassification approach to binomial presence-absence surfaces using the maximization of sensitivity and specificity. Distributional shifts were characterized by mirror density plots reflecting species' potential latitudinal changes and by producing aggregated maps reflecting gained and lost habitats from near present-day conditions to future times.

The average and maximum predicted depth was determined per species by crossing a bathymetry layer obtained from Bio-ORACLE with the reclassified binomial maps. Depth shifts were assessed by comparing the median depth of species distributions in the present and future scenarios. Finally, the 50% and 75% kernel density of the distribution of fishing effort was estimated to assess if areas of current high fishing effort might suffer future changes of suitable habitats for demersal fish. The assessment was made by comparing the proportion of species' distributions in areas of high fishing activity in near-present day conditions and in future conditions.

Results

Species Distribution Models

The distribution models using the optimal combination of hyperparameters (Appendix S3) produced predictions with high performance rates, both when tested in cross-validation (average AUC in CV of BRT: 0.86 ± 0.03; average AUC in CV of AdaBoost: 0.82 ± 0.04; Table 1; Appendix S3) and when ensembled in unique models (average AUC: 0.92 ± 0.02; Table 1). The ensembles reflected each species known distributional and depth ranges (see Appendix S2 for maps contrasting occurrence records and predicted distributions). Focal fish species distributions were mostly predicted in the Celtic, Irish and North Seas, and along the coasts of Norway and Iceland (Fig. 1a).

Table 1 Modelled species, their known depth range (in meters) and performance of Boosted Regression Trees (BRT) and Adaptive Boosting (AdaBoost) distribution models in cross-validation and when ensemble in a final predictive model. For more comprehensive information of model performance refer to Appendix S3.

[1](Wright et al., 2000) ; [2](Coad & Reist, 2004); [3](Frimodt, 1995); [4](Cohen et al., 1990); [5](Muus & Nielsen, 1999); [6](Lloris et al., 2005); [7](Relini et al., 1999).

Figure 1 Proportion of near present-day suitable habitats, fishing effort and distributional range shifts (loss and gain of suitable habitats from near present-day conditions, 2000-2017, to future RCP climate change scenarios, 2090-2100; please refer to Appendix S2 for individual projections per species). Colour gradients reflect the proportion of species (panel a) predicted with suitable habitats and (panels c-f) who lost or gained suitable habitats (yellow to dark red depicting >0 to 1 proportion scale). In panel b, the 50% (blue) and 75% (red) kernel utilization distribution of the fishing activity in the study area are represented.

The predictors considered in the models significantly increased predictive performances (> 0.8 proportion of improved models; Fig. 2). Temperatures (i.e., maximum, and minimum) alongside productivity were the main drivers explaining distributions, with a combined average contribution of 79.9% (TempMax: 27.9%; TempMin: 36.4%; Productivity: 15.6%; Fig. 2a). Oxygen and salinity had lower contributions (oxygen: 12.1%; salinity: 7.9%; Fig. 2a) nevertheless, for some species, these predictors reached up to 23.0% and 17.2% contribution, respectively (e.g., *Dicentrarchus labrax*). Additional contribution extremes/outliers were verified for *M. poutassou* (minimum temperature: 58.6%; salinity: -0.8%; productivity 1.4%) and *Ammodytes marinus* (productivity: 30.5%; for species specific variable contributions see Appendix S3). These findings are supported by the overall low correlation found between predictors; only minimum and maximum temperatures showed stronger correlation (Pearson's Correlation 0.82; VIF > 5; Appendix S4 - Figure S4a; Table S4), yet their opposite monotonic fit in both BRT an AdaBoost (positive for minimum temperature and negative for maximum temperature) allowed removing potential confounding inferences about the contribution of both predictors.

Focal species were predicted to find suitable habitat conditions in areas with near present-day average minimum temperatures between 0.1°C - 5.4°C, maximum temperatures ranging from 13.6°C - 20.2°C, dissolved oxygen concentrations inside the range 160.4 $mol.m^{-3}$ - 248.3 $mol.m^{-3}$, and salinity between 7.8 PSS - 33.9 PSS. Productivity tipping points were found above oligotrophic conditions of 0 - 0.1 $g.m-3.day^{-1}$ (Fig. 2b; for species specific variable tipping points see Appendix S3).

Figure 2 Average relative contribution (a) and physiological tipping point (b) of each predictor inferred with Boosted Regression Trees and Adaptive Boosting across all species. Horizontal lines represent the mean contribution and tipping points (i.e., physiological tolerances) of each predictor. Values above boxes indicate the proportion of models developed for each species where predictors retrieved significantly higher contributions to their performance. Variable units: Oxygen ($mol.m^{-3}$); MinTemp, MaxTemp (°C); Salinity (PSS); Productivity ($g.m^{-3}.day^{-1}$).

Latitudinal and depth distributional shifts

All species were projected to shift distributions poleward in both future scenarios, yet with greater changes in suitable areas (Fig. 1c-f; Table 2) and latitudinal limits (Fig. 3) when considering RCP8.5 (average range gain: 54.5±35.7%; average range loss: 40.9±13.4%) than with RCP2.6 (average range gain: 17.9±11.8%; average range loss: 13.4±4.1%). Latitudinal shifts were often coupled with depth shifts to deeper waters, which were also greater with RCP8.5 (average depth gain= 25.4±21.5m; 7 out of 10 species shift to deeper waters) than with RCP2.6 (average depth gain= 10.4±7.9m; 8 out of 10 of species shift to deeper waters; Fig. 3).

In terms of suitable habitats, *C. harengus, Gadus morhua*, *Melanogrammus aeglefinus* and *M. poutassou* had the greatest range gain, while being among those with lower range loss (Table 2). These species have the potential to colonize coastal and open waters in the Barents, Kara, Norwegian, Greenland, and Iceland Seas, the Hudson Bay and Western Arctic ocean (see Appendix S2 for species specific distribution projections under all scenarios analysed). Contrarily, *A. marinus*, *D. labrax, Merluccius merluccius*, *Pleuronectes platessa*, *Raja clavata* and *Solea solea* had smaller range gain and greater loss (with loss being concentrated in the southern section of their ranges). These species mostly colonize coastal waters in Norwegian, Iceland, and Greenland Seas (Appendix S2). Changes in latitudinal range were a result of the colonization of the northernmost regions of the study area (especially for species with greater range gain) and the loss of southern suitable range (particularly evident for species with greater range loss; Fig. 3).

Figure 3 Latitudinal and depth shifts projected for demersal fish in the northern Atlantic with the scenarios RCP2.6 and RCP8.5 (future scenarios cover the time period 2090-2100). Yellow represents near present-day distributions; purple and blue represent distributions under RCP2.6 and RCP8.5, respectively. Dashed lines represent the median latitude and median depth of occurrence.

Table 2 Near present-day (from year 2000 to year 2017): total area (km^2) and percentage of species' distributions inside areas of high fishing effort (FE50 and FE75). RCP2.6 and RCP8.5 (from 2090-2100): Percentage of lost and gained habitats in each future global change scenario, and percentage of future distribution inside areas of high fishing effort. FE50 and FE75 represent 50% and 75% kernel utilization distribution of fishing effort, respectively. Bold values depict area changes above 50% and values between parentheses show difference in percentage of species distributions inside areas of high fishing effort between near present-day and each future scenario.

Loss of suitable range is mostly concentrated in the Mediterranean Sea, Celtic and Irish Seas, southern areas of the North Sea (especially along the English Channel), and in the NE North American coast (Fig. 1c, Fig. 1d). Poleward shifts are mostly projected towards the Barents, Greenland, Kara, Norwegian, Iceland Seas, Hudson Bay and Western Arctic Ocean (Fig. 1e, Fig. 1f). The geographic pattern of where species might lose or gain suitable areas are similar in both scenarios, yet more pronounced in RCP8.5 (Fig. 1c-f; Table 2).

Areas of high fishing effort are predominantly distributed in the northeast Atlantic, particularly in the Celtic, North, Iceland, Norwegian and Barents Seas (Fig. 1b). This matched regions where species are predicted to be distributed in near present-day conditions (suitable habitats overlapping areas of high fishing effort: FE50=61.75±16.54%, Table 2) and projected in the future, (suitable habitats overlap ranging from 52.16±27.16% to 79.36±16.19, depending on the climate scenario and fishing effort, Table 2). The projected distributional changes in areas of high fishing effort are more pronounced in RCP85 than RCP26 (Table 2), while the gain in suitable habitats in these areas (i.e., in Iceland, Norwegian and Barents Seas) surpass the projected losses, regardless of the climate scenario (i.e., in Celtic and North Seas; Fig. 1c-f; Table 2).

Discussion

In the present study we anticipate future distributional shifts for demersal fish of high commercial value in the northern Atlantic Ocean. On rare occasions, past studies have modelled species distributions based on predictors beyond temperature (e.g. Jones & Cheung, 2015), yet, to our knowledge, this is the first attempt to integrate biologically meaningful predictors like oxygen, primary productivity, and salinity alongside temperature conditions, to assess the potential consequences of future climate changes to marine fish biodiversity at such large scales. Along the lines of previous research looking at species' response to past and future climate change (Morato et al., 2020; Pinsky et al., 2020), our models predicted generalized poleward shifts across all modelled species. As hypothesized, greater changes to species' distributions (i.e., suitable areas, latitudinal and depth distributions) were predicted under the higher greenhouse gas emission scenario (RCP8.5), suggesting that broad compliance with the Paris Agreement might potentially mitigate the negative impacts of global climate change to fish biodiversity, benefiting commercial fisheries and resource management (Baudron et al., 2020; Bell et al., 2015; Miller & Munro, 2004).

Overall, the most important predictors shaping demersal fish distributions (i.e., extreme temperatures and productivity) are in line with previous studies (Valavanis et al., 2004). Temperature directly impacts species' physiology, and the modelled species, with contrasting distributional patterns, exhibited specific thermal limits and predictor affinities. Minimum temperature, for instance, contributed more than average to *M. poutassou*, a species with its northern range bordering the Arctic waters, where extreme cold conditions potentially impose an important physiological barrier. Contrarily, the lower contribution of maximum temperature to *D. labrax* can result from its warmer affinity (Beare et al., 2004), allowing the species to extend ranges to the low latitude limits of our study area. Besides temperature dependent niche affinities, fish species favour high productivity waters (Cheung et al., 2008), and this was evident for most modelled species (productivity tolerance limits above oligotrophic conditions). In particular, *A. marinus* strongly relied on this variable since its distribution exclusively comprises the productive waters of the North and Irish Seas and the inner seas of the West coast of Scotland (Capuzzo et al., 2018). Beyond these areas, productivity sharply decreases and so does the species known and predicted distribution. Contrastingly, productivity had a lower contribution for *M. poutassou*. In pair with its wide-ranging distribution in the northern Atlantic Ocean, this species is also found in the Mediterranean Sea, a region known for poor nutrient / productivity conditions (Huertas et al., 2012). Salinity and dissolved oxygen were further identified as important drivers to model demersal fish species. The first controls osmoregulation mechanisms, with areas falling outside tolerance limits presenting sharp distributional barriers (Evans & Claiborne, 2009). Such premise was verified for the species with salinity tolerance limits above 28 PSS and absent from the Baltic Sea, the wider hyposaline region of the study area (Bagdonas et al., 2011). The more tolerant species *P. platessa* and *C. harengus* (tolerance limits of 7.66 PSS and 9.66 PSS, respectively) can expand ranges into such conditions. Low oxygen barriers prevail where species oxygen demand, as well as their capacity for extraction and metabolic suppression exceeds local availability (Pörtner & Knust, 2007). Overall, the inferred tolerance limits largely match known thresholds of hypoxia for marine fish (average of approx. 200 mol.m^{-3}; Vaquer-Sunyer & Duarte, 2008), highlighting the key role of this variable for marine fish and strengthening the ecological significance of our models.

Distribution models reflecting meaningful biological traits showed the species favouring cold and eutrophic conditions that might change in the years to come. In particular, the critically identified regions with potential habitat losses (i.e., the Mediterranean Sea, the Celtic and Irish Seas, the southern proportion of the North Sea and the NE coast of North America) have been previously signed for faster warming rates and prone to future losses across biodiversity (Dulvy et al., 2008; Lejeusne et al., 2010; Saba et al., 2016; Weinert et al., 2016). Projected latitudinal shifts were further coupled with depth shifts, as hypothesized. Much like altitudinal shifts in terrestrial climates, stable deeper regions, less prone to abrupt warming when compared to superficial waters, seem crucial refugia for species to successfully cope with future climate conditions (Jorda et al., 2020). However, for some of the modelled species, distributional shifts produced shallower ranges, stemming from the loss of suitable deeper areas in near present-day conditions. This is likely to occur in deep areas of low latitude ranges where near present-day environmental conditions already border physiological tolerances (Osovitz & Hofmann, 2007).

Ensemble model projections showed how higher emission scenarios might translate into synergistic climate interactions linked to global warming, and greater distributional changes for demersal fish species. For instance, reduced dissolved oxygen is associated with warming conditions (Pörtner & Knust, 2007). This is particularly evident in projections along the coastlines of the northern Atlantic Ocean (Appendix S4 – Fig. S4d), acting synergistically with temperature in creating unsuitable habitats. Salinity is also projected to change in the years to come, yet with some regions impacted by an overall increase (Saba et al., 2016), while others by salinity reductions due to freshwater runoff from melting ice (Belkin et al., 1998). The spatial variation of this driver in the future ocean is likely to pose great challenges to species distributional ranges. In terms of primary productivity, projections show an actual increase in coastal waters (Appendix S4 – Fig. S4f), benefiting fish populations inhabiting regions where future temperatures do not surpass species' specific tolerance limits.

The produced biodiversity impact assessment has an inherent degree of uncertainty and oversimplification that should be acknowledged and discussed. Firstly, it did not account for biotic interactions that might impact the capacity of species to shift distributions and successfully colonize new suitable areas (Selden et al., 2018). Neglecting this component might have led to overestimating species' potential to colonize new habitats in previously unsuitable areas. Secondly, it did not consider species' ability to adapt to new conditions imposed by climate change. While adaptation to new conditions has much relevance in the scope of anticipating climate-induced distributional shifts, itis highly unlikely to take place within the time frame considered (the next 80 years; Henson et al., 2017; Pinsky et al., 2020). Thirdly, other potential meaningful predictors such as sea bottom substrate (e.g. Koubbi et al., 2006; Maravelias et al., 2000; Maxwell et al., 2009) were not included in the SDM framework due to their unavailability at this study's spatial scale. This may have led to overestimated predicted distributions, hence, our results should be interpreted as estimates of abiotic niche conditions rather than fully realized niches. Finally, given the large spatial scale of this study, it is also possible that local conditions were not completely captured by AOGCM, like upwelling areas structuring future climate refugia (Lourenço et al., 2016). Nevertheless, models mimicked species' distributions and physiological tolerances, while integrating the best bioclimatic data available beyond thermal conditions alone.

Minimal climate change mitigation translated into greater environmental changes (RCP8.5) might produce larger negative consequences for demersal fish and the fisheries industry as a whole. Such is the case because more severe poleward shifts associated with greater environmental changes will be reflected in (i) increased need for investment in new fishing gear to adapt to new fishing conditions (Poloczanska, 2013; Sumaila et al., 2011) and (ii) will raise fishing trip costs to reach fishing grounds further north when compared to the potential cost associated with contained poleward shifts (Weatherdon et al., 2016). Coincidently, areas that currently have higher fishing effort were among those predicted to suffer greater species turnover in the future (area losses: Celtic and North Seas; area gain: Iceland, Norwegian and Barents Seas). By limiting distributional shifts, the need for fishing adaptation and changes in effort distribution is minimized. Furthermore, it allows species to more efficiently allocate resources to tackle additional threats alongside current climate change (e.g. overfishing and invasive processes). For instance, the combined effects of climate change, high fishing pressure and invasive processes have already caused great biodiversity loss in the Mediterranean Sea (Marbà et al., 2015; Occhipinti-Ambrogi, 2007). Together, our results emphasize the potential benefits of complying to the Paris Agreement, limiting global warming levels (Wang et al., 2018) and therefore changes to range shifts in commercially valuable demersal fish. Nonetheless, in either climate change scenario, adaptive measures such as fishing effort redistribution and fishing stock allocation are needed to reach sustainable exploitation of fish stocks and achieve SDG 14 targets. When rearranging the distribution of fishing effort, managers should strive to guide fishers to areas where targeted species are found, allowing for greater yield per fishing trip. Additionally, the allocation of fishing stocks per country should reflect species' distributions at time of allocation and their vulnerability to environmental conditions. Lack of consideration of climate change induced range shifts has already caused overfishing, massive discarding of fished volume and conflicts between neighbouring regions due to poor allocation of fishing effort and fish stocks (Baudron et al., 2020; Baudron & Fernandes, 2015). Conservation planning strategies should consider climate change impacts to achieve their maximum effectiveness. Marine spatial planning and MPAs in particular are promising conservation tools yet, the inclusion of climate change threats is still rare which reduces their potential effectiveness (Rilov et al., 2019). Accurate predictions that truly grasp species' physiological limitations as the ones here presented are key to provide a reliable policy-relevant biodiversity impact assessment (e.g., IPCC) and contribute with baseline projections for fishing stocks distribution and allocation of fishing effort.

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Data Accessibility Statement

The data that support the findings of this study are available from the corresponding author, upon reasonable request.

Conflict of Interest Statement

Authors declare no conflict of interest.

Table 1 Modelled species, their known depth range (in meters) and performance of Boosted Regression Trees (BRT) and Adaptive Boosting (AdaBoost) distribution models in cross-validation and when ensemble in a final predictive model. For more comprehensive information of model performance refer to Appendix S3. [1](Wright et al., 2000) ; [2](Coad & Reist, 2004); [3](Frimodt, 1995); [4](Cohen et al., 1990); [5](Muus & Nielsen, 1999); [6](Lloris et al., 2005); [7](Relini et al., 1999).

Scientific name	**Common name**	**Depth range (m)**	**Cross-validation**	**Final ensemble**	
			AUC (BRT / AdaBoost)	AUC	Sensitivity
Ammodytes marinus	Lesser sand eel	10-150[1]	0.92 / 0.89	0.97	0.95
Clupea harengus	Atlantic herring	0-364[2]	0.82 / 0.73	0.87	0.79
Dicentrarchus labrax	European seabass	0-100[3]	0.83 / 0.80	0.92	0.95
Gadus morhua	Atlantic cod	0-600[4]	0.82 / 0.73	0.89	0.89
Melanogrammus aeglefinus	Haddock	0-450[5]	0.86 / 0.81	0.93	0.92
Merluccius merluccius	European hake	30-1075[6]	0.87 / 0.85	0.93	0.92
Micromesistius poutassou	Blue whiting	150-3000[4]	0.84 / 0.82	0.92	0.79
Pleuronectes platessa	European plaice	0-200[5]	0.89 / 0.86	0.95	0.97
Solea solea	Common sole	0-150[5]	0.86 / 0.82	0.93	0.88
Raja clavata	Thornback ray	0-700[7]	0.84 / 0.81	0.93	0.91

Table 2 Near present-day (from year 2000 to year 2017): total area (km^2) and percentage of species' distributions inside areas of high fishing effort (FE50 and FE75). RCP2.6 and RCP8.5 (from 2090-2100): Percentage of lost and gained habitats in each future global change scenario, and percentage of future distribution inside areas of high fishing effort. FE50 and FE75 represent 50% and 75% kernel utilization distribution of fishing effort, respectively. Bold values depict area changes above 50% and values between parentheses show difference in percentage of species distributions inside areas of high fishing effort between near present-day and each future scenario.

Species	**Near present-day**			**RCP2.6**				
	Area (x10^3 km^2)	% FE50	% FE75	Area loss (%)	Area gain (%)	% FE50	% FE75	Area los
Ammodytes marinus	1,014.39	90.75	99.06	13.44	6.86	88.67 (-2,08)	99.35 (+0.29)	**74.7**
Clupea harengus	4,393.32	48.14	74.21	13.01	31.78	39.43 (-8.71)	64.98 (-9.23)	36.6
Dicentrarchus labrax	1,170.77	67.92	85.92	9.67	8.1	75.91 (+7.99)	90.55 (+4.63)	30.8
Gadus morhua	4,993.17	36.97	61.28	6.64	32.51	27.79 (-9.18)	49.82 (-11.45)	29.7
Melanogrammus aeglefinus	3,394.86	49.91	72.65	9.39	25.2	41.25 (-8.66)	65.82 (-6.83)	30.5
Merluccius merluccius	2,051.04	57.72	78.12	20.14	10.88	68.49 (+10.77)	86.02 (+7.9)	37.7
Micromesistius poutassou	4,392.44	44.82	66.54	18.92	37.7	40.55 (-4.27)	62.09 (-4.44)	33.2

Pleuronectes platessa	1,624.06	80.31	94.76	13.45	9.76	78.52 (-1.79)	90.18 (-4.57)	**55.3**
Raja clavata	2,066.72	62.78	79.44	16.89	10.91	73.8 (11.02)	88.35 (+8.92)	42.0
Solea solea	1,323.13	78.11	93.43	12.25	5.13	83.67 (5.56)	96.48 (+3.05)	37.7
	Average	61.75	80.54	13.38	17.88	61.81	79.36	40.8
	SD	16.54	11.9	4.06	11.82	20.97	16.19	13.3

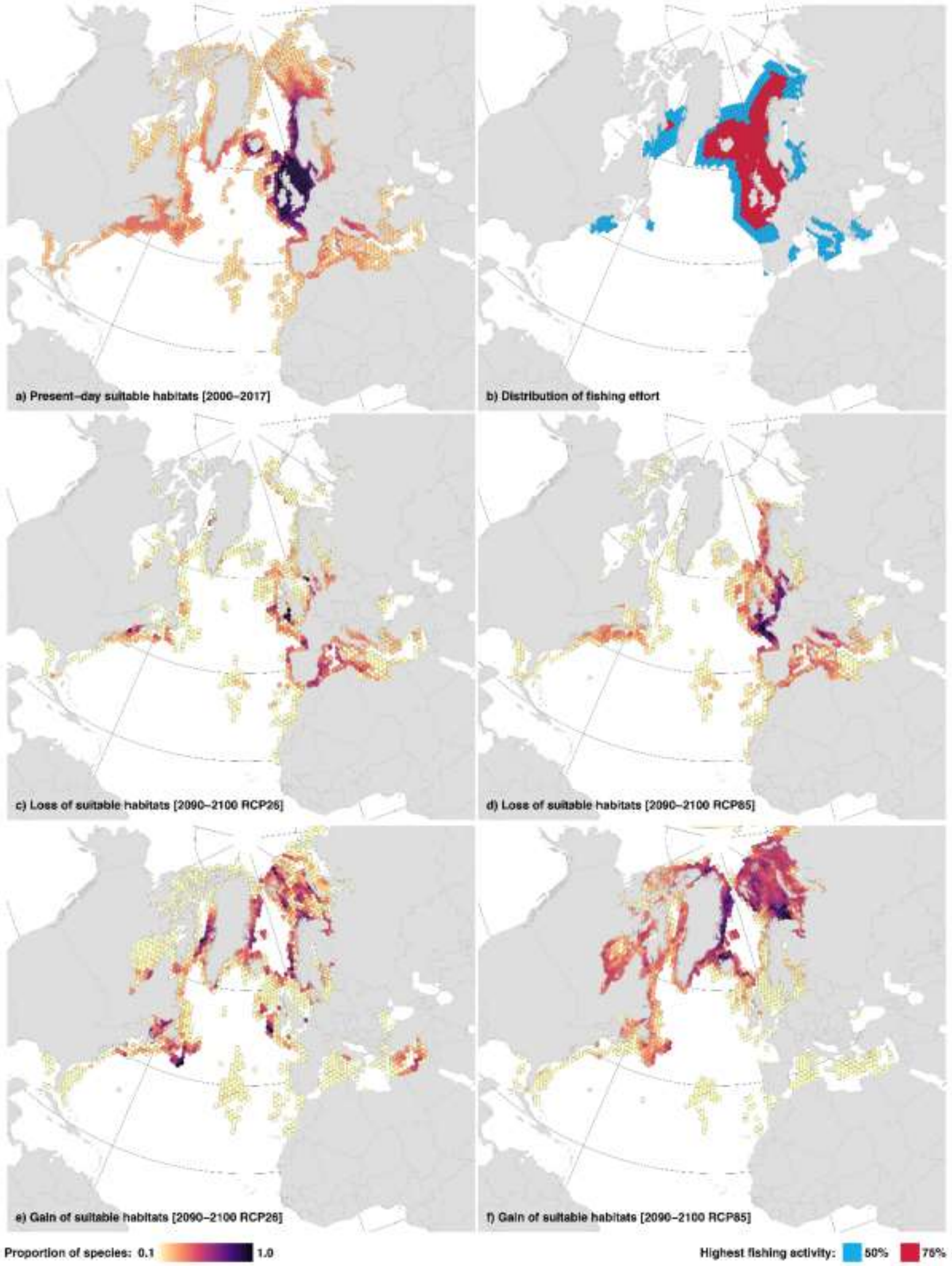

Figure 1 Proportion of near present-day suitable habitats, fishing effort and distributional range shifts (loss and gain of suitable habitats from near present-day conditions, 2000-2017, to future RCP climate change scenarios, 2090-2100; please refer to Appendix S2 for individual projections per species). Colour gradients

reflect the proportion of species (panel a) predicted with suitable habitats and (panels c-f) who lost or gained suitable habitats (yellow to dark red depicting >0 to 1 proportion scale). In panel b, the 50% (blue) and 75% (red) kernel utilization distribution of the fishing activity in the study area are represented.

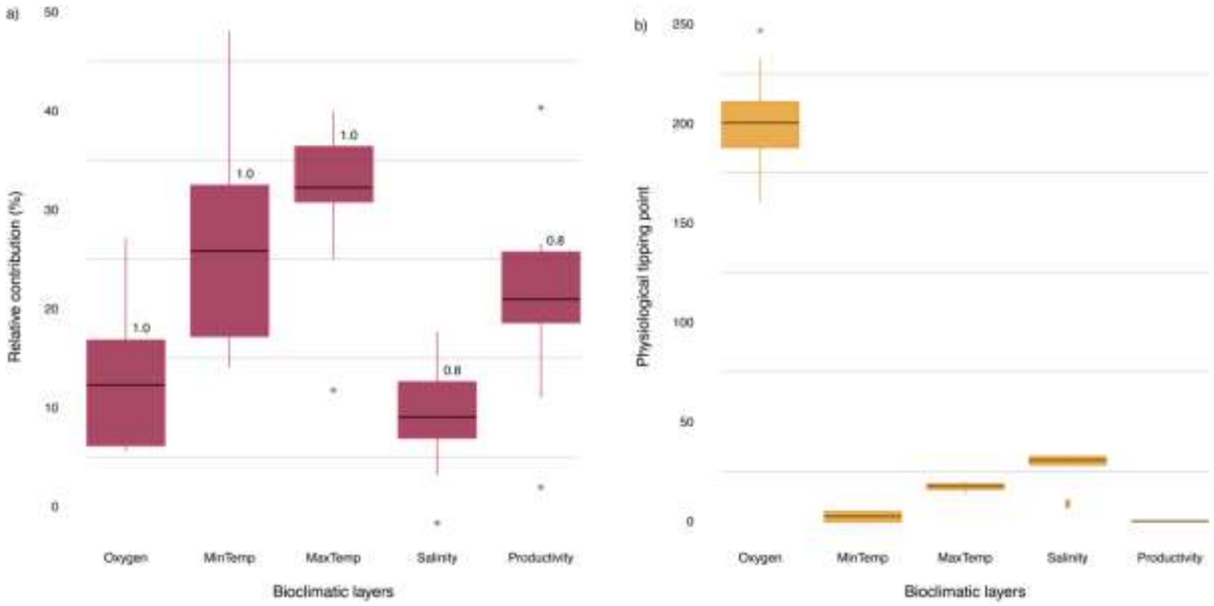

Figure 2 Average relative contribution (a) and physiological tipping point (b) of each predictor inferred with Boosted Regression Trees and Adaptive Boosting across all species. Horizontal lines represent the mean contribution and tipping points (i.e., physiological tolerances) of each predictor. Values above boxes indicate the proportion of models developed for each species where predictors retrieved significantly higher contributions to their performance. Variable units: Oxygen (mol.m^{-3}); MinTemp, MaxTemp (^{o}C); Salinity (PSS); Productivity (g.m^{-3}.day^{-1}).

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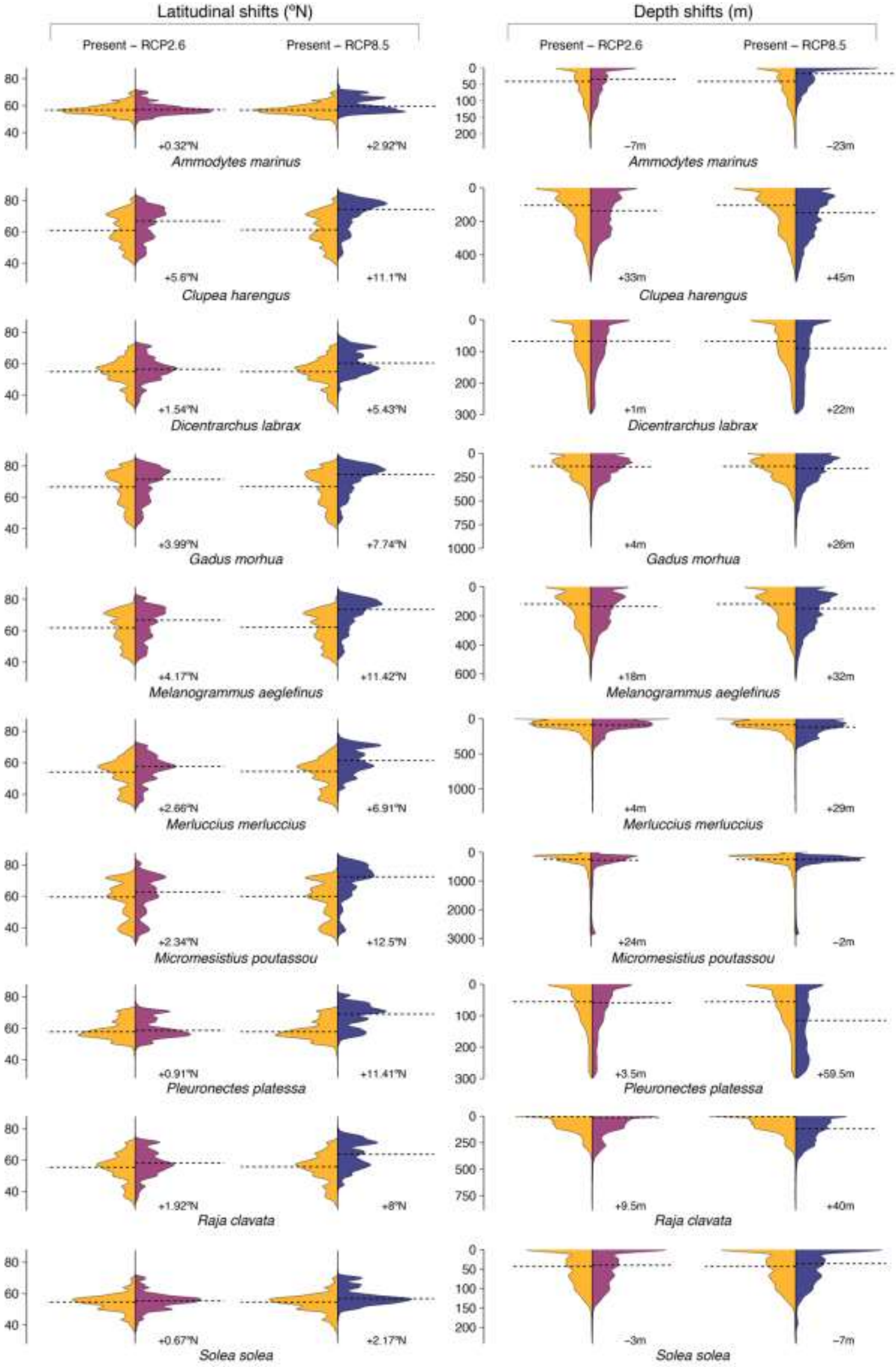
Latitudinal shifts (°N)
Depth shifts (m)
Present – RCP2.6
Present – RCP8.5
Present – RCP2.6
Present – RCP8.5
Ammodytes marinus
+0.32°N
+2.92°N
−7m
−23m
Clupea harengus
+5.6°N
+11.1°N
+33m
+45m
Dicentrarchus labrax
+1.54°N
+5.43°N
+1m
+22m
Gadus morhua
+3.99°N
+7.74°N
+4m
+26m
Melanogrammus aeglefinus
+4.17°N
+11.42°N
+18m
+32m
Merluccius merluccius
+2.66°N
+6.91°N
+4m
+29m
Micromesistius poutassou
+2.34°N
+12.5°N
+24m
−2m
Pleuronectes platessa
+0.91°N
+11.41°N
+3.5m
+59.5m
Raja clavata
+1.92°N
+8°N
+9.5m
+40m
Solea solea
+0.67°N
+2.17°N
−3m
−7m
40
60
80
0
50
100
150
200
250
300
400
500
600
750
1000
2000
3000

753

Figure 3 Latitudinal and depth shifts projected for demersal fish in the northern Atlantic with the scenarios RCP2.6 and RCP8.5 (future scenarios cover the time period 2090-2100). Yellow represents near present-day distributions; purple and blue represent distributions under RCP2.6 and RCP8.5, respectively. Dashed lines represent the median latitude and median depth of occurrence.

Appendix S1

Citations on previous work on focus species SDM and habitat preferences

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Appendix S2 – Species specific occurrence points and distribution projections in present and future (RCP2.6 and RCP8.5) scenarios

Ammodytes marinus

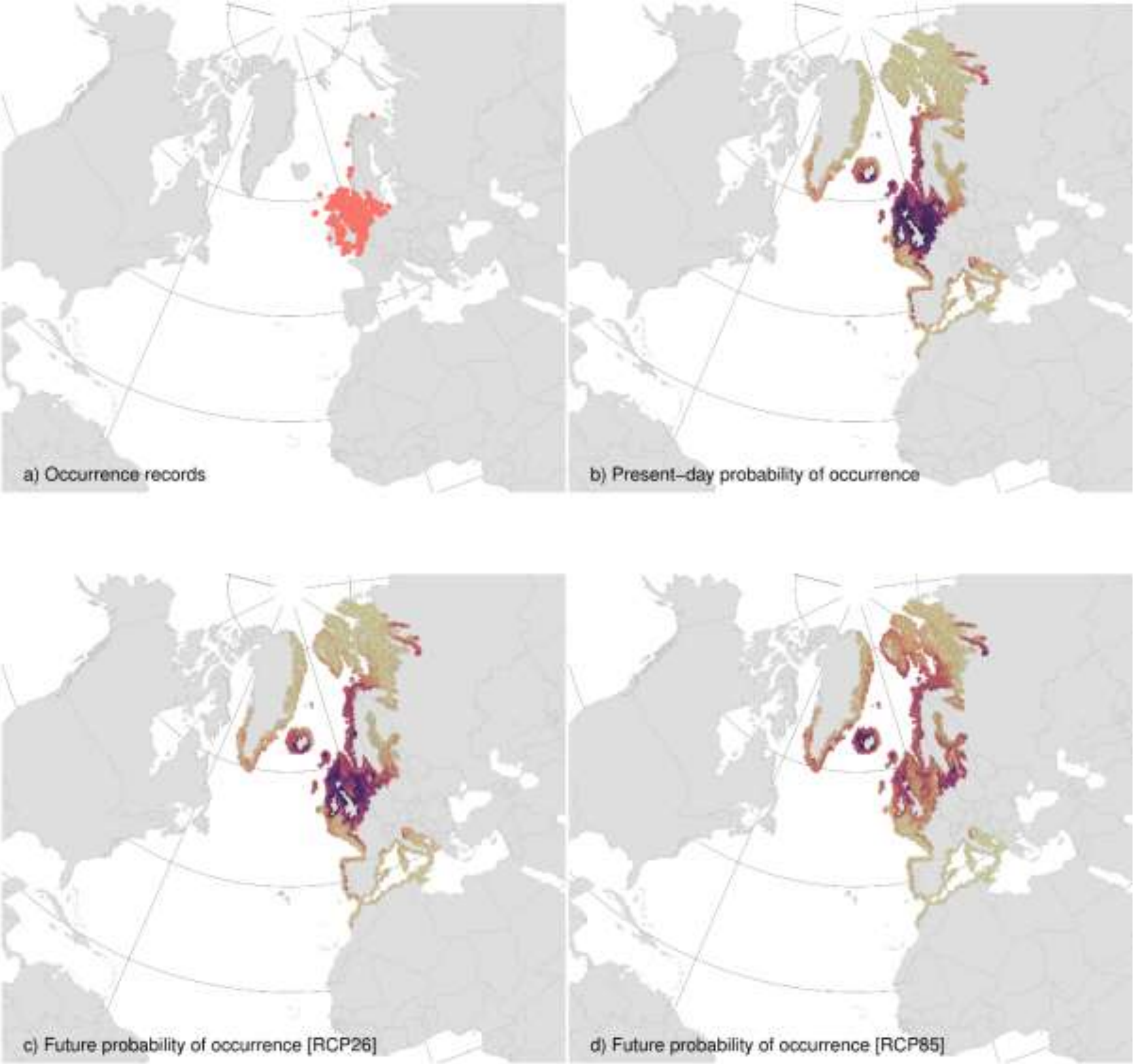

Fig S2a Occurrence points included in model (panel a) and habitat suitability in all scenarios modelled (panel b: near present-day scenario; panel c: scenario RCP2.6; panel d: scenario RCP8.5) for *Ammodytes marinus*. In panels b-d colour scale of yellow to dark red depicting habitat suitability from >0 to 1 where 1 is maximum suitability.

Clupea harengus

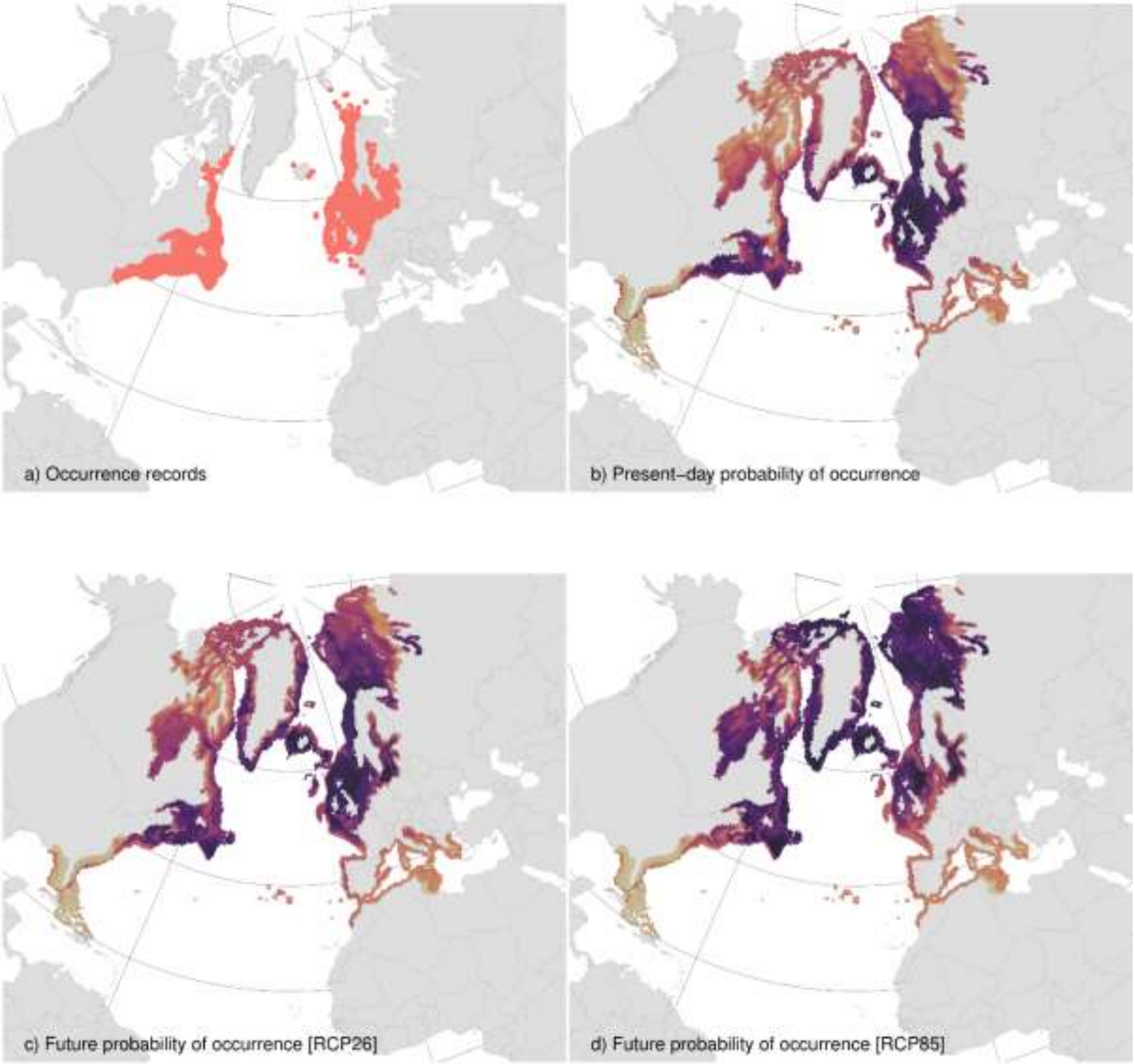

Fig S2b Occurrence points included in model (panel a) and habitat suitability in all scenarios modelled (panel b: near present-day scenario; panel c: scenario RCP2.6; panel d: scenario RCP8.5) for *Clupea harengus*. In panels b-d colour scale of yellow to dark red depicting habitat suitability from >0 to 1 where 1 is maximum suitability.

Dicentrarchus labrax

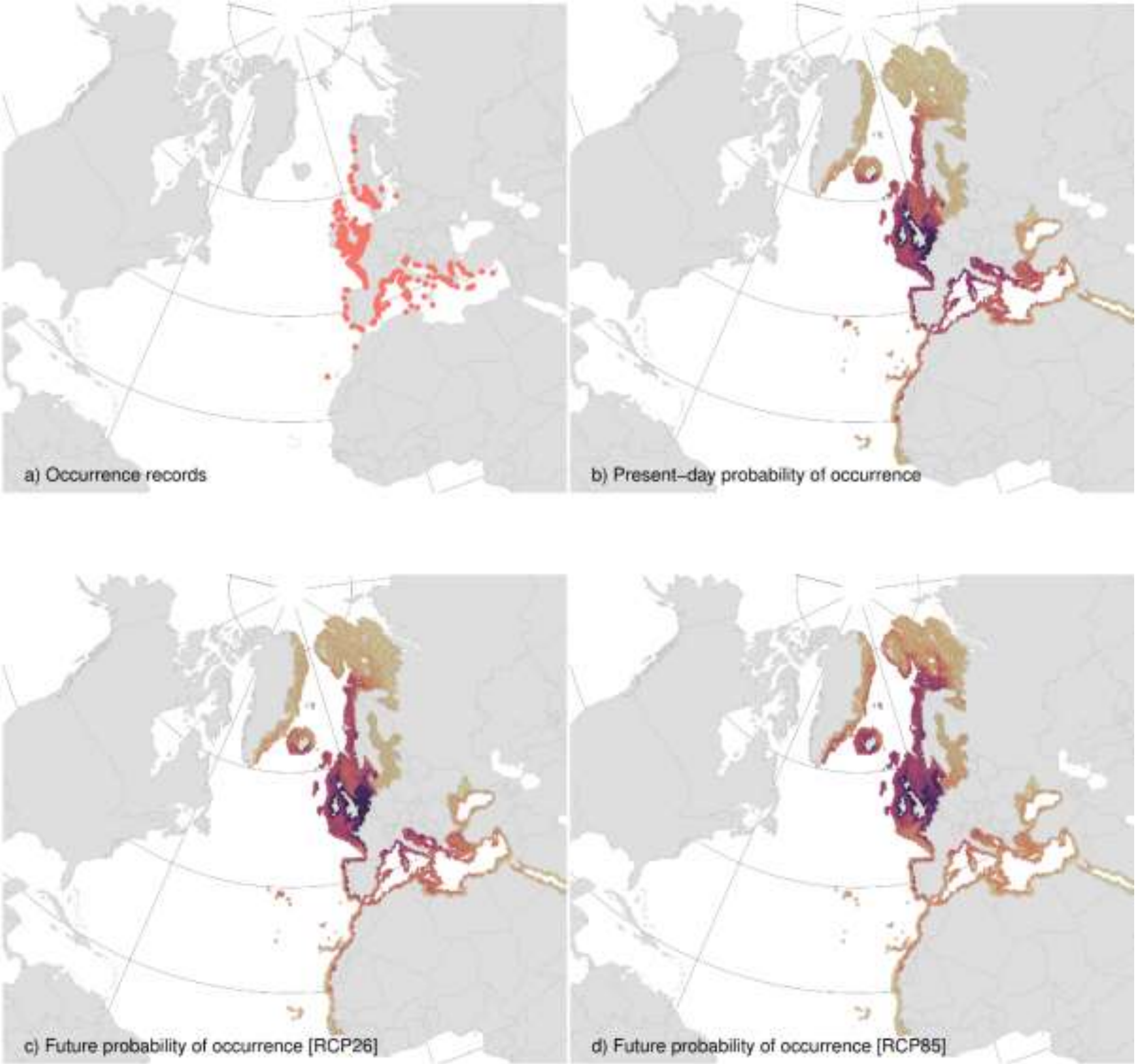

Fig S2c Occurrence points included in model (panel a) and habitat suitability in all scenarios modelled (panel b: near present-day scenario; panel c: scenario RCP2.6; panel d: scenario RCP8.5) for *Dicentrarchus labrax*. In panels b-d colour scale of yellow to dark red depicting habitat suitability from >0 to 1 where 1 is maximum suitability.

Gadus morhua

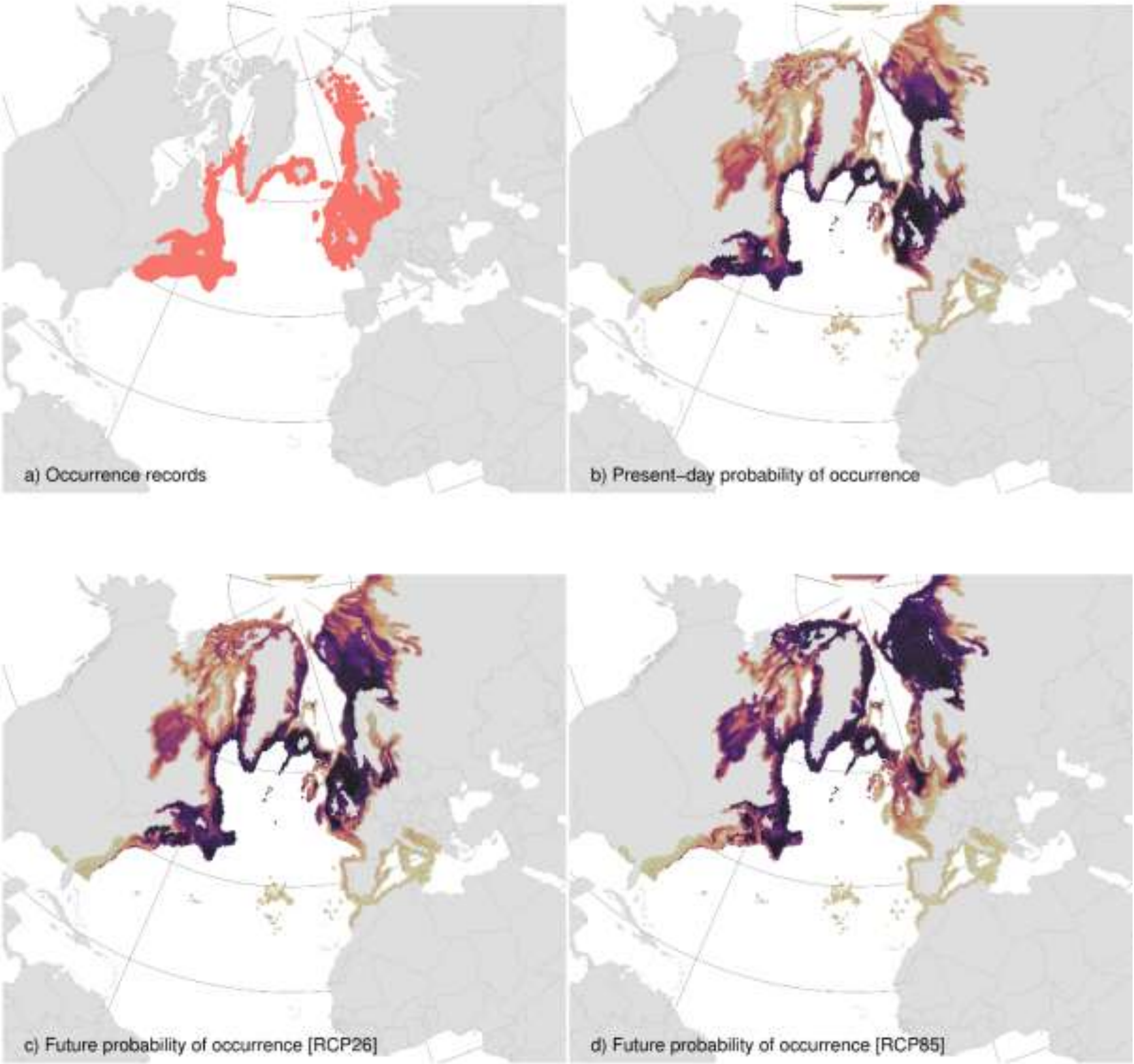

Fig S2d Occurrence points included in model (panel a) and habitat suitability in all scenarios modelled (panel b: near present-day scenario; panel c: scenario RCP2.6; panel d: scenario RCP8.5) for *Gadus morhua*. In panels b-d colour scale of yellow to dark red depicting habitat suitability from >0 to 1 where 1 is maximum suitability.

Melanogrammus aeglefinus

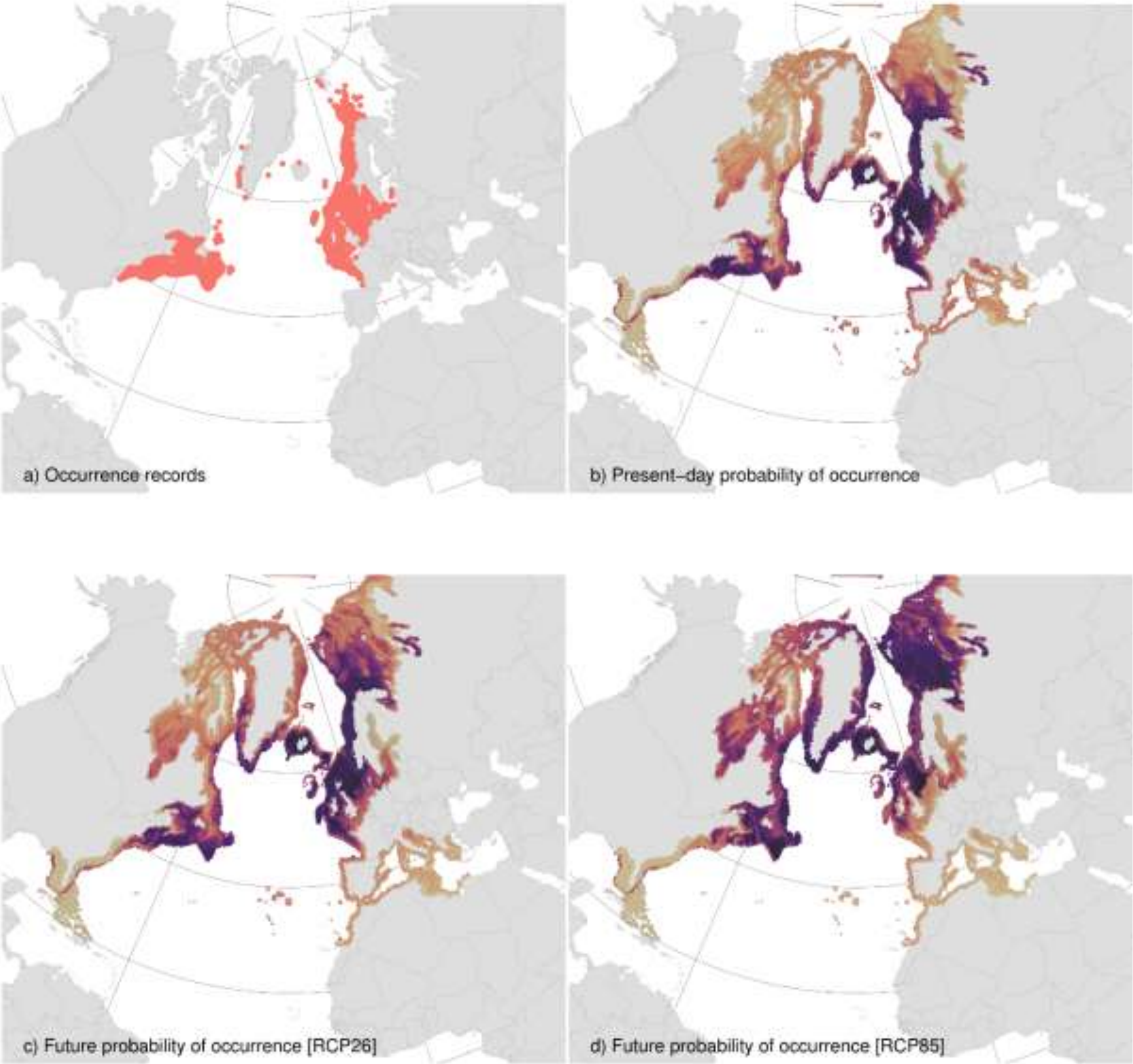

Fig S2e Occurrence points included in model (panel a) and habitat suitability in all scenarios modelled (panel b: near present-day scenario; panel c: scenario RCP2.6; panel d: scenario RCP8.5) for *Melanogrammus aeglefinus*. In panels b-d colour scale of yellow to dark red depicting habitat suitability from >0 to 1 where 1 is maximum suitability.

Merluccius merluccius

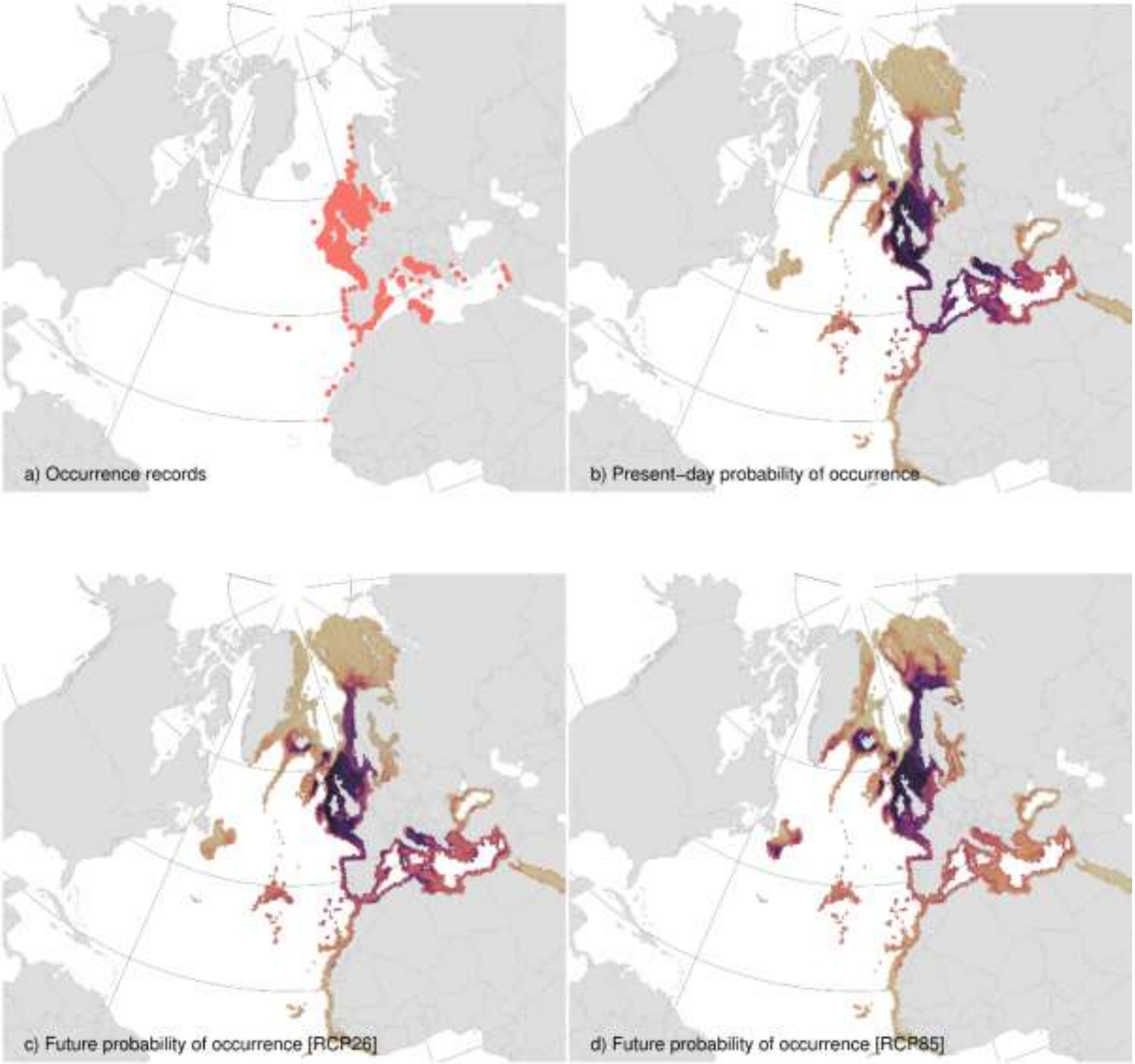

Fig S2f Occurrence points included in model (panel a) and habitat suitability in all scenarios modelled (panel b: near present-day scenario; panel c: scenario RCP2.6; panel d: scenario RCP8.5) for *Merluccius merluccius*. In panels b-d colour scale of yellow to dark red depicting habitat suitability from >0 to 1 where 1 is maximum suitability.

Micromesistius poutassou

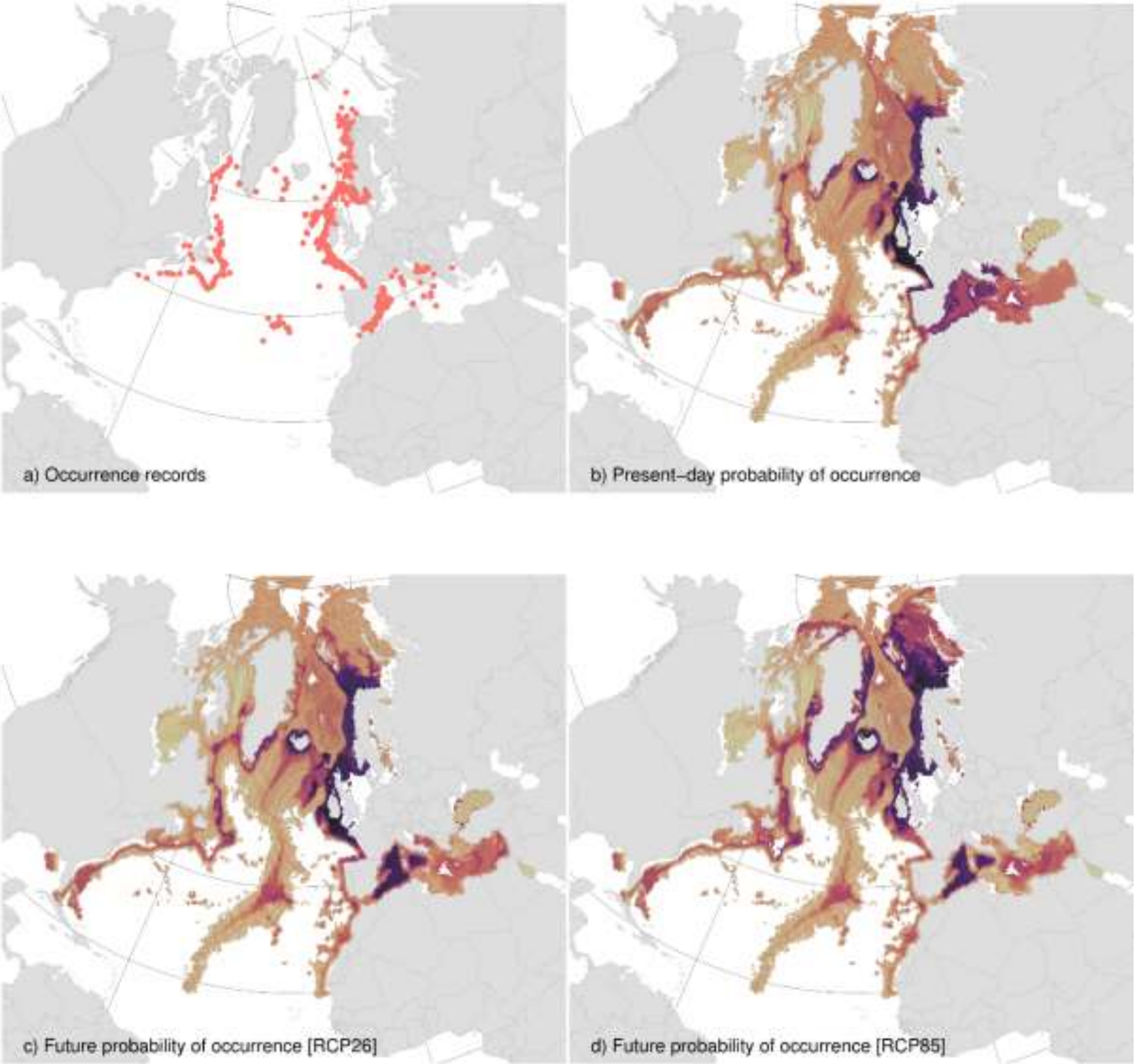

Fig S2g Occurrence points included in model (panel a) and habitat suitability in all scenarios modelled (panel b: near present-day scenario; panel c: scenario RCP2.6; panel d: scenario RCP8.5) for *Micromesistius poutassou*. In panels b-d colour scale of yellow to dark red depicting habitat suitability from >0 to 1 where 1 is maximum suitability.

Pleuronectes platessa

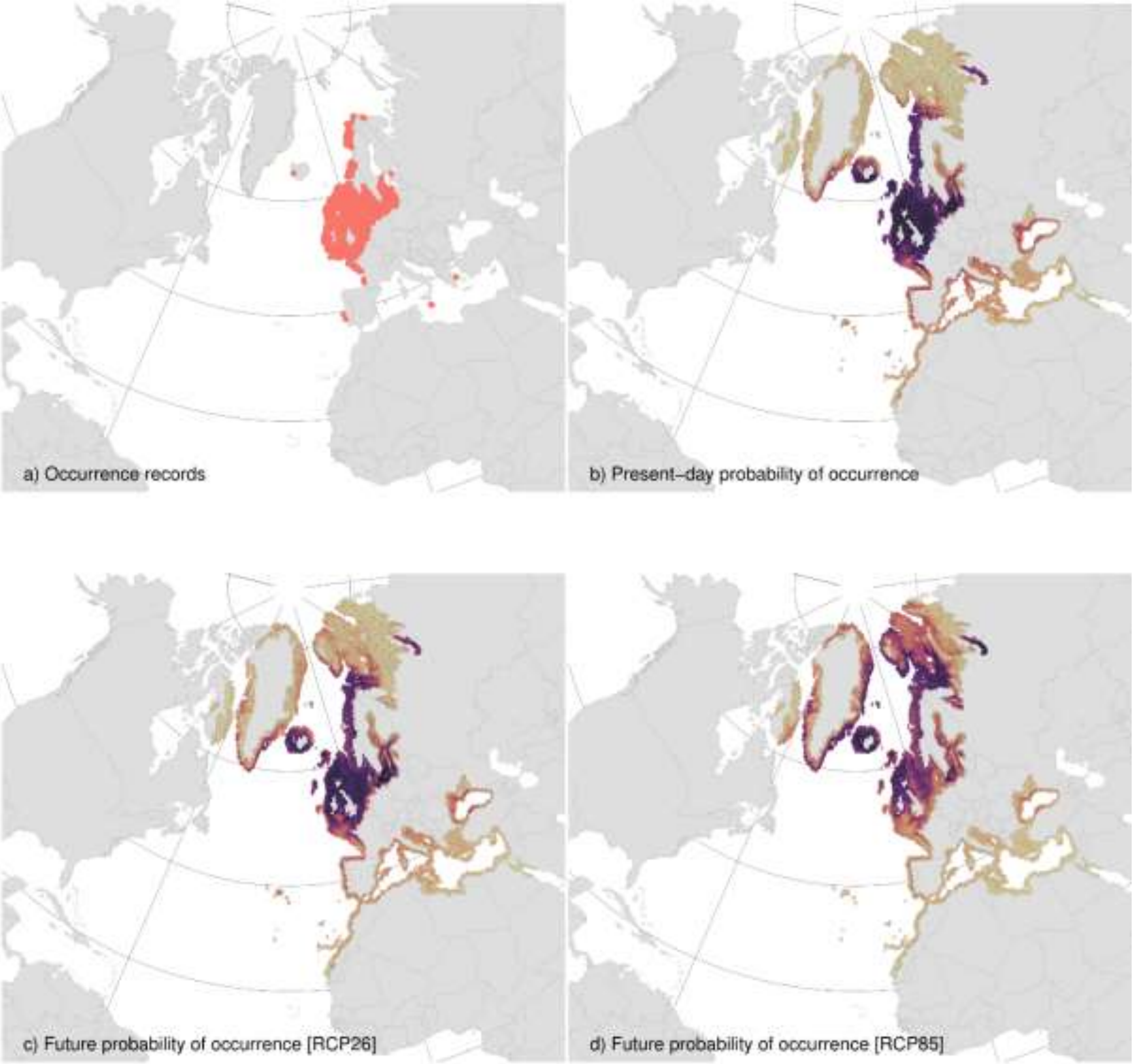

Fig S2h Occurrence points included in model (panel a) and habitat suitability in all scenarios modelled (panel b: near present-day scenario; panel c: scenario RCP2.6; panel d: scenario RCP8.5) for *Pleuronectes platessa*. In panels b-d colour scale of yellow to dark red depicting habitat suitability from >0 to 1 where 1 is maximum suitability.

Raja clavata

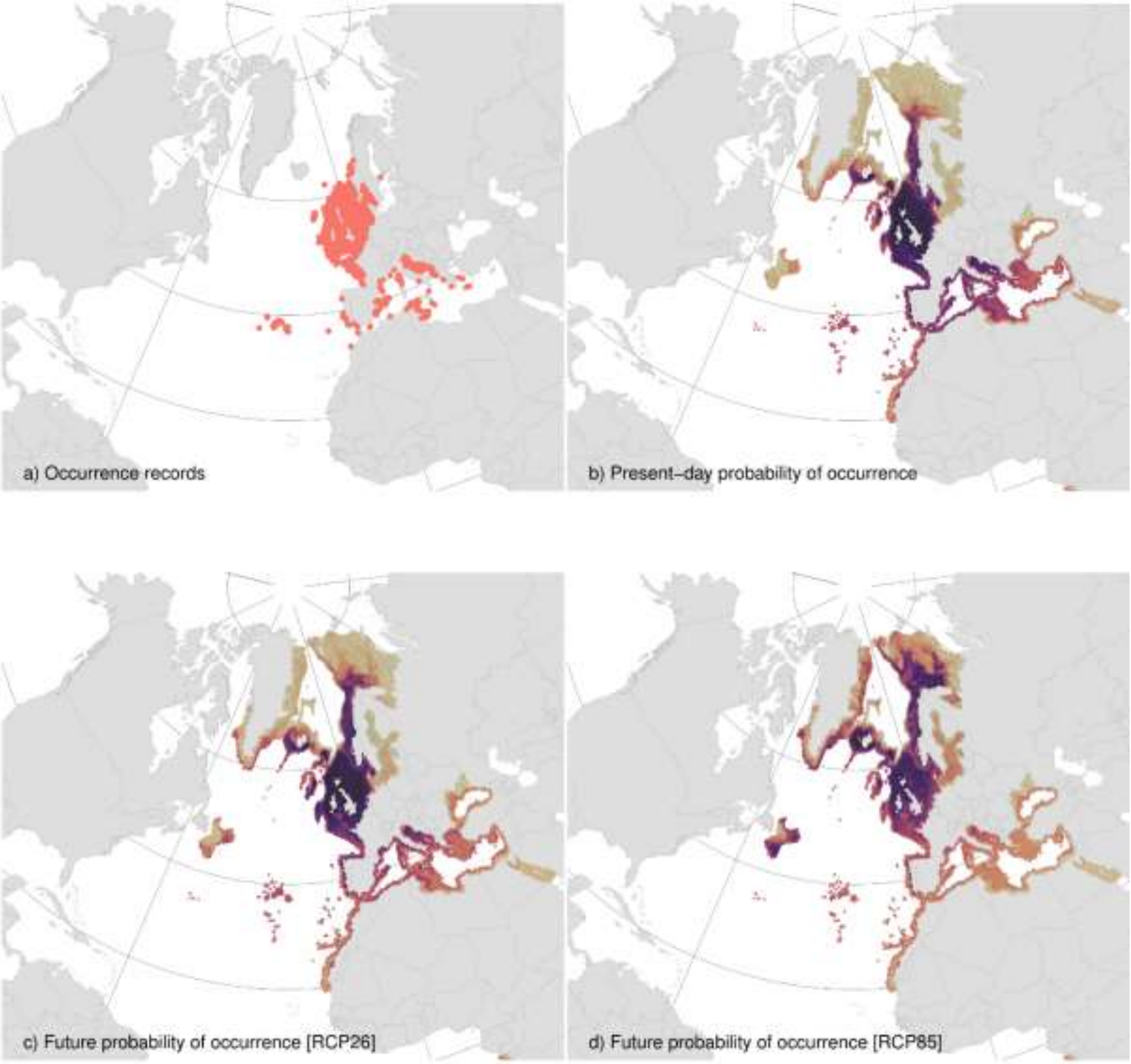

Fig S2i Occurrence points included in model (panel a) and habitat suitability in all scenarios modelled (panel b: near present-day scenario; panel c: scenario RCP2.6; panel d: scenario RCP8.5) for *Raja clavata*. In panels b-d colour scale of yellow to dark red depicting habitat suitability from >0 to 1 where 1 is maximum suitability.

Solea solea

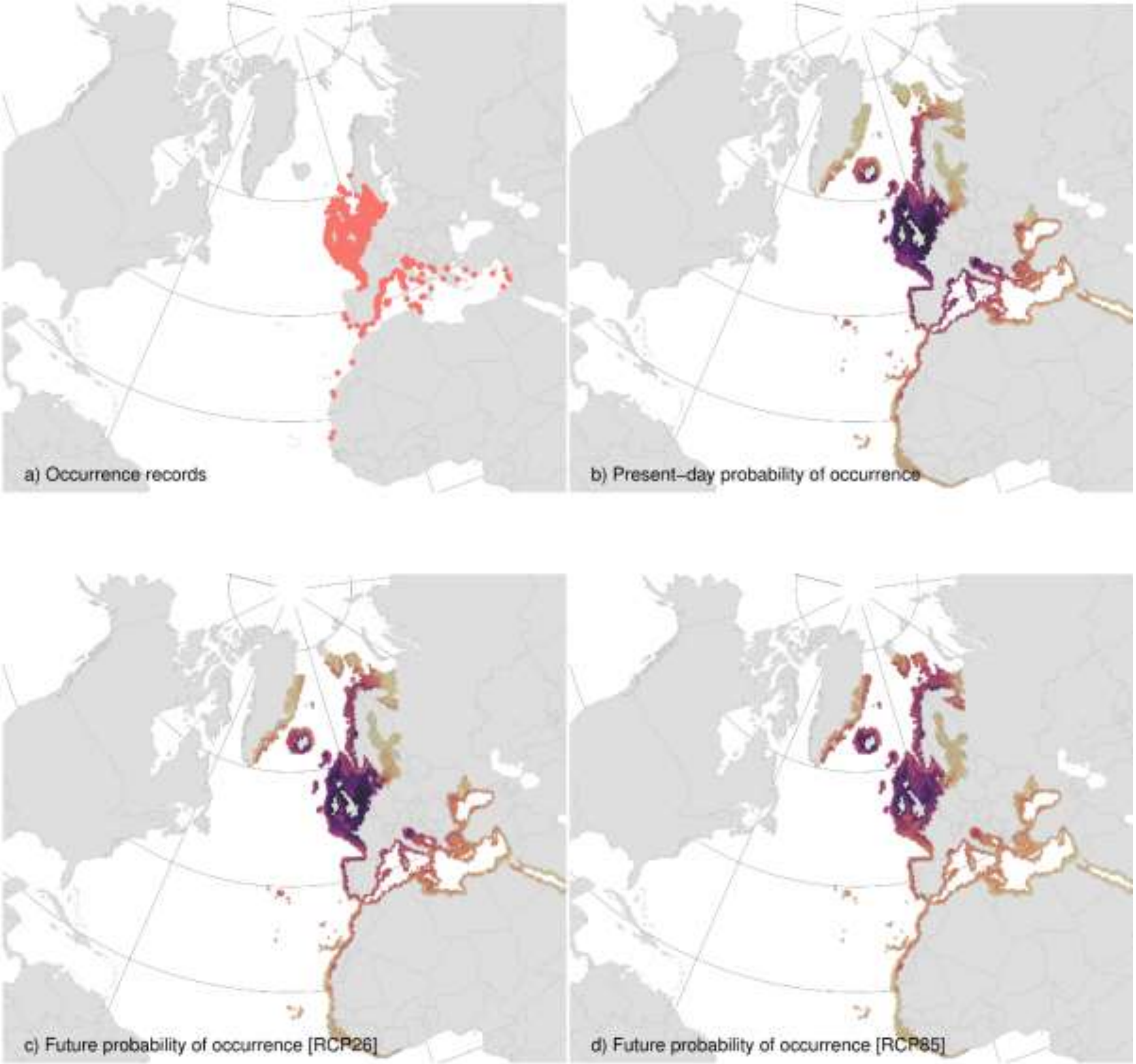

Fig S2j Occurrence points included in model (panel a) and habitat suitability in all scenarios modelled (panel b: near present-day scenario; panel c: scenario RCP2.6; panel d: scenario RCP8.5) for *Solea solea*. In panels b-d colour scale of yellow to dark red depicting habitat suitability from >0 to 1 where 1 is maximum suitability.

Appendix S3 – Excel file named Appendix S3

Appendix S4 – Environmental predictor statistic

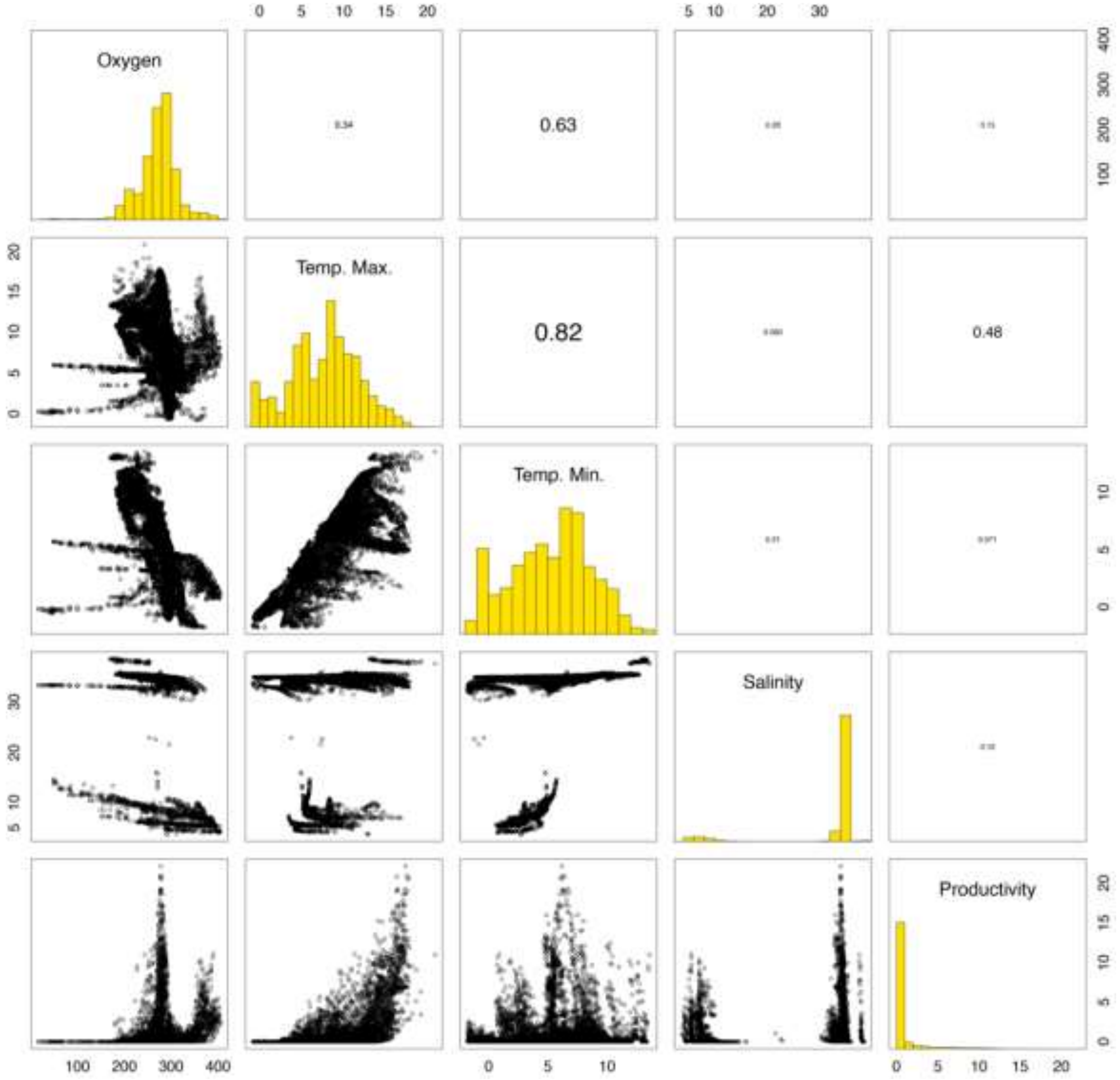

Figure S4a Correlogram showing Pearson's Correlation between predictors included in species distribution modelling (SDM).

Table S4. Variance inflation factors (VIF) for each predictor used in SDM. Variance inflation factors range from 1 upwards, with values above 5 showing strong collinearity (Everitt & Skrondal, 2010).

Predictor variable	**VIF**
Dissolved oxygen	2.105
Maximum temperature	8.070
Minimum temperature	8.394
Salinity	1.103
Productivity	2.309

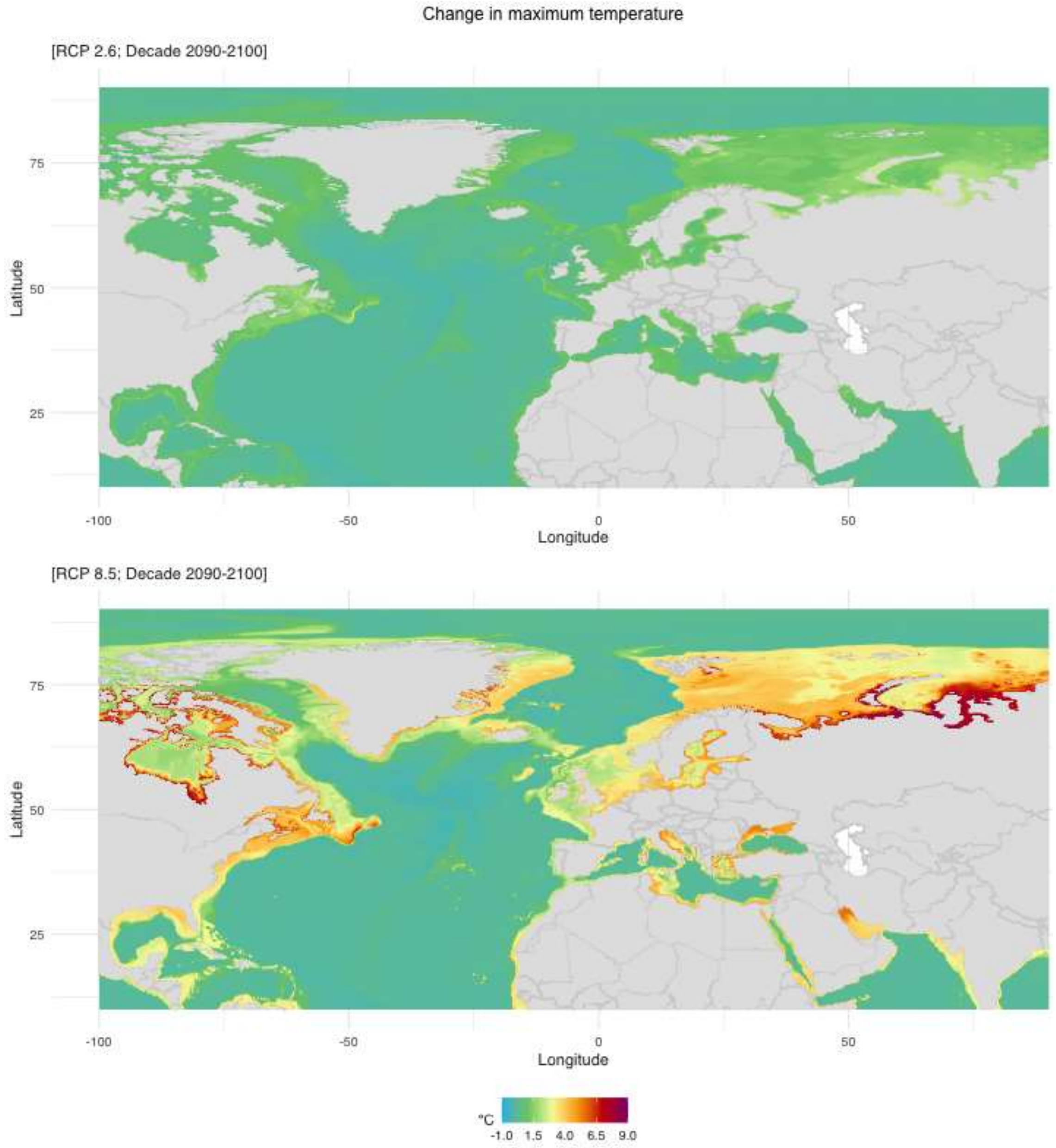

Figure S4b Difference between present and future (RCP2.6 and RCP8.5) maximum temperature (°C) in the benthos of the North Atlantic.

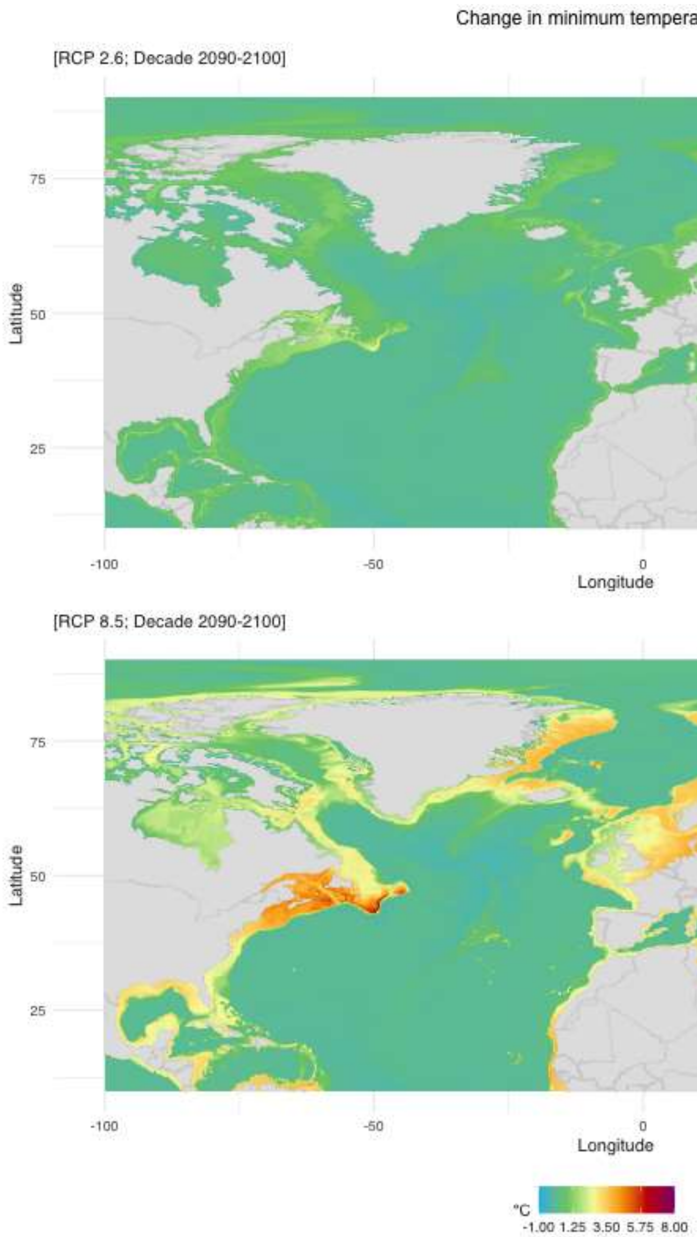

Figure S4c Difference between present and future (RCP2.6 and RCP8.5) minimum temperature (°C) in the benthos of the North Atlantic.

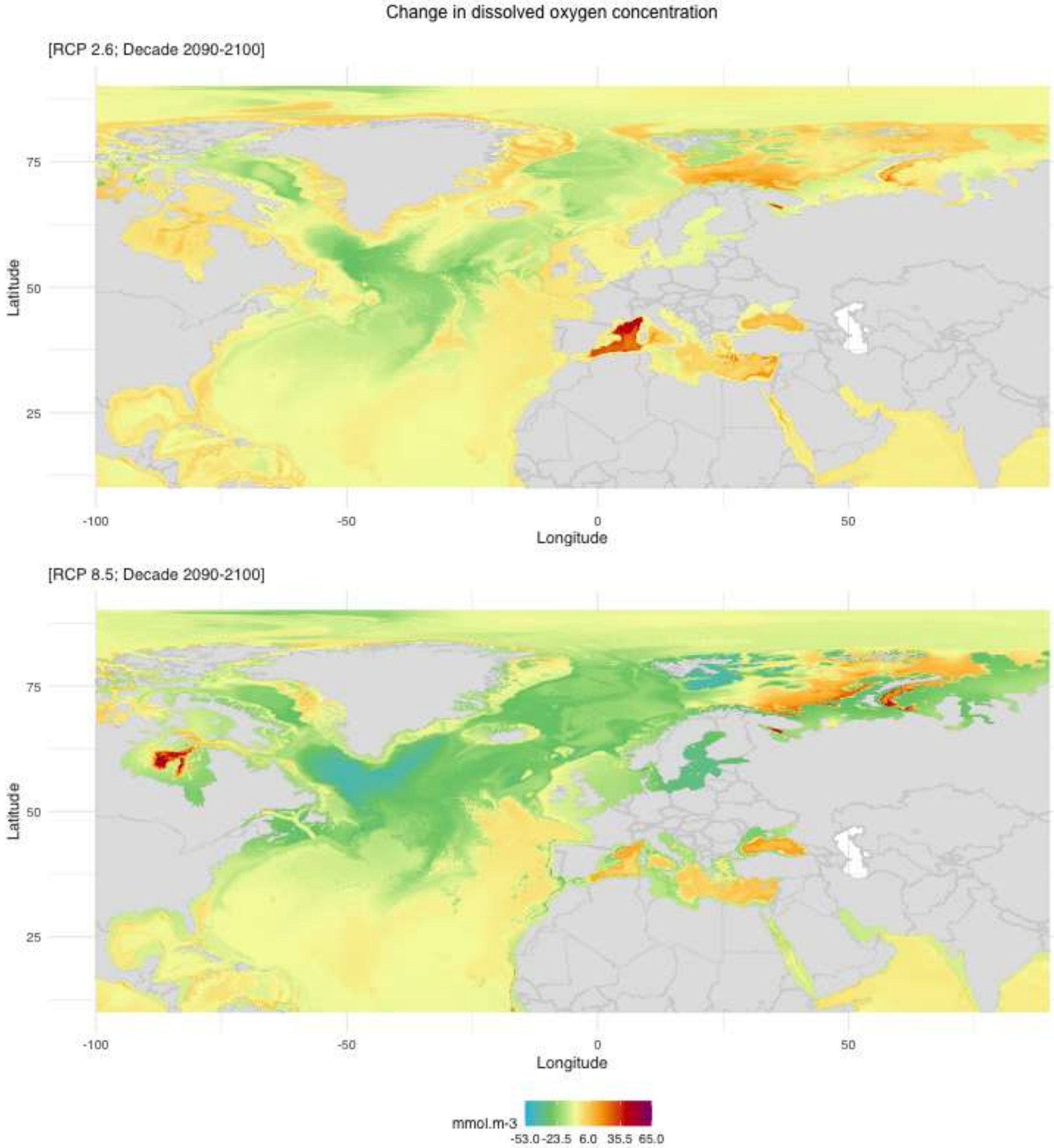

Figure S4d Difference between present and future (RCP2.6 and RCP8.5) dissolved molecular oxygen (mol.m^{-3}) in the benthos of the North Atlantic.

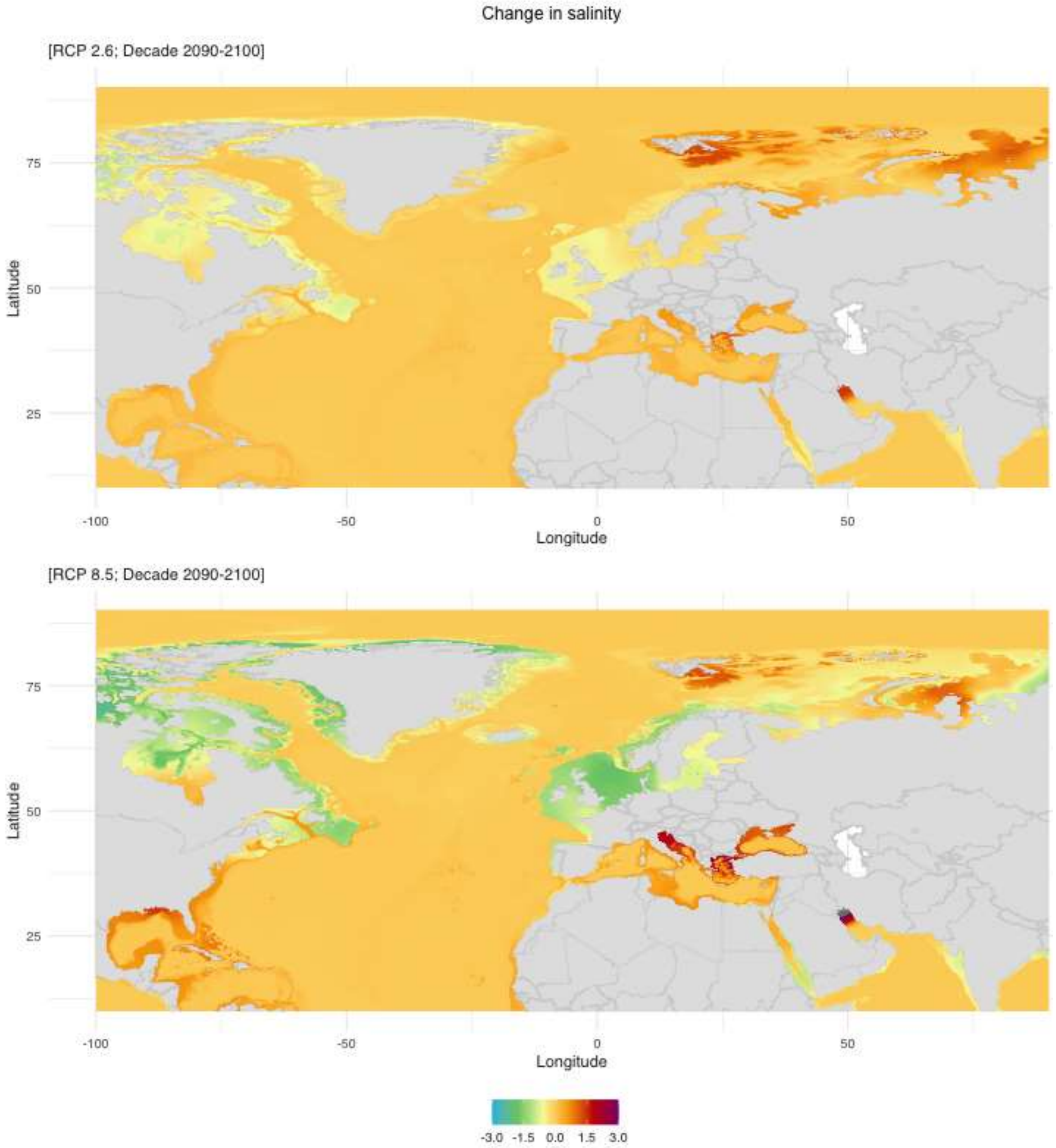

Figure S4e Difference between present and future (RCP2.6 and RCP8.5) salinity (PSS) in the benthos of the North Atlantic.

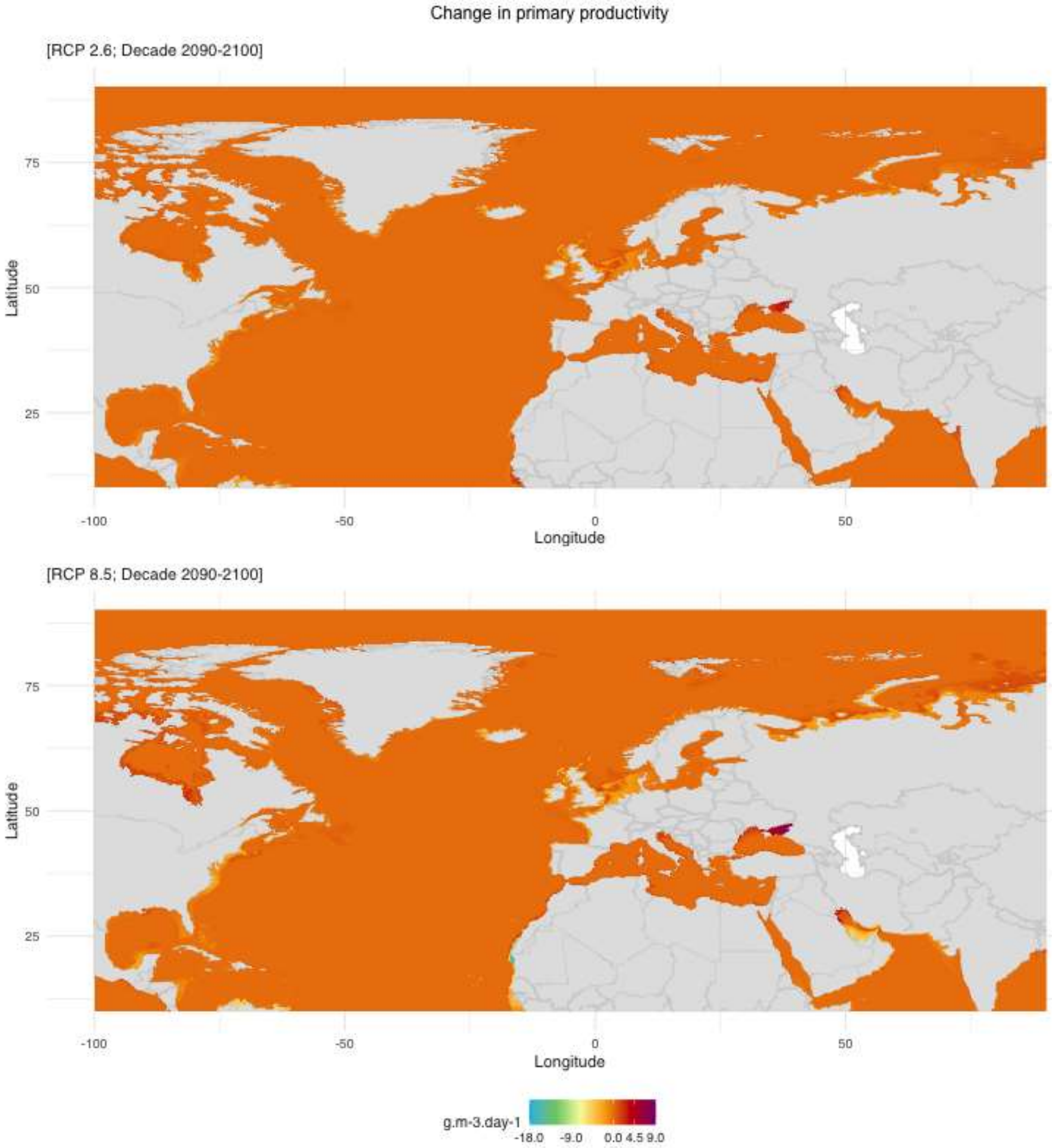

Figure S4f Difference between present and future (RCP2.6 and RCP8.5) primary productivity (g.m^{-3}.day^{-1}) in the benthos of the North Atlantic.

References

Everitt, B., & Skrondal, A. (2010). The Cambridge Dictionary of Statistics (4th Edition). Cambridge University Press.

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