

Climate change projections of commercial fish distribution and suitable habitat around north western Europe

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Abstract

Under future climate change, modification of temperature and salinity are expected to result in distribution shifts of marine organisms, including commercial fish and shellfish. Changes are anticipated everywhere, including in the seas of many important fishing nations. Species turnover will in turn result in both opportunities and threats to fishing industries. To determine the impacts for northwest European shelf fisheries, we project changes for 49 commercially important fish and shellfish species using an ensemble of five ecological niche models and three different downscaled climate change projections. The habitat suitability and latitudinal shifts projected from the recent past (1997–2016) to two futures (2030–2050; 2050–2070) were calculated for waters around the United Kingdom. Of the species examined, around half were projected to have consistently more suitable habitat in the future, including European seabass (*Dicentrarchus labrax*, Moronidae), sardine (*Sardina pilchardus*, Alosidae) and anchovy (*Engraulis encrasicolus*, Engraulidae). Conversely, it is suggested that UK waters will become less suitable for species including Atlantic cod (*Gadus morhua*, Gadidae) and saithe (*Pollachius virens*, Gadidae). Our comprehensive approach using a number of models and climate change scenarios shows that while there are differences in the magnitude of change between models, and while some models perform better for certain species compared with others, overall, the general trends in habitat suitability and abundance are robust across models and climate scenarios. This emphasises the value in using more than one modelling technique with different climate scenarios (i.e., an ensemble approach) to capture the uncertainty or agreement around climate change projections.

KEYWORDS

ecological niche model (ENM), fishing, marine, salinity, species turnover, temperature

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1 | INTRODUCTION

Long-term changes in temperature and other ocean variables often coincide with observed changes in fish distribution (Montero-Serra et al., 2015; Perry et al., 2005). Globally, fisheries catches are already impacted by changing sea temperatures, and catch composition has become more dominated by warm water species in the past few decades (Bindoff et al., 2019). Around Europe, distribution shifts and abundance changes have been observed. In a retrospective analysis of 50 abundant fish species in the waters around the United Kingdom and Ireland, 72% were shown to have responded to warming in the region already, by changing distribution and abundance (Simpson et al., 2011). Specifically, warm water species have increased in abundance while cold water species have decreased, with these trends expected to continue in the future (Poloczanska et al., 2016). In general terms, in the northern hemisphere, warming results in a distributional shift northward (Weinert et al., 2016), whereas in the southern hemisphere species typically shift south (Melbourne-Thomas et al., 2021), although species and different life history stages vary in their thermal or salinity preferences and so respond differently to long-term climate change (Petitgas et al., 2013). These changes are also often modulated at the local scale by depth preferences, sea bed features, food availability and/or the influence of fishing and other pressures (Poloczanska et al., 2016). Such changes in distribution can have consequences for commercial fisheries, because it is likely to affect the distance that fishers have to travel to catch their traditional target species. In addition, species distributions may shift across the political boundaries where quotas belong to different nations, or fishing communities (Link et al., 2011; Pinsky et al., 2020). Often it is not the individual fish themselves that are shifting their distribution, rather it is the population centre that is shifting as a result of increased relative mortality or reduced reproductive success at the edge of the distribution (southern in the northern hemisphere), and sometimes enhanced survival or reproductive success elsewhere (e.g., further north in the northern hemisphere; Engelhard et al., 2014).

Modelling strategies for projecting the potential impacts of climate change on the natural distribution of species and consequently the effects upon fisheries have often focused on the characterisation of a species' 'bioclimate envelope' (Pearson & Dawson, 2003). In other words, by looking at the current range of environmental conditions, such as temperature, tolerated by a species, it is possible to predict the future suitable habitat, if we know how the physical environment in an area will likely change in the future (Araújo & Peterson, 2012 and references therein). Model simulations suggest that distributions of exploited species will continue to shift in the next five decades both globally and in the north-east Atlantic specifically. A world-wide analysis using this technique, suggested that climate change may lead to numerous local extinction events by the year 2050, especially the tropics and semi-enclosed seas (Cheung et al., 2009). Pelagic species were projected to move pole-ward by up to 600 km and demersal species by an average of 223 km.

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Ecological Niche Models (ENMs), aiming to establish the species environmental requirements based on statistical analysis of distribution data, come in different types and varieties, each with different assumptions and biases, and can lead to different projections. For 14 commercial fish, three different ENMs were applied to the same datasets and same geographic region (the North Sea and north-east Atlantic) with each modelling method producing plausible predictions of habitat suitability (Jones et al., 2012). However, there were often marked disparities between projected distributions despite exhibiting similar 'goodness-of-fit'. A separate study of 252 models found that uncertainty in niche models can exceed that in the earth system models (Brodie et al., 2022). These studies show that authors should not assume that there is necessarily a 'best' model, and that a multi-model ensemble is useful to bracket the level of uncertainty in future projections and produce a more robust forecast (Araújo & New, 2007).

The term 'niche' or 'habitat suitability' is used here to describe the bathymetry and the environmental hydrographic conditions (temperature and salinity) that are suitable for each species, and does not include characteristics of bottom substrate (since sufficient data for the study region was not available), or local species interactions within communities (i.e., food availability, etc.). These may conceivably be important in certain instances. In this study, we employ an approach that can be applied across a very broad range of species to investigate and compare how different species might respond to climate change in the future.

The seas around the British Isles, and in particular, the southern North Sea have been identified as one of 20 sites globally that have warmed the fastest over the past 50 years – so-called global marine climate change 'hotspots' (Hobday & Pecl, 2014). Sea surface temperatures (SSTs) in the north-east Atlantic have generally risen over the past century, with the rate of warming particularly rapid since the 1980s and in the eastern English Channel and southern North Sea (Tinker et al., 2015), and expected to continue in the future (Tinker

et al., 2015, 2016). Ensemble mean outputs suggested a self-averaged, mean SST rise of $2.90 \pm 0.82^\circ\text{C}$ over the next 80 years, and a freshening of -0.41 ± 0.47 psu (Tinker et al., 2016). There is a spatial pattern to the warming, with greatest winter/spring warming anticipated in the south-eastern North Sea, and greatest summer/autumn warming in the Celtic Sea. In the winter and autumn, the near-bed temperature across the shelf is projected to warm at a similar rate as SST (Tinker et al., 2016). Changes in SST and salinity are different for different climate scenarios. The changes for the three scenarios used in this work are shown in Figure 1. These are the A1B 'medium' emissions scenario from the Coupled Model Intercomparison Project (CMIP) 3 Special Report Emissions Scenarios (SRES) dataset, and the CMIP5 Representative Concentration Pathway (RCP) 4.5 (medium emissions, high mitigation) and 8.5 (high emissions, low mitigation) projections.

Regional studies to date have tended to either look at a large number of species with one or a low number of ENMs, or focus on a few species but with a larger ensemble of models, while global studies are unable to use downscaled climate models to capture the

detailed climatic changes that happen in a specific region. Here, we generate an ensemble of five ENMs, applied to 49 commercial fish and shellfish species, out to the middle of the century (to 2040 and 2060) under three climate change scenarios. We aim to answer the questions:

- How will habitat suitability change across the northwest European shelf and in the United Kingdom Exclusive Economic Zone (EEZ) for key commercial species?
- Which species will be 'winners' (will have an increase in suitable habitat) and which will be 'losers' (will have a decrease in suitable habitat) as a result of future climate change?

2 | METHODS

Five Ecological Niche Models were trained for each of the 49 species, under three different climate scenarios, one of which (the A1B scenario) had 11 ensemble members (yielding 65 models for each

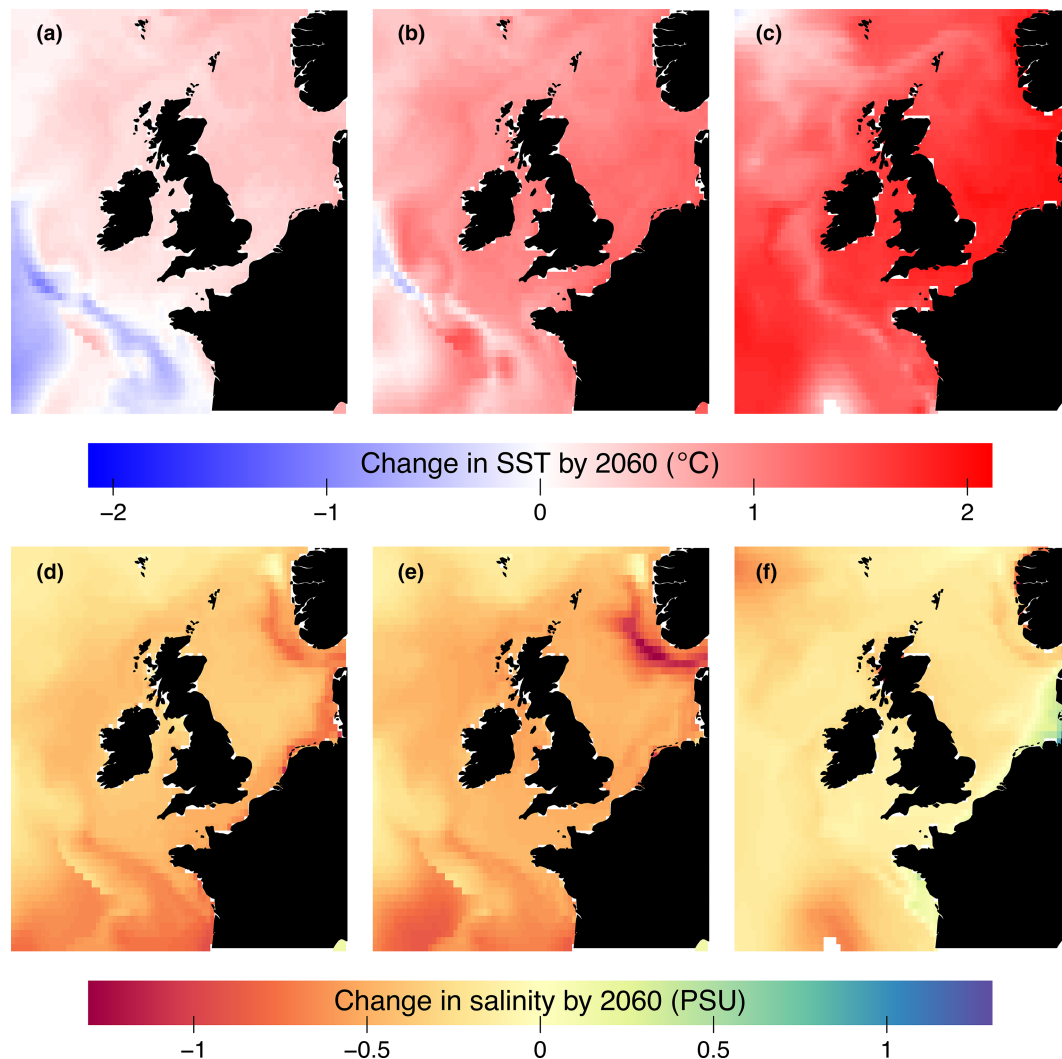


FIGURE 1 Projected changes in sea surface temperature (SST, top plots) and salinity (SSS, bottom plots) for the 20-year period centred on 2060 with respect to the training period 1997–2016, under the RCP 4.5 (a, d), RCP 8.5 (b, e) and the SRES A1B scenario (c, f).

species, or a total of 3185 ENMs, 2695 of which corresponded to the 11 ensembles of the A1B scenario).

2.1 | Species

Forty nine species (Table 1) were chosen by the authors, with wider consultation with scientists and policy makers. The species list includes those that are currently commercially important to the UK, and some warm water species that are important in France and Spain, but not yet in the United Kingdom.

Species occurrence data were obtained from the International Council for Exploration of the Sea (ICES) – Groundfish Survey Monitoring and Assessment Data Product (DATRAS) for the North-east Atlantic Area, which contains all of the groundfish survey datasets uploaded to the ICES system (Moriarty et al., 2017), and from the Ocean Biogeographic Information System (OBIS; <http://www.obis.org>), the largest free-access online database on the occurrences of marine species world-wide. Additional Spanish groundfish survey data was obtained from the Spanish Institute of Oceanography. Species occurrence data from 1997 to 2016 were used, which corresponds with the 'present' period for the climate variables. Any duplicated data or points on land were removed.

The fish species were categorised according to their 'geographical extent' (Table 1), so that the geographical area from which environmental data were extracted was constrained. For example, for an Atlantic species, it would not be appropriate to take into account Pacific Ocean environmental data to determine the species' habitat suitability. The species were split into global, Atlantic, North Atlantic, and North Atlantic plus northern seas (which includes the Labrador Sea, the Greenland Sea and the Barents Sea).

2.2 | ENM models

The five models chosen for the multi-model approach include Maxent (Phillips et al., 2006), BIOCLIM (Busby, 1991), Generalised Linear Models (GLMs; Nelder & Wedderburn, 1972), Random Forest (Breiman, 2001) and Support Vector Machines (SVM; Drake et al., 2006; Moguerza & Muñoz, 2006).

The Maximum Entropy (MaxEnt) ecological niche model is widely applied and provides a robust method for assessing habitat suitability compared with other, similar modelling methodologies (Elith et al., 2006; Reiss et al., 2011; Vierod et al., 2015). MaxEnt estimates a probability distribution for the grid, defined by the environmental variables, by finding the distribution that has the maximum entropy (i.e., most uniform), subject to the constraints of incomplete information (Phillips et al., 2006). Similar to MaxEnt, BIOCLIM uses only presence records. It is the earliest model developed to characterise species habitats, and the simplest of the five used in this study. It defines a bioclimatic envelope for a species as the range in all the environmental/climatic variables at which the species is found. BIOCLIM has been widely used, although it has been shown that it tends to

underpredict in climate change studies (Hijmans & Graham, 2006). However, because of this, it can be considered as providing a more conservative estimate of potential range shifts.

GLMs are a regression method which allow for response variables with error distributions other than a normal distribution (Nelder & Wedderburn, 1972). A link function is used to relate the model to the response variables and the magnitude of the variance is a function of the predicted value. We fitted GLMs with binomial responses using an adjusted-score approach to bias reduction (Firth, 1993), as implemented in the R package 'brglm' (Kosmidis, 2021). Random Forest is a method based on an ensemble of classification tree models, each built by sequentially splitting the data into two groups based on the value of the environmental or climatic variables. Random Forest uses an ensemble of trees to improve predictive accuracy, by training multiple classification trees on bootstrap samples of the training set, with each split of the trees being determined using only a randomly chosen subset of the environmental variables (so as to induce variations between the trees). Tree-based techniques are able to model non-linear relationships and interaction effects and have been shown to be among the top performing ENMs in studies of fish habitats (Knudby et al., 2010). The Random Forest models were trained in R using the package 'randomForest' (Liaw & Wiener, 2002).

Also a machine-learning technique, Support Vector Machines (SVMs) estimate a species' habitat by fitting a hyperplane to separate presence and absence data in the eco-space defined by all environmental/climatic variables, after applying some transformation to the variables so that the separation can be found by linear analysis. Being relatively recent, it has not been as widely used as some of the other methods, but it has been applied successfully in marine studies (e.g., Reiss et al., 2011). The SVM implementation in the R library 'e1071' was used (Meyer et al., 2020).

2.3 | Climate projections

The climate projections used here are based on three different trajectories of future carbon emissions and are taken from two different sources. These are the CMIP3 SRES A1B 'medium' emissions scenario, and the RCP 4.5 (medium emissions, high mitigation) and 8.5 (high emissions, low mitigation) projections from the more recent IPCC CMIP5 RCP dataset. The SRES A1B scenario projections are described in Tinker et al. (2015, 2016). Global ~300km resolution (with 1.25° ocean) projections were from a Perturbed Physics Ensemble (PPE; Collins et al., 2011) of the Atmosphere–Ocean Global Climate Model HadCM3 (with a 3.75° × 2.75° resolution atmosphere and 1.25° ocean; Gordon et al., 2000; Pope et al., 2000). To span the range of uncertainty in climate sensitivity (the amount of global mean warming associated with a doubling of CO₂), the PPE consisted of 11 ensemble members, which each have a number of atmospheric parameters perturbed. All 11 ensemble members were used in this modelling to examine the full range of distribution shifts that could be expected, based on the SRES A1B 'medium' emission scenario. The ensemble

TABLE 1 The commercial species chosen for the ecological niche modelling.

Scientific name and family	Common name	Distribution
<i>Amblyraja radiata</i> , Rajidae	Starry ray	Atlantic and northern seas
<i>Anarhichas lupus</i> , Anarhichadidae	Atlantic wolffish	Atlantic and northern seas
<i>Capros aper</i> , Caproidae	Boarfish	North Atlantic
<i>Chelidonichthys cuculus</i> , Triglidae	Red gurnard	Atlantic
<i>Chelidonichthys lucerna</i> , Triglidae	Tub gurnard	Atlantic
<i>Clupea harengus</i> , Clupeidae	Atlantic herring	Atlantic and northern seas
<i>Dicentrarchus labrax</i> , Moronidae	European seabass	Atlantic
<i>Dipturus batis</i> , Rajidae	Blue skate	North Atlantic
<i>Engraulis encrasicolus</i> , Engraulidae	European anchovy	Atlantic
<i>Eutrigla gurnardus</i> , Triglidae	Grey gurnard	North Atlantic
<i>Gadus morhua</i> , Gadidae	Atlantic cod	Atlantic and northern seas
<i>Glyptocephalus cynoglossus</i> , Pleuronectidae	Witch	Atlantic and northern seas
<i>Hippoglossoides platessoides</i> , Pleuronectidae	Plaice	Atlantic and northern seas
<i>Hippoglossus hippoglossus</i> , Pleuronectidae	Halibut	Atlantic and northern seas
<i>Lepidorhombus whiffiagonis</i> , Scophthalmidae	Megrim	North Atlantic
<i>Limanda limanda</i> , Pleuronectidae	Dab	Atlantic and northern seas
<i>Loligo forbesii</i> , Loliginidae	Veined squid	Global
<i>Loligo vulgaris</i> , Loliginidae	European squid	Atlantic
<i>Lophius piscatorius</i> , Lophiidae	Angler	North Atlantic
<i>Melanogrammus aeglefinus</i> , Gadidae	Haddock	Atlantic and northern seas
<i>Merlangius merlangus</i> , Gadidae	Whiting	North Atlantic
<i>Merluccius merluccius</i> , Merlucciidae	European hake	North Atlantic
<i>Micromesistius poutassou</i> , Gadidae	Blue whiting	Atlantic and northern seas
<i>Microstomus kitt</i> , Pleuronectidae	Lemon sole	Atlantic and northern seas
<i>Molva molva</i> , Lotidae	Ling	North Atlantic
<i>Mullus surmuletus</i> , Mullidae	Surmullet	North Atlantic
<i>Nephrops norvegicus</i> , Nephropidae	Norway lobster	North Atlantic
<i>Pleuronectes platessa</i> , Pleuronectidae	Plaice	Atlantic and northern seas
<i>Pollachius pollachius</i> , Gadidae	Pollack	North Atlantic
<i>Pollachius virens</i> , Gadidae	Saithe	North Atlantic
<i>Raja clavata</i> , Rajidae	Thornback ray	Atlantic
<i>Raja montagui</i> , Rajidae	Spotted ray	North Atlantic
<i>Reinhardtius hippoglossoides</i> , Pleuronectidae	Greenland halibut	Global
<i>Sardina pilchardus</i> , Alosidae	Sardine	North Atlantic
<i>Scomber scombrus</i> , Scombridae	Atlantic mackerel	North Atlantic
<i>Scophthalmus maximus</i> , Scophthalmidae	Turbot	North Atlantic
<i>Scophthalmus rhombus</i> , Scophthalmidae	Brill	North Atlantic
<i>Scyliorhinus canicula</i> , Scyliorhinidae	Lesser spotted dogfish	North Atlantic
<i>Sepia officinalis</i> , Sepiidae	Common cuttlefish	Atlantic
<i>Solea solea</i> , Soleidae	Sole	North Atlantic
<i>Spondyliosoma cantharus</i> , Sparidae	Black seabream	Atlantic
<i>Sprattus sprattus</i> , Clupeidae	European sprat	North Atlantic
<i>Squalus acanthias</i> , Squalidae	Picked dogfish	Global
<i>Thunnus thynnus</i> , Scombridae	Atlantic bluefin tuna	Atlantic
<i>Trachurus trachurus</i> , Carangidae	Atlantic horse mackerel	Atlantic

TABLE 1 (Continued)

Scientific name and family	Common name	Distribution
<i>Trisopterus esmarkii</i> , Gadidae	Norway pout	Atlantic and northern seas
<i>Trisopterus luscus</i> , Gadidae	Pouting	North Atlantic
<i>Trisopterus minutus</i> , Gadidae	Poor cod	North Atlantic
<i>Zeus faber</i> , Zeidae	John Dory	Global

Note: The distributions were categorised and used as the geographic extent for model training.

members have been dynamically downscaled with the shelf seas model POLCOMS (Proudman Oceanographic Laboratory Coastal Ocean Modelling System; Holt et al., 2001; Holt & James, 2001) to produce the northwest European shelf seas projection (Tinker et al., 2015, 2016) used here, with a resulting resolution of 12 km (1/9° latitude by 1/6° longitude), covering 43°N – 63°33'20"N and 18°20'W – 13°E.

The RCP projections were produced using the POLCOMS-ERSEM coupled model at a 10km resolution, underpinned by the global climate model MPI-ESM-LR (Kay et al., 2018; available from Copernicus Climate Data Store, 2020). The global model, resolution about 1.5°, provided lateral boundary conditions, while surface forcing at 0.11° resolution came from a downscaled atmospheric model, MPI-ESM-LR_RCA4, under the EURO-CORDEX initiative. The river discharge and nutrient loadings were created using the E-HYPE hydrological model (Donnelly et al., 2016), also driven by downscaled versions of MPI-ESM-LR.

Following a similar methodology to Townhill et al. (2017), the SRES and RCP downscaled shelf seas projections were nested within the driving global projections with a resulting global dataset at 1/3° resolution. The global ocean fields were bi-linearly interpolated from their native resolution to 1/3°, and the downscaled regional cells were aggregated up (averaged) from their native resolution to the required 1/3°. These were then nested into the global data. This resolution still captures the local-scale processes of the shelf seas model, such as tides and riverine inputs while not reducing the resolution of the global data more than is appropriate. This 1/3° resolution grid of the recent past environmental parameters was then used as the driver for the ecological niche model, with the projections being carried out for the 2060 grid.

Environmental variables used to train the ENMs were near-bed sea temperature, sea surface temperature, near-bed salinity, sea surface salinity, the difference in near-bed and surface salinity and temperature (an approximation of stratification), and depth. The stratification variables were excluded from the modelling because they were strongly correlated to the others (i.e., with a Pearson correlation coefficient >0.7; see Figure S1 for full correlation analysis). Detailed substrate data were not available for the whole geographic area covered by the models, and so was not included.

For each SRES ensemble member and each RCP, the training period of 1997 to 2016 (hereafter referred to as “present day”) was used to determine each species' current habitat suitability, and the models run was used to calculate 20-year averages from 2010 to 2070. We present results for each 20-year period, referred to by

their central year (i.e., the time period of 2051–2070 is hereafter referred to as 2060).

2.4 | Modelling

Since our species occurrence data came from such large and heterogeneous dataset, abundance values were not directly comparable and only presence data was considered. Presence/absence models compare conditions at sites where a species is known to be present with those of sites where it is known to be absent. For 44 species, absences were defined as the locations and dates where an IBTS or Spanish survey was carried out using a relevant gear but the species was not found. In particular, bottom dwelling species were considered absent when either otter or beam trawling gears were used in the survey, while pelagic species were only considered absent if otter trawls were used. There were five species for which this procedure could not be followed, either because they were typically not captured by any of the gears used in the surveys or because their possible presence was not recorded. These species were Atlantic bluefin tuna, the two squid species (*Loligo forbesii* and *Loligo vulgaris*), cuttlefish and Norway lobster. For these five species, pseudoabsences (sometimes referred to as background points) were generated by choosing random sites within the species' range which were at least 20km away from any presence sites. The use of pseudoabsences instead of real absences for ENM modelling is well established and leads to robust models (Barbet-Massin et al., 2012), in addition of being routinely done by some ENM techniques, such as MaxEnt, which frequently ranked among the top performers of the five models we used (see below). The ENM models were trained with all the presence/absence data aggregated for the 20-year training period (1997–2016), and it was expected that using such an extensive training period would provide good coverage of the species' true habitats even for those species that were harder to detect, in addition to minimising the effect of combining heterogeneous and non-standardised observations.

For each species, climate model and ENM technique combination, an additional 10 models were trained for model validation (to test model performance). All the occurrence data were randomly divided into 10 groups, with each model trained with data from 9 of the 10 groups, leaving a different group out each time. Model performance was then tested on the data not used for model training. Area Under the Curve (AUC) values of the Receiver Operating Characteristic (ROC) curves were calculated to get an indication of

model fit (see [Figure S2](#)). Those models with an AUC value <0.7 were excluded from further analysis. All the models with AUC value of 0.7 or greater were given the same weight.

On completion of the modelling, projections were made for 2060, and the percentage change in habitat suitability for the United Kingdom EEZ calculated by averaging the changes for all models that had passed the AUC test for each particular species. The latitudinal shift in kilometres within the EEZ was also calculated for each decade, showing how the suitable habitat for each species is projected to move north or south over the century. To produce maps of the suitable habitat, the model projections were converted to binary presence/absence data using the thresholds that optimised the True Skill Statistics (TSS) of each model, to produce model agreement maps showing the likely suitable habitat for each species for the training period and the future decades. We additionally produced maps with the number of species with suitable habitat, using the same presence/absence thresholds and counting each species when at least half of the ENM methods with acceptable performance projected a suitable habitat for it.

3 | RESULTS

3.1 | Model performance

Model performance varied across the 49 species and was highest on average for black seabream, Greenland halibut, boarfish and Atlantic wolffish ([Figure S2](#)). All five ENMs performed well for most species, but for some species (e.g., European anchovy, veined squid, Norway lobster, Atlantic mackerel) only one or two distribution models had sufficient skill. Bioclim was the weakest-performing model of the five studied, and the one that more often did not meet the 0.7 AUC cut-off (for 44% and 34% of the species, for the models trained on data from the RCP and A1B climate scenarios respectively). For veined squid, only one model performed suitably well: Maxent. Model performance was species-dependent and was impacted by the extent in which the occurrence data managed to capture the actual distribution, and whether the environmental variables used are the main drivers of the species' distribution (for example, if a species is so widespread that it is able to tolerate a wider range of temperatures, or if bottom substrate has more bearing on the ecological niche).

3.2 | Habitat suitability and distribution shifts

Of the 49 commercial species examined, the waters around the United Kingdom are predicted to become more suitable in the future for around half of them (i.e., 'winners'), including black seabream, European seabass, sardine, surmullet, pouting, anchovy, sole and John Dory ([Figure 2](#)). The models projected that the waters will become less suitable for others, including saithe, Atlantic wolffish, starry ray, halibut, ling, lemon sole, Atlantic cod, haddock

and megrim (i.e., 'losers'). [Figure 2](#) shows the overall habitat suitability trend for the UK EEZ. For some species, there is an initial increase in suitable habitat, and then a decrease as the century progresses.

The different combinations of ENM and climate scenarios showed some differences in their projections, which are not clear from the overall mean trends shown in [Figure 2](#). The projected changes in habitat suitability and latitudinal centroid for the different models are given in [Figure 3](#). For some species, the models gave a large range of projections, with some models showing a greater change than others. The RCP4.5 projections generally yielded the smallest responses of the three. It should be noted that the range of projected change often spans zero for many species (including bluefin tuna, whiting, herring and cod), that is, some model formulations suggest negative consequences and others suggest positive consequences, highlighting the uncertainty implicit in such modelling and the value of using an 'ensemble approach'. For some species, the models showed very different magnitude of changes, for example, black seabream and European seabass. In these cases, all models showed an increase in suitable habitat, but this varied greatly (between 0% and nearly 400%) between models.

The distributions of the majority of species modelled were projected to shift northwards around the United Kingdom by 2060, with the exact number varying with the model used ([Figure 3](#)). Those with the greatest projected northward shift include boarfish, spotted ray, European plaice, dab and grey gurnard. However, for a number of species, including sardine, anchovy, surmullet, pouting (bib) and European squid, while some models project an overall northward shift, other models anticipate a southward shift. The highest northward shifts are generally projected with the SRES A1B scenario and the RCP8.5 scenario.

The median latitude of each species centroid for the present day and for 2060 are also shown in [Figure 3](#). Again, this shows that the majority of species are projected to move northwards, including those which currently have a more northerly distribution (such as Greenland halibut, saithe, halibut, ling and cod) and those with a more southerly distribution (such as black seabream, European seabass, turbot and pouting (bib)).

Maps are included ([Figures 4 and 5](#)) showing the projected habitat suitability change for two southerly species, black seabream, European seabass, and for two northerly species, Atlantic cod and saithe. These show the present day habitat suitability, and the projected change in habitat suitability to 2060 under RCP8.5. The projected changes under the A1B and RCP4.5 scenarios are provided in the [Figures S3–S6](#). Black seabream and European seabass are both projected to experience an increase in habitat suitability in the future, with their distributions shifting north around the United Kingdom ([Figure 4](#)). The present day distributions for these species are currently predominantly in France, Spain and the Mediterranean, and suitable habitat in the United Kingdom is only around the south and southwest of England. By 2060, the

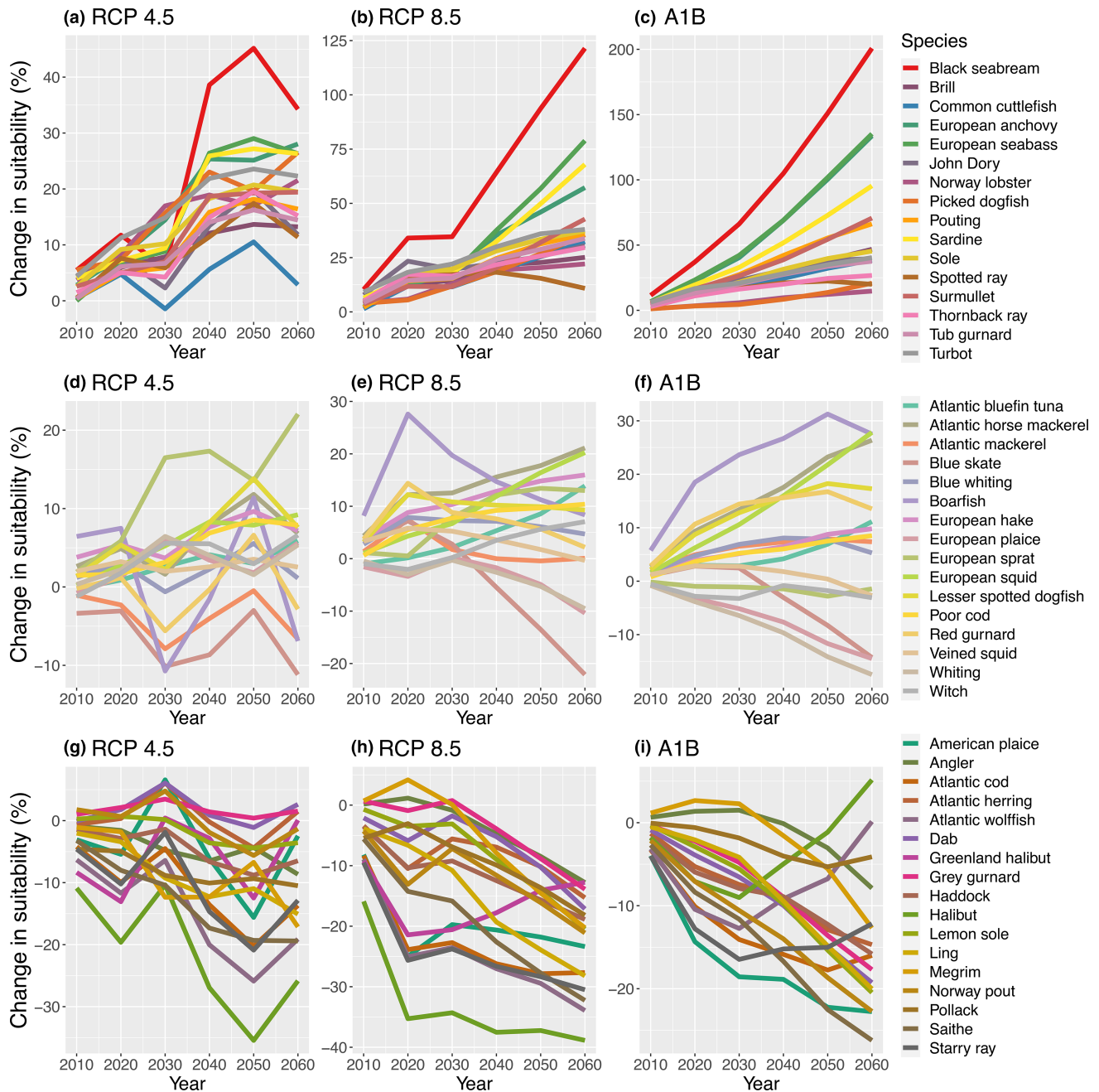


FIGURE 2 The model ensemble mean for the UK's EEZ for each species from 2010 to 2060 under RCP 4.5 (a, d, g), RCP 8.5 (b, e, h) and A1B (c, f, i). The first row (a–c) shows those species whose habitat suitability is projected to increase for a majority of climate models, whereas the second and third rows show species with suitable habitat mostly projected to experience little variation (d–f) or to decrease (g–i).

suitable habitat is projected to increase around the United Kingdom and Ireland, and particularly in the North Sea for black seabream. Atlantic cod and saithe by contrast are both projected to experience a decrease in suitable habitat during the century (Figure 5). The most suitable habitat for these species is currently in the northern North Sea and around Scotland, extending to Scandinavia. By 2060, suitable habitat in the UK EEZ is projected to have decreased substantially as the species' distribution shifts northwards. Maps showing the projected changes around northwest Europe for all species are shown in the Appendix S2.

Considering all species together, suitable habitat is projected to increase around the central and northern North Sea, and the north of Scotland, and to decrease in the English Channel, southern North Sea and the Irish Sea. Figure 6 shows the number of species which have at least half of the models projecting suitable habitat out of the 49 modelled under the RCP scenarios (maps for A1B are provided in the Figure S7). This can be considered a proxy for the number of species projected to be present in each area by 2060 under each scenario. More species are projected to have suitable habitat under RCP8.5 than in RCP4.5, in those same more northerly areas.

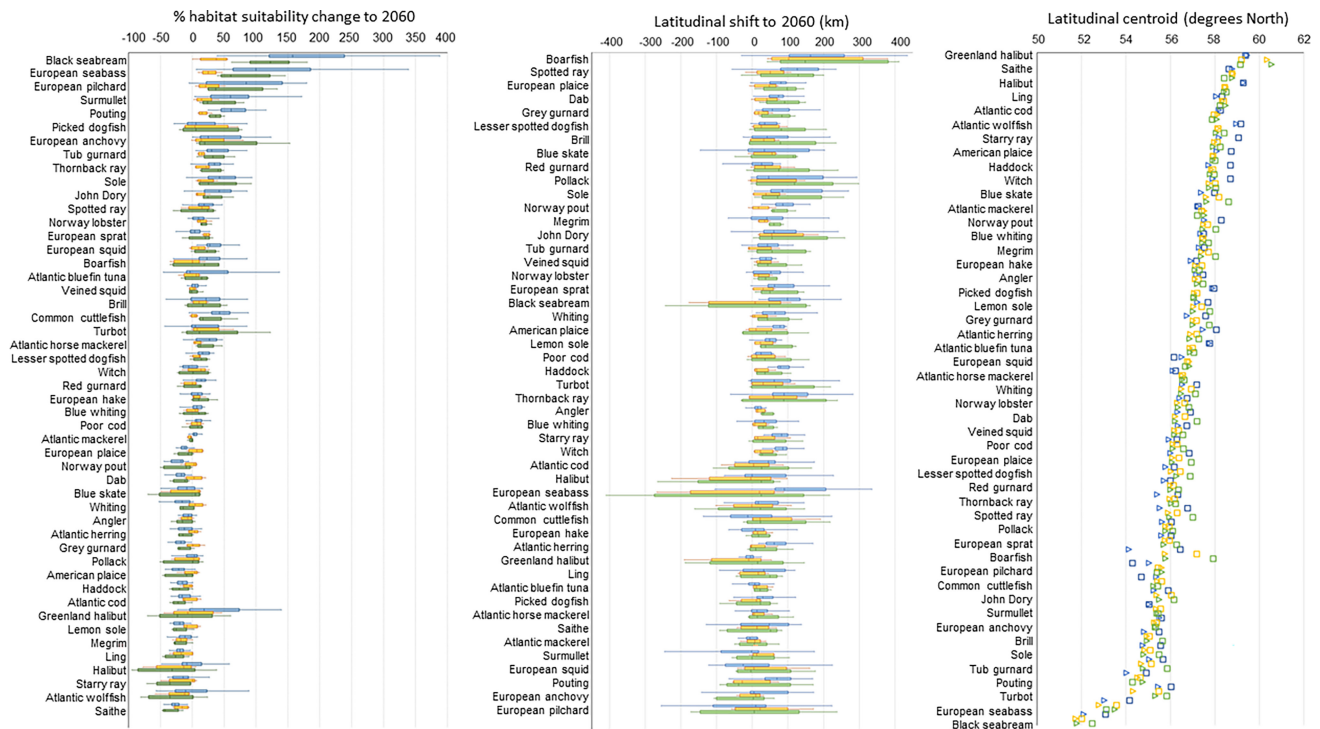


FIGURE 3 The percentage change in suitable habitat in the UK EEZ to 2060 under the different climate change scenarios (left). A positive habitat suitability change indicates that the area will become more suitable in the future for the species. A negative habitat suitability change shows that the habitat is less suitable for that species in the future. The latitudinal shift of suitable habitat in the UK EEZ to 2060 under the different climate change scenarios (middle). Negative latitudinal shift values show a projected southward movement of habitat suitability, and positive shifts reflect a northward movement of habitat suitability. The latitudinal centroid for the present day (Δ) and for 2060 (\square) (right). Blue = A1B. Orange = RCP4.5. Green = RCP8.5.

4 | DISCUSSION

This work suggests that climate change is likely to have implications for many (if not all) commercial fish around the northwest of Europe and the UK, with substantial turnover of species anticipated. The suitable habitat of around half of those species modelled was projected to increase, with the other half decreasing. The models indicate that northwest European waters are likely to become less suitable for the more traditional commercial fish species, such as cod, haddock and saithe, and more suitable for species which are more widespread in southern Europe, such as black seabream, European seabass, sardine and anchovy. As such, the modelling shows that climate change is expected to present both opportunities and threats to the local fishing industries, in agreement with other studies (Payne et al., 2021). For those species which currently have their most northerly distribution (leading edge) around northern France and the south of England, suitable habitat is projected to shift northwards, into the Irish Sea and the southern and central North Sea. For trailing edge species which are currently present only in northern parts of the British Isles, their suitable habitat is projected to retreat further north, away from the United Kingdom. A broad analysis of the UK Sea Fisheries Statistics (MMO, 2020) for UK landings to UK ports (which shows the main species groups caught) shows that in 2019, 81,000 tonnes were caught of species which are projected to increase

around the UK, with a value of £211 million, whereas 203,000 tonnes were caught of species projected to decrease, with a value of £307 million. This is mainly due to the high catch of species such as haddock, cod and mackerel, which are projected to have a reduced habitat suitability under climate change.

The range of model results shown for each species, which sometimes span zero, illustrates that while these techniques are valuable in understanding how environmental changes can conceivably affect species distributions, the results are heavily dependent upon the particular model that is chosen and that there is no 'best' or 'correct' model overall. However, while there are differences in the magnitude of change between models, and while some models perform better for certain species compared with others, overall, the general trends in habitat suitability and abundance are robust across models and climate scenarios. By using an ensemble of different models, some of which are more or less conservative in their species projections, we can demonstrate how robust or consistent the particular projections are to the assumptions that have been made. The ensemble method shows that while the absolute values of any change should not be relied upon, and should not be considered a prediction, the direction of change is generally consistent as a projection. Caution should be used for those species where the projected direction of change is not consistent across models. When considering changes in a specific species, it is important to consider the uncertainty in the projections, and not only focus on the average results.

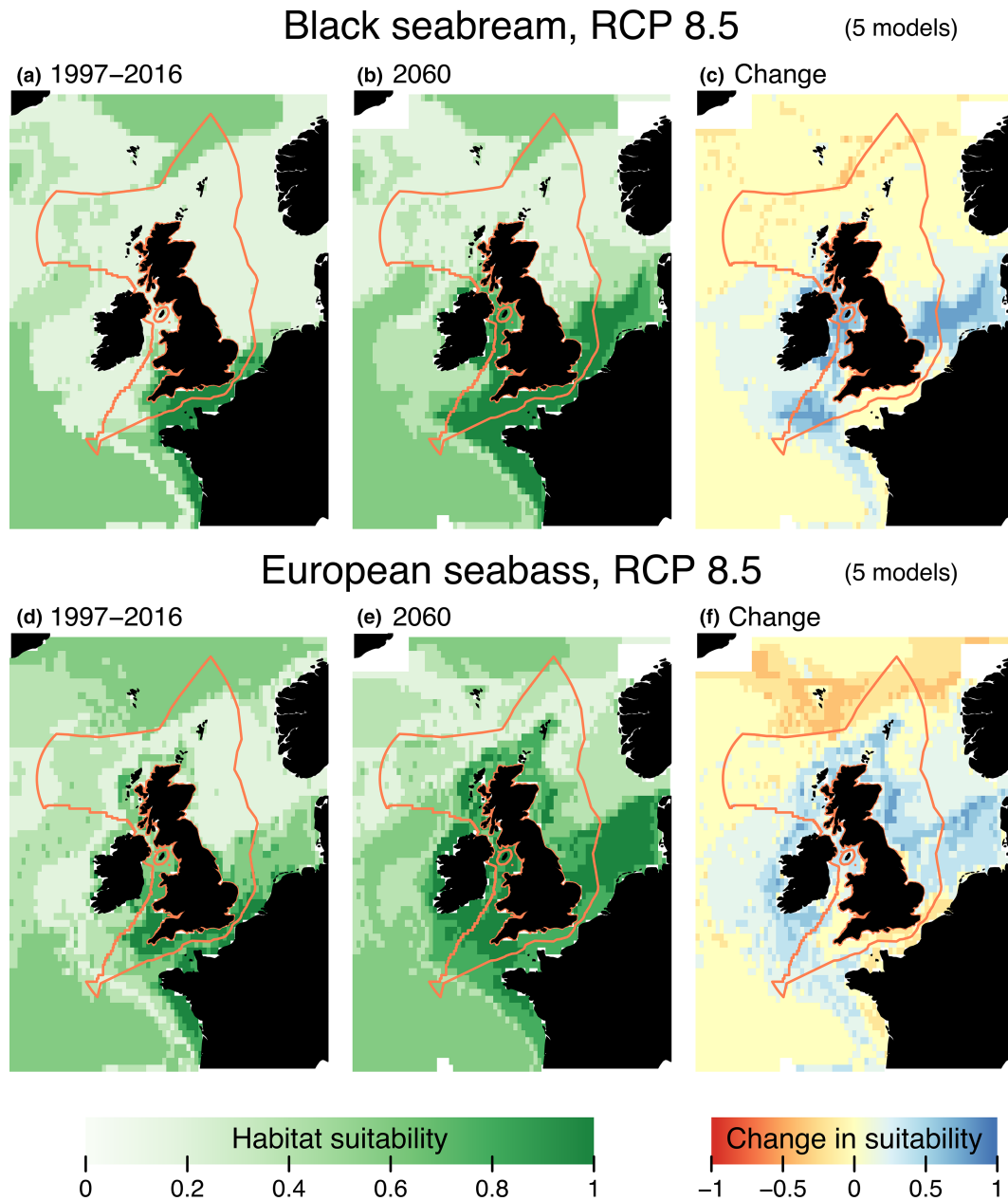


FIGURE 4 The suitable habitat for the training period (1997–2016; left), for 2060 (middle) and the change in suitability (right) for black seabream (top) and European seabass (bottom), corresponding to RCP 8.5. The UK EEZ is shown in red for reference. The scale shows model agreement. A value of “1” in suitability indicates that all models with acceptable performance agree that the habitat is suitable for the species, a value of “0” indicate all models agree habitat is not suitable. Similarly, a change of suitability of “1” corresponds to areas where all models initially agreed was not suitable in the training period but is suitable in 2060, and a value of “-1” to the opposite situation. Also shown in parenthesis next to the species name is the number of ENM models with acceptable performance (i.e., AUC score of 0.7 or above).

Overall, we suggest that the projections of changes in habitat suitability within the United Kingdom EEZs are more useful than the projections of latitudinal shift, since the latter can yield counter-intuitive results because of the complex coastal geomorphology and oceanography (depth, local temperature variations etc.) of the European shelf. The maps showing the number of species projected to have suitable habitat in the future (Figure 6; Figure S7) are useful in understanding the areas which might support more commercial fish and fisheries in the future. These show that there is projected to

be suitable habitat in the future for more commercial species in the central and northern North Sea and north and west of Scotland, and less in the English Channel, southern North Sea and the Irish Sea.

However, as an example of the complexity of the geographical shifts, some species, such as surmullet and sardine, are projected to experience more suitable habitat around the UK as a whole, but also that the overall direction of distribution shift will be southwards (i.e., opposite direction to that generally anticipated), because they are anticipated to spill into the North Sea from the top

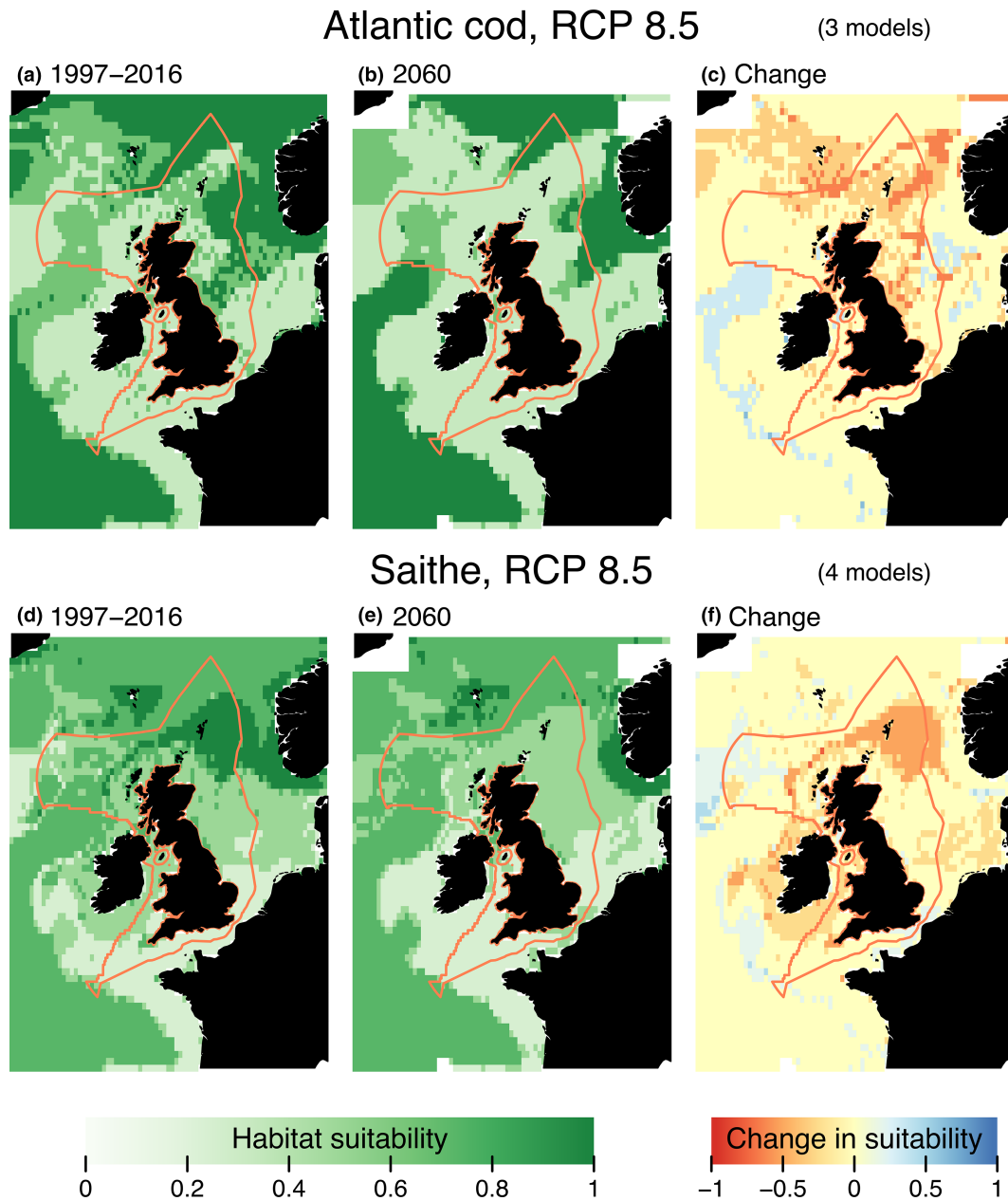


FIGURE 5 The suitable habitat for the training period (1997–2016; left), for 2060 (middle) and the change in suitability (right) for cod (top) and saithe (bottom), corresponding to RCP 8.5. The UK EEZ is shown in red for reference. Also shown in parenthesis next to the species name is the number of ENM models with acceptable performance (i.e., AUC score of 0.7 or above). The scale shows model agreement, as in Figure 4.

of Scotland rather than via the English Channel, in line with previous evidence (Beare et al., 2004). The maps of individual species are most useful in showing the areas where suitable habitat will increase or decrease, rather than an overall metric of latitudinal shift.

Similar changes were projected for many species, including Atlantic cod, using the Size Spectra-Dynamic Bioclimate Envelope Model (SS-DBEM) and the same POLCOMS-ERSEM RCP projections as used here (Copernicus, 2020). For other species, such as anchovy and European seabass, slower changes in suitable habitat are seen in the SS-DBEM model than in the present study. The SS-DBEM

includes parameters, such as trophic interactions, which could account for some of the differences. Similarly, ENM modelling using global climate models rather than downscaled models, yielded similar projections to the current study. The future distributions of 14 commercial species around the northwest shelf have been modelling using three ENM models, including Maxent (Jones et al., 2012). Similar to the present study, this showed that while some ENMs project an increase in suitable habitat, others suggest a decrease. Overall, the suitable habitat for traditional cold-water species was found to likely decrease this century, again agreeing with the present study (Frontiers Economics, 2013; Jones et al., 2012).

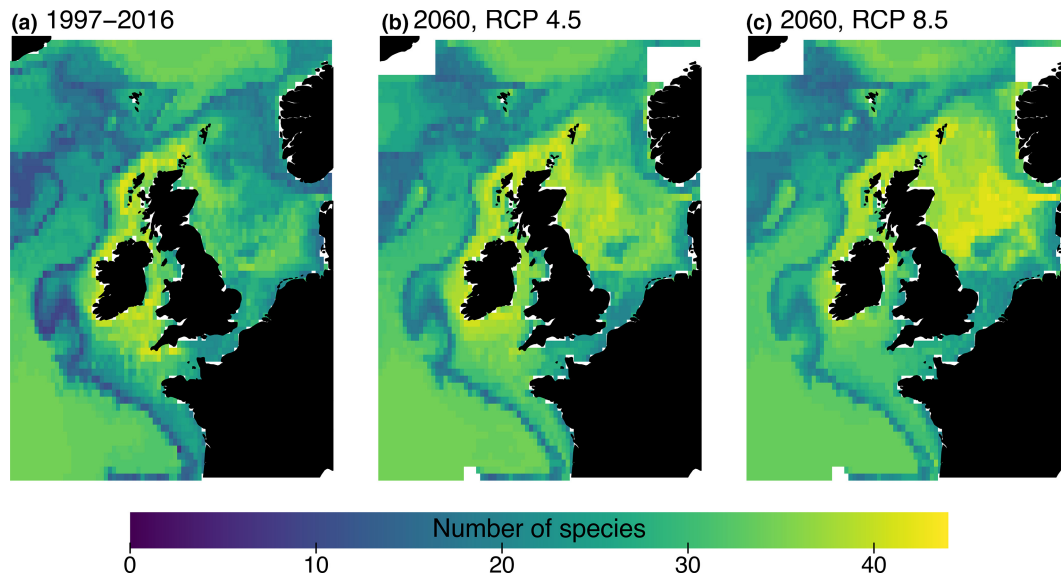


FIGURE 6 Number of species projected to have suitable habitat by at least half of the ENM methods with acceptable performance for the training period (a) and by 2060 under RCP 4.5 (b) and 8.5 (c).

The models used here include depth as a driving variable. However, previous work has shown that depth may become a limiting factor in the northerly distribution shifts of some demersal and benthic species (Rutterford et al., 2015; Weinert et al., 2016). Fish may not be able to move northwards to keep up with their temperature preferences, because the waters become too deep (although see Dulvy et al., 2008, showing that the North Sea demersal fish assemblage did shift deeper on average by ~3.6 m per decade between 1980 and 2004). Similarly, demersal fish may be constrained by prey availability or a particular substrate type (e.g., gravel for spawning) as their distribution shifts, and so they may not be able to track the changing temperatures by shifting northwards or deeper.

The models here include only certain variables (temperature, salinity and depth), and there are others which affect the suitable habitat for fish, such as seabed substrate, currents, pH, chlorophyll and prey availability. These variables were not available either for the future periods examined or at the resolution required, and so were not included in this study. However, as more data become available, these could be included in future modelling. While the present study used only a small number of variables, the technique is valuable in that the same methodology can be used on a large number of species without the need for detailed mechanistic understanding of life histories and physiology, allowing comparisons to be made, and the relative increases or decreases in habitat to be evaluated. If only a small number of species were modelled, or a smaller geographical area, additional variables could also be included, such as the inclusion of substrate for demersal species.

Not all of the ENMs performed well for each species, although each species had at least one ENM which met the criteria for inclusion. Those species for which the models did not perform well included pelagic species such as mackerel and anchovy which are not well sampled by the survey, which uses a demersal trawl, and

those which only occur on specific substrates (such as Norway lobster). As such, the projections for these models are less certain than for some of the other species for which the model performance was higher. Models for these species could be improved using additional acoustic survey or catch data, or including substrate data where available.

Our study has focused on changes in environmental niche and has not considered species interactions or other human pressures which can also affect the niche (Brierley & Kingsford, 2009; Wilkinson et al., 2019). Further work could use the model outputs to consider predator–prey interactions, species turnover, functional groups or traits, nursery areas, recruitment and economic values of the species (e.g., Izquierdo et al., 2021; Paradinas et al., 2017). These analyses would have wide interest and could be combined with any projections of invertebrates, biogenic habitat engineers, or higher predators such as marine mammals or birds.

Knowing which species may increase ('winners') or decrease ('losers') at a particular locality can be useful in fisheries management (Barange, 2019). Such insights can be used to identify the species for which precautionary fisheries management might be needed. For example, fishery researchers (Núñez-Riboni et al., 2019) have suggested that some areas of the North Sea will still be suitable for Atlantic cod, and may still support a sustainable fishery in the future, but only at very much lower levels of fishing mortality. Hence management reference points and Harvest Control Rules may need to be adapted to reflect changes in the prevailing climate.

Equally, fishing fleets and seafood consumers may need to adapt to accommodate emerging, warmer water species, which United Kingdom fishers do not traditionally target. These species could present an opportunity for fishers whose traditional species are no longer available. An example of this in recent years has been the development of summer squid fisheries off north-east Scotland (the

Moray Firth), reflecting a localised increase in squid abundance (van der Kooij et al., 2016). This has been viewed as a 'fishery of last resort' by fishers in response to limited availability or quota of more traditional species such as haddock.

Results could also be used to identify areas for species protection, where other human impacts can be managed or reduced to build climate resilience (Bernhardt & Leslie, 2013). However, species already subject to protection through closed areas (such as plaice in the North Sea 'Plaice Box') may no longer be found in those areas in the future, and so any future area-based management should take into account potential species shifts and evolve to be more 'adaptive'. For example, Weinert et al. (2021) found that the current locations of Marine Protected Areas in the North Sea may no longer be suitable for the vulnerable and protected species which they are designed to protect in the future.

This work has shown that climate change is likely to have implications for commercial fish around the UK and the north western shelf. The models indicate that north western European waters are likely to become more suitable for certain species but less suitable for others, presenting both opportunities and threats to the fishing industry. The discrepancies shown across models illustrates that while these techniques are valuable in understanding how environmental changes can conceivably affect ecological niches, the results are heavily dependent upon the individual model that is chosen. As such, this approach of modelling a large number of species, using an ensemble approach and a number of different climate change scenarios, is a way to take these differences into account, yet still revealing useful insights into potential future changes and yielding useful data for use in management. These results can be used in a number of different ways, in fisheries management and conservation, either considering only individual species or commercial fish as a whole.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data with the model agreement on the habitat of the 49 fish species from 2020 to 2060 under all 3 emission scenarios is available

to download from the Cefas Data Hub at: <https://doi.org/10.14466/CefasDataHub.138>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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