Received: 29 November 2019 | Accepted: 3 July 2020

DOI: 10.1111/1365-2664.13724

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Projected impacts of warming seas on commercially fished species at a biogeographic boundary of the European continental shelf

Katherine M. Maltby[1,2] | Louise A. Rutterford[2,3] | Jonathan Tinker[4] | Martin J. Genner[3] | Stephen D. Simpson[2]

[1]Centre for Environment Fisheries and Aquaculture Science (Cefas), Lowestoft, UK

[2]Biosciences, College of Life & Environmental Sciences, University of Exeter, Exeter, UK

[3]School of Biological Sciences, Life Sciences Building, University of Bristol, Bristol, UK

[4]Met Office Hadley Centre, Exeter, UK

Correspondence
Stephen D. Simpson
Email: s.simpson@exeter.ac.uk

Funding information
Centre for Environment, Fisheries and Aquaculture Science; Natural Environment Research Council

Handling Editor: Andre Punt

Abstract

1. Projecting the future effects of climate change on marine fished populations can help prepare the fishing industry and management systems for resulting ecological, social and economic changes. Generating projections using multiple climate scenarios can provide valuable insights for fisheries stakeholders regarding uncertainty arising from future climate data.
2. Using a range of climate projections based on the Intergovernmental Panel on Climate Change A1B, RCP4.5 and RCP8.5 climate scenarios, we modelled abundance of eight commercially important bottom dwelling fish species across the Celtic Sea, English Channel and southern North Sea through the 21st century. This region spans a faunal boundary between cooler northern waters and warmer southern waters, where mean sea surface temperatures are projected to rise by 2 to 4°C by 2098.
3. For each species, Generalized Additive Models were trained on spatially explicit abundance data from six surveys between 2001 and 2010. Annual and seasonal temperatures were key drivers of species abundance patterns. Models were used to project species abundance for each decade through to 2090.
4. Projections suggest important future changes in the availability and catchability of fish species, with projected increases in abundance of red mullet *Mullus surmuletus* L., Dover sole *Solea solea* L., John dory *Zeus faber* L. and lemon sole *Microstomus kitt* L. and decreases in abundance of Atlantic cod *Gadus morhua* L., anglerfish *Lophius piscatorius* L. and megrim *Lepidorhombus whiffiagonis* L. European plaice *Pleuronectes platessa* L. appeared less affected by projected temperature changes. Most projected abundance responses were comparable among climate projections, but uncertainty in the rate and magnitude of changes often increased substantially beyond 2040.
5. *Synthesis and applications*. These results indicate potential risks as well as some opportunities for demersal fisheries under climate change. These changes will challenge current management systems, with implications for decisions on target fishing mortality rates, fishing effort and allowable catches. Increasingly flexible

and adaptive approaches that reduce climate impacts on species while also supporting industry adaptation are required.

KEYWORDS
Celtic Sea, climate change, English Channel, fish, fisheries, North Sea, regional projections, uncertainty

1 | INTRODUCTION

Climate change has affected the abundance, dynamics and distribution of marine fish populations and their associated fisheries, resulting in substantive social and economic consequences (Barange et al., 2018; Brander, 2007; Cheung, Dunne, Sarmiento, & Pauly, 2011; Perry, Low, Ellis, & Reynolds, 2005). Projections of climate change impacts on marine systems provide important insights into future species responses to increased temperatures, as well as the future availability, productivity and catchability of stocks for dependent fisheries (Barange et al., 2014; Blanchard et al., 2012; Cheung et al., 2011).

The north-west European shelf has warmed particularly rapidly over the last four decades (Hughes et al., 2017). This warming has affected the phenology, behaviour, abundances and distributions of many fish species in these waters (Engelhard, Pinnegar, Kell, & Rijnsdorp, 2011; Pinnegar, Garrett, Simpson, Engelhard, & van der Kooij, 2017; Poloczanska et al., 2016; Simpson et al., 2011). For species with Lusitanian affinities such as red mullet *Mullus surmuletus* L., anchovy *Engraulis encrasicolus* L. and red gurnard *Chelidonicthys cuculus* L., warming temperatures have led to abundance increases and range expansion, leading to fishery level effects (Montero-Serra, Edwards, & Genner, 2015; Pinnegar et al., 2017; Simpson et al., 2011). Boreal species such as Atlantic cod *Gadus morhua* L., anglerfish *Lophius piscatorius* L. and European plaice *Pleuronectes platessa* L., which typically prefer cooler waters, have in some cases declined in abundance, shifted their distributions polewards, and/or deepened as they track preferred thermal ranges (Dulvy et al., 2008; Perry et al., 2005; van Hal, van Kooten, & Rijnsdorp, 2016).

Spatially explicit projections capturing the effects of future climate change on the abundance and distribution of fish populations underpin assessments of fisheries consequences. For the Northeast Atlantic region, Species Distribution Models (SDMs) have generally projected further poleward movements and/or deeper distributions of those species with preference for cooler waters (Cheung et al., 2011; Jones et al., 2013). However, a study using Generalized Additive Models (GAMs) suggested that many bottom dwelling (demersal) species in the North Sea could not move further polewards because they were constrained by availability of habitat at suitable depth (Rutterford et al., 2015). Differences between model projections highlight the need to examine the uncertainty associated with future projections to guide future model development and decision-making.

Identifying and disclosing the sources and extent of uncertainty associated with modelled projections provides insight into their strengths and weaknesses and can guide appropriate responses to, and treatment of, projections during decision-making (Cheung, Frölicher, et al., 2016; Freer, Partridge, Tarling, Collins, & Genner, 2018; Payne et al., 2015). Research comparing model approaches and performances or using different climate scenarios can help to quantify levels of uncertainty arising from these different potential sources (Cheung, Frölicher, et al., 2016; Cheung, Jones, et al., 2016; Freer et al., 2018). Recent attempts to consider uncertainty within the marine literature include exploring future long-term responses of individual species (Gårdmark et al., 2013), habitat suitability (Jones et al., 2013), ocean marine animal biomass (Lotze et al., 2019) and fisheries catch potentials and revenues (Cheung, Jones, et al., 2016; Lam, Cheung, Reygondeau, & Sumaila, 2016). While progress has been made in this area, there remains a significant lack of ecological research exploring the effects of uncertainty arising within and across climate scenarios, which could have important consequences for interpretation of resulting modelled projections (Freer et al., 2018; Payne et al., 2015).

The Celtic Sea, English Channel and southern North Sea sections of the European continental shelf comprise a faunal boundary between cooler northern waters and warmer southern waters (Hinz, Capasso, Lilley, Frost, & Jenkins, 2011). Sea temperatures in this region have warmed 0.17–0.45°C per decade between 1985 and 2014 (Hughes et al., 2017), and climate projections suggest further sea warming of 2–4°C by 2098 (Tinker, Lowe, Pardarns, Holt, & Barciela, 2016). The region is fished by many countries including the UK, Ireland, France and the Netherlands, with major fishing ports based along the coastline including Newlyn, Brixham, IJmuiden and Le Havre. Given the significance of this region for fisheries (STECF, 2017), and extent of projected climate change within the region (Tinker et al., 2016), we aimed to project responses of commercially important species while incorporating climate uncertainty. Specifically, we trained GAMs based upon multiple downscaled climate projections for the north-west European shelf seas alongside extensive fisheries survey data, and used these models with climate projections to estimate changes in the abundance of eight demersal fish species through the 21st century.

2 | MATERIALS AND METHODS

2.1 | Study area

The region of study included all marine areas from 47–53°N and 12°W–3°E, represented in our analyses as 72 1°× 1° sea grid cells.

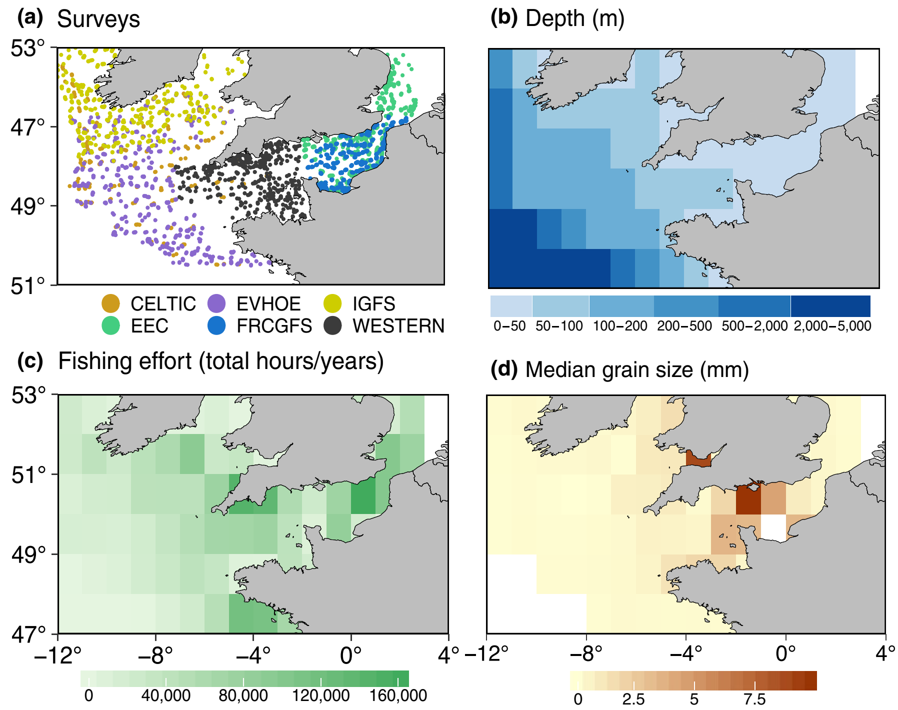

FIGURE 1 Study region and environmental data; (a) survey haul locations 2001–2010; (b) average depth; (c) average total fishing effort; (d) whole-sediment median grain size

Collectively, the region spans the English Channel, Celtic Sea, the Bristol Channel and parts of the southern North Sea (Figure 1).

2.2 | Data sources

2.2.1 | Depth, fishing effort and habitat

Average depth was calculated for each 1 × 1° grid cell using bathymetry data generated by the UK Met Office Hadley Centre (Figure 1b). Average decadal fishing effort (total hours/year) per 1 × 1° grid cell (Figure 1c) was calculated using data from the European Commission's Scientific, Technical and Economic Committee for Fisheries (STECF) database for the available time period 2003–2013 (STECF, 2014; see Table S1). Whole-sediment median grain size for each 1 × 1° grid cell was generated using data from Wilson, Spiers, Sabatino, and Heath (2018; Figure 1d).

2.2.2 | Temperature and salinity

In all, 13 climate projections for the region were obtained from the UK Met Office Hadley Centre. In total, 11 projections were generated from a project that dynamically downscaled, using the POLCOMS shelf seas model, an ensemble of perturbed global Atmosphere-Ocean climate model projections [based upon the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios (SRES) A1B scenario] for the entire north-west European shelf seas region (Tinker, Lowe, Holt, Pardaens, & Wiltshire, 2015; Tinker et al., 2016). Developing an ensemble of projections allowed uncertainty associated with atmosphere-physics model parameters to be explored, which is an important aspect of climate uncertainty often overlooked. The resulting 11 ensemble-member projections represent a range of possible future temperature and salinity ranges within a single climate scenario (Figure 2; see Tinker et al., 2016). The Tinker et al. (2016) projections are the only set of north-west European shelf sea projections (to date) that systematically and extensively consider this aspect of climate uncertainty (Tinker & Howes, 2020). These projections' annual and ensemble mean sea surface temperature and salinity absolute biases were <0.2°C and 0.2 psu when averaged over the shelf compared to observed data over the same time period and area: (1986–2006: Roberts-Jones, Fiedler, & Martin, 2012; 1960–2001: Ingleby & Huddleston, 2007).

Using this SRES ensemble enabled exploration of aspects of uncertainty *within* a single climate scenario through the use of different ensemble-members and examining their relative effects on projected species responses. A further two climate projections were obtained to compare uncertainty on projected species responses *across* climate scenarios. These climate projections represented Relative Concentration Pathway (RCP) 4.5 and RCP 8.5 scenarios, which were developed from a regional shelf sea model (AMM7) that dynamically downscaled long-term simulations of two CMIP5 Global Climate Models (HadGEM2-ES and MPI-ESM-LR) for the north-west European shelf (Hermans et al., 2020).

For all projections, decadal annual and seasonal (winter: January–March; summer: July–September) average sea surface temperatures (SST; °C), near bottom temperatures (NBT; °C) and near bottom salinity (NBS; psu) were calculated per 1 × 1° grid cell for each decade from 2001–2090 (2001–2010, 2011–2020, etc.). Across the SRES ensemble, there is a projected increase in annual SST of 3.26°C (southern North Sea), 3.13°C (English Channel) and 3.01°C (Celtic Sea) compared with

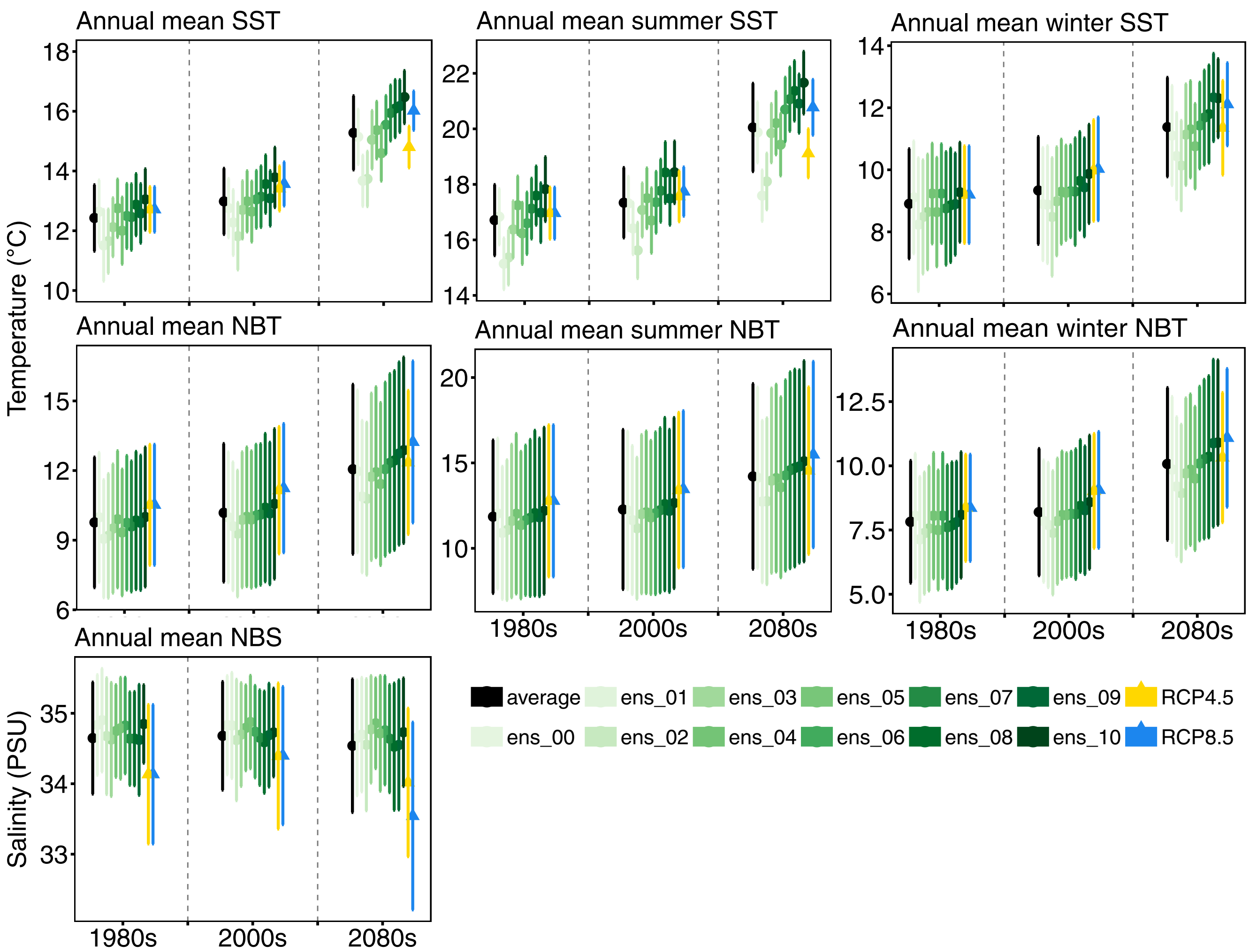

FIGURE 2 Decadal climate trends as projected for the 11 SRES ensemble-members (ens 00–ens 10), the average across the ensemble-members (black), and the two RCP projections. Y axes are independently scaled. Uncertainty in projections is represented by upper and lower 1 standard deviation from the mean

1960–1989, and a respective decrease in annual average sea surface salinity of −0.51, −0.08 and −0.11 psu by 2069–2098 compared with 1960–1989 (Tinker et al., 2016).

2.2.3 | Fish abundance data

Eight demersal fish species with a range of biogeographic affinities were selected, based on prior assessment of landing statistics and their social and economic importance to fisheries within the region (Table 1). These were anglerfish, Atlantic cod, Dover sole *Solea solea* L., European plaice, John dory *Zeus faber* L., lemon sole *Microstomas kitt* L., megrim *Lepidorhombus whiffiagonis* L. and red mullet. Abundance data were derived from six survey datasets [Cefas Eastern English Channel Survey (EEC), Cefas South Western Beam Trawl Survey (WESTERN), Cefas Celtic Sea Groundfish Survey (CELTIC), Irish Marine Institute Irish Groundfish Survey (IGFS), IFREMER French Southern Atlantic Bottom Trawl Survey (EVHOE) and IFREMER French Channel Groundfish Survey (FRCGFS)], which were obtained through the ICES DATRAS online database (http://www.ices.dk/data/data-portals/Pages/DATRAS.aspx) and from the UK Centre for Environment, Fisheries and Aquaculture Science (Cefas; Figure 1a).

Surveys only partially overlap in space, differ in temporal coverage and use different sampling methods and gears (Table S2). Consequently, we used data from 2001 to 2010 (2000s) when all surveys operated. We standardized abundance data to reduce inherent survey biases (see Supporting Information). Species abundances from individual hauls were converted to a catch per unit of effort (CPUE; effort = 1 hr), averaged for each 1 × 1° grid cell and the whole time series, and fourth root transformed to reduce the influence of outliers. In all, 62 grid cells with sufficient abundance data (more than three hauls recorded) were used for further analysis. To standardize species CPUE across different survey methods and gears, CPUE was included in a general linear model (CPUE ~ grid cell + decade + survey) using R v.3.4.1 (R Core Team, 2017) to generate standardized least-square mean CPUE estimates for each 1 × 1° grid cell using the LSMEANS package (Lenth, 2016; Searle, Speed, & Milliken, 1980; see Tables S3–S5).

TABLE 1 Species current geographical tendencies, thermal experience and fisheries commercial catch weights within the study region

Species	Central latitude (°)[a]	Central longitude (°)[a]	Mean temperature (°C)[a]	Fisheries catch (2017; tonnes, wet weight)[b]
Anglerfish	50.2	−7.1	12.84	22,623[c]
Atlantic cod	50.8	−5.1	12.36	2,595
Dover sole	50.4	−4.8	12.52	13,267
European plaice	50.9	−5.0	12.37	16,815
John dory	50.1	−6.5	12.88	1,818
Lemon sole	50.8	−4.9	12.37	2,572
Megrim[c]	50.1	−9.0	13.13	10,081[c]
Red mullet	50.0	−3.3	12.61	2,430

[a]Calculated from survey data analysed in this study.

[b]Total catch calculated from EU vessels in 2017 for ICES areas 27.4c, 27.7d, 27.7e, 27.7f, 27.7g, 27.7h and 27.7j (ICES, 2017).

[c]Statistics derived from, respectively, all Lophiidae (the dominant species in the area is anglerfish *Lophius piscatorius*), and all Lepidorhombus species (the dominant species in the area is the megrim *Lepidorhombus whiffiagonis*).

2.2.4 | Generalized additive models

Eight GAMs were developed; a 'full' model incorporating all variables and seven other models developed with different sets of environmental variables (Table S6). These were trained on abundance data for each species for 2001–2010, using all climate projections. Analyses were conducted using the MGCV package in R (Wood, 2011) and after trialling GAMs with different distributions, GAMs were fitted with a Gaussian distribution and 'identity' link function as this provided the best model fit. Abundance data were zero-bounded, and any resulting modelled abundance values less than zero were replaced with zero. A smoothing term was applied to all explanatory variables with knots set to $k = 5$ for smoothing to limit the degrees of freedom and avoid overfitting. Model fit was checked using *gam.check* and *gam.plot* functions. The relatively short time series prevented further training, and it was not possible to test the ability of GAMs to robustly project into the future when trained on different lengths of time series. However, previous work where equivalent historical fisheries and climate data were used with GAMs to generate future projections suggest that training with data from a single decade can provide meaningful projections (Rutterford et al., 2015). While some variables were collinear (Table S7), most were under a 0.7 threshold, and as informed by Dormann et al. (2012), this was not expected to significantly affect resulting projections due to these relationships not changing with future projection data, and due to projecting only within the geographical area on which GAMs were trained.

To identify which model should be considered for generating future projections, GAMs were compared and selected based on a range of model statistics; Akaike Information Criterion (AICc), Akaike weights, adjusted R squared, Generalized Cross Validation (GCV) scores and strength of correlations between projected and observed abundances. The optimal set of variables to include in the final GAM were chosen based on a balance between model simplicity and predictive ability (Table S8). Due to the high number of model outputs (832), one final GAM was required to use the same set of variables across species to allow the effect of different climate projections to be assessed while keeping all other explanatory variables constant. To identify the model that overall was most optimal across most species–climate combinations, each model statistic was included in a general linear model with climate projection and species as predictor variables. Least-square means were then generated, using the LSMEANS package in R, to determine the model with the best performance across all species (Table S9; Lenth, 2016).

The final GAM model was used for each species–climate projection combination for each decade separately from 2001–2010 to 2081–2090 to project future species' abundance. The present spatial pattern of fishing effort was assumed to be constant when generating future projections. 'Mean abundance' projections for each species were also calculated by averaging projections across the 11 SRES ensemble-members and for each RCP projection. The difference in mean abundance between the 2000s (2001–2010) and 2040s (2041–2050) was determined for each species using back-transformed projected fourth rooted abundance data to allow comparison of abundances within the timeframe over which there was strong agreement between climate projections and had greatest relevance from ecological and management perspectives.

3 | RESULTS

3.1 | GAM performance

Least-square mean analysis identified that for most model statistics Model A, the model with all variables included, provided the optimal combination of variables to model patterns of species abundance (Figure 3; Table S9). This was the most parsimonious model owing to low AICc and GCV scores (Figure 3) and a high mean Pearson correlation score of 0.92 between observed and projected abundances across

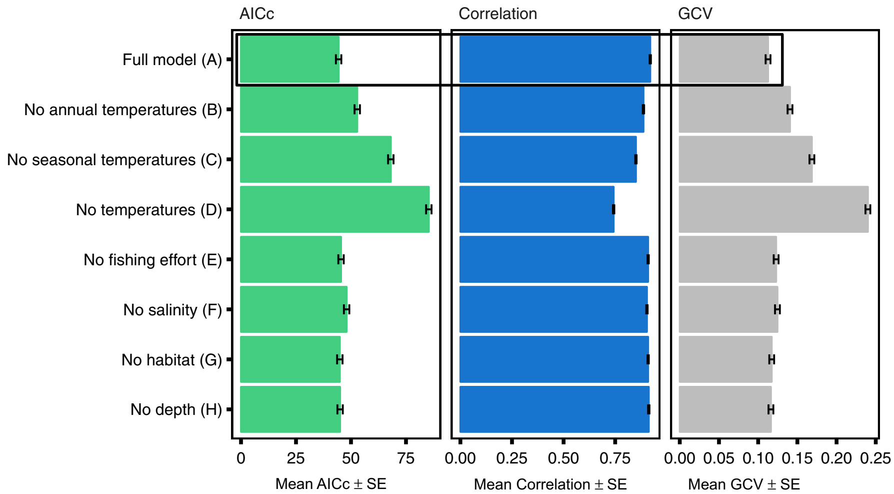

FIGURE 3 Least-square mean model statistic scores for each trialled model. Left panel: Akaike Information Criterion corrected for small samples; Mid panel: Correlation; Right panel: Generalized Cross Validation. Bars show standard errors

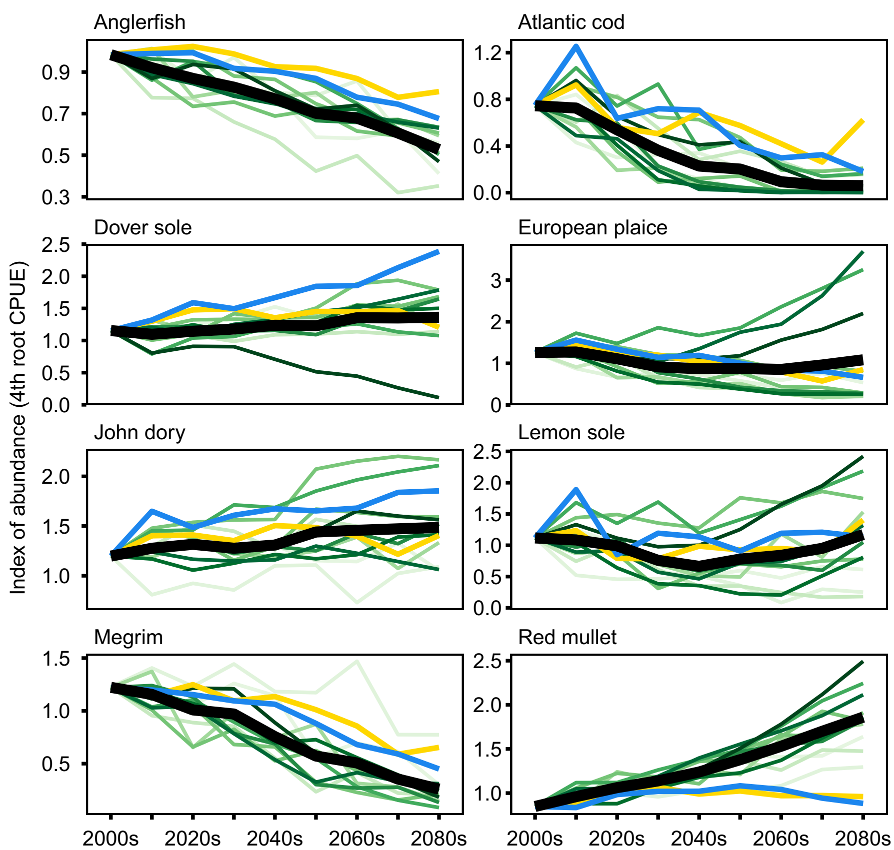

FIGURE 4 Projected changes in an index of abundance (4th rooted CPUE) from 2000s until 2080s for all species. Each line represents an SRES or RCP projection (colour codes follow Figure 2). Black lines represent the mean across SRES ensemble-members

all species and climate projections (Table S9). For most species, all variables improved model fit, but importantly, model statistics consistently indicated that temperature was a key driver of species responses; models that did not include temperature variables, particularly Model D, had some of the highest AICc and GCV scores and often poor fit and/or predictive ability compared to other models (Figure 3; Table S9).

3.2 | Projected abundance

Region-wide declines in abundance were projected towards the 2080s for anglerfish, Atlantic cod and megrim (Figure 4; Table 2). The majority of projections indicated similar declining trends, although RCP-based projections showed less of a decline compared to the average of SRES-based projections. Increases in red mullet were projected with all climate projections up to 2040s, but after this point SRES-based projections showed further increases compared to RCP-based projections (Figure 4; Table 2). Dover sole, John dory and lemon sole increased in mean abundance, but responses projected with different climate projections were more variable. Projections for European plaice were relatively stable across all climate scenarios up to 2040s, but their projected responses differed by 2080s. For most species, there was greater variability in projected mean abundance among climate projections later into the 21st century.

TABLE 2 Mean CPUE index of abundance (back-transformed CPUE; catch per hour) for each time period and climate projection. Bold numbers represent mean abundance across all ensemble-members (SRES only) and grid cells. Standard deviation is in brackets

	SRES			RCP 4.5			RCP 8.5		
Species	Mean CPUE 2000s	Mean CPUE 2040s	Mean CPUE 2080s	Mean CPUE 2000s	Mean CPUE 2040s	Mean CPUE 2080s	Mean CPUE 2000s	Mean CPUE 2040s	Mean CPUE 2080s
Anglerfish	**2.08** (2.02)	**1.29** (1.55)	**0.51** (0.79)	**2.08** (2.03)	**1.92** (1.76)	**1.24** (1.15)	**2.07** (1.96)	**1.71** (1.61)	**0.82** (0.82)
Atlantic cod	**0.94** (1.45)	**0.13** (0.51)	**0.02** (0.15)	**0.92** (1.25)	**0.87** (1.31)	**0.79** (1.23)	**0.92** (1.20)	**1.08** (1.57)	**0.04** (0.10)
Dover sole	**3.69** (6.38)	**5.15** (7.96)	**8.54** (13.73)	**3.55** (5.62)	**6.03** (7.68)	**4.63** (6.45)	**3.66** (6.54)	**12.77** (13.87)	**50.34** (55.76)
European plaice	**11.12** (23.01)	**10.84** (39.81)	**53.78** (153.65)	**10.39** (17.37)	**7.80** (19.37)	**2.35** (4.78)	**10.55** (18.22)	**10.27** (20.77)	**1.30** (2.27)
John dory	**3.60** (2.99)	**5.53** (6.59)	**12.29** (19.65)	**3.63** (2.93)	**10.05** (9.05)	**9.52** (9.89)	**3.58** (2.86)	**11.55** (8.96)	**19.30** (18.01)
Lemon sole	**5.43** (8.77)	**1.66** (3.81)	**15.99** (32.09)	**5.45** (9.29)	**3.85** (7.22)	**12.13** (18.65)	**5.61** (9.70)	**5.92** (10.55)	**9.42** (20.65)
Megrim	**17.49** (27.33)	**11.67** (40.99)	**8.67** (77.13)	**17.18** (26.62)	**16.02** (26.40)	**4.48** (14.45)	**17.34** (27.84)	**14.91** (31.67)	**2.31** (10.11)
Red mullet	**1.97** (3.28)	**6.80** (10.37)	**24.34** (33.60)	**2.02** (3.34)	**3.98** (7.27)	**3.65** (6.63)	**2.04** (3.40)	**4.32** (7.81)	**3.18** (5.41)

Spatial abundance patterns revealed some variation in the magnitude and directionality of projected change for each species (Figure 5a,b; Figure S3a–h). Almost all of the SRES ensemble-members agreed on the directionality in abundance change for anglerfish, Atlantic cod and red mullet across the region, but the magnitude of change differed. For all other species, there was less agreement across ensemble-members regarding directionality and/or magnitude of change, particularly for Dover sole, lemon sole and John dory. Comparing SRES- and RCP-based projections revealed differences in the magnitude of change for some species. For example, Dover sole and John dory showed greater increases for RCP-based projections, while for European plaice, megrim and red mullet SRES-based projections indicated greater increases/decreases. Spatial abundance changes showed similar directionality across climate projections for most species with the exceptions of anglerfish and Atlantic cod (Figure 5a,b).

Red mullet was projected to show a region-wide increase in abundance from the 2000s to 2040s, particularly in the English Channel. Dover sole and John dory were also projected to increase in most parts of the study area. Anglerfish (with the exception of RCP 4.5) and megrim were projected to decline across their range, with some localized increases for megrim to the west. Lemon sole was projected to decline in the northern extent of the region but increase towards the south. European plaice showed increases to the east of the region but decreases to the west.

4 | DISCUSSION

For the first time for this region, we provide projections of species abundance in response to future warming that are based on multiple climate projections and use survey information to identify variables influencing these responses. On average, projections towards 2090 suggest increased abundance for warm-water-associated species (e.g. red mullet and John dory) and declines for those associated with cooler waters (e.g. Atlantic cod and anglerfish). Projections presented here can help to inform the fishing industry and management systems about the potential social, economic and ecological risks and opportunities resulting from these changes.

Our projections suggest that fisheries within the region could benefit from projected increases in Lusitanian species such as Dover sole, John dory and red mullet. Projected increases and expansions across the region for John dory and red mullet continue a trend that has been documented since the mid-1990s within the North Sea and Celtic Sea (Beare et al., 2004; Simpson et al., 2011; ter Hofstede, Hiddink, & Rijnsdorp, 2010). Such expansions may provide new fishing opportunities, as seen with other species in the region such as boarfish *Capros aper* off the south of Ireland (Pinnegar et al., 2013). However, the extent to which these opportunities can be realized depends on factors including fishers' capacity to modify fishing practices and the development of consumer demand and emergence of export markets (Jennings et al., 2016; Perry, Barange, & Ommer, 2010; Pinsky & Mantua, 2014). John dory and red mullet are currently subject to no fishing regulations or quota. A lack of

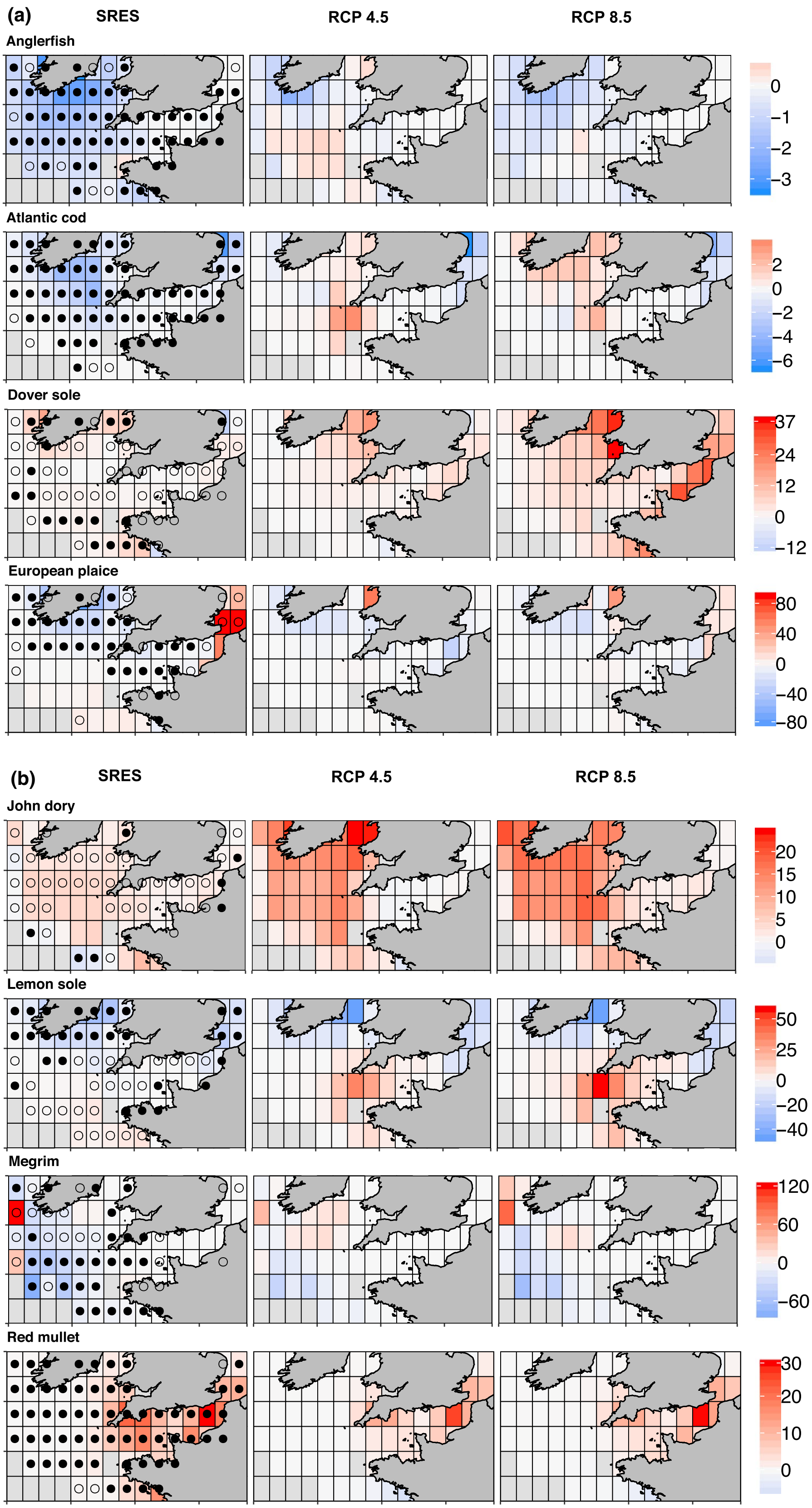

FIGURE 5 (a) Differences in projected abundance between 2000s and 2040s, using back-transformed CPUE (catch per hour) data for anglerfish, Atlantic cod, Dover sole and European plaice. Left panel: average projected abundance across SRES ensemble-members. Proportion of individual ensemble-members agreeing in directionality of projected change is reflected through closed dots ● (90% or more ensemble-members agree), open ○ (50%–90% ensemble-members agree) or no dots (fewer than 50% ensemble-members agree) for each grid cell. Mid and right panel: projected abundance for RCP4.5 and RCP8.5 projections. Grey grid cells represent no training data and therefore no projections. (b) Differences in projected abundance between 2000s and 2040s, using back-transformed CPUE (catch per hour) data for John dory, lemon sole, megrim and red mullet. Full legend description in (a)

regulation could enable easier access for fishers into these potential fisheries, but this would also likely risk the long-term sustainability of these species, which are often data-limited and can have a lack of understanding of how stressors such as climate change and fishing affect them (ICES, 2012; Pinsky & Mantua, 2014). Future management would need to balance facilitating access for fishers while also determining appropriate harvesting levels, or Total Allowable Catches, to ensure long-term sustainability.

Projected future declines in the boreal species anglerfish, Atlantic cod and megrim appear to be highly likely given that the majority of climate projections indicate declines. The projected trends add to wider literature demonstrating poleward (northward) shifts and/or deepening of these species in response to warming (Dulvy et al., 2008; Perry et al., 2005; van Hal et al., 2016). Such responses suggest reduced availability of these traditionally valuable species for fishers, alongside implications for the composition of catches. Many of the fisheries operating within this region are multispecies in nature (e.g. Mateo, Pawlowski, & Robert, 2016), catching many species simultaneously with the same gears. Species experiencing localized declines will most likely have reduced fishing mortality rates imposed by management systems and thus traditionally targeted species could become 'choke' species, restricting the capture of other species that are still abundant or are increasing. Flexible, adaptive management systems that enable responsive regulatory action to changing catch compositions and resources is therefore crucial to allow fishers to adapt to future changes (Holsman et al., 2019; Pinsky & Mantua, 2014).

Alterations in future fishing effort or management decisions were not incorporated in our projections, but such changes are likely (Haynie & Pfeiffer, 2012; Melnychuk, Banobi, & Hilborn, 2014). Projected abundance decreases would likely be linked to requirements to reduce fishing mortality and fishing effort to meet lower reference points for spawning stock biomass (Brander, 2007; Holsman et al., 2019). If abundances increased, the converse would occur. Increases in stock distribution owing to distribution–abundance relationships (Fisher & Frank, 2004) may also lead to fishing opportunities in new areas and effort spreading more widely, depending on management restrictions. Future research could explore the effects of different distributions of fishing activity and mortality for particular vessels and gears, resulting from prescribed or climate responsive management regimes.

All parameters included in the full model used have been demonstrated in wider research to affect species abundance and distributions, such as the role of depth in providing thermal relief for species or associations of demersal fish with benthic habitat type (Dulvy et al., 2008; Johnson, Jenkins, Hiddink, & Hinz, 2013). Crucially however, iterative removal of individual parameters across the model set suggested that the mean effects of temperature are important in driving species responses. Varying depth and climatic conditions have already shaped marine species assemblages within the region (Hinz et al., 2011; ter Hofstede et al., 2010). Given the importance of temperature affecting species responses, incorporating temperature driven effects within projections from stock assessments is crucial for anticipating future climate effects on stock dynamics and informing management decisions to help consider broader ecosystem effects (Sguotti et al., 2019; Skern-Mauritzen et al., 2015). Yet, for many stocks within this region, incorporating such environmental variability within assessments is still lacking.

Assessing model performance and understanding the uncertainty associated with projections is important from both scientific and fisheries management perspectives (Cheung, Frölicher, et al., 2016; Freer et al., 2018). Using GAMs provided a data-driven, statistical approach, but differences in the design, coverage and duration of fisheries surveys used limited training data duration and precluded in-depth testing of GAMs using iteratively partitioned time series. However, we have relatively high confidence in our approach for making projections through to 2040, and potentially beyond, as model statistics and comparisons for the tested time period indicated good model fits and there were relatively consistent patterns among climate projections. The performance of the approach has been systematically tested in the North Sea where annual surveys have been conducted in a relatively standardized way since the early 1980s (Rutterford et al., 2015). This study showed that projections using GAMs trained on data from the early part of the time series provided relatively reliable predictions of distribution and abundance for eight of 10 demersal species over a period of 30 years. Additional uncertainty about mid- to long-term projections and their consequences may result from factors we do not address directly such as changes in interspecific interactions (e.g. predator–prey dynamics) or fishing activity.

Using multiple climate projections provides greater transparency regarding the confidence in resulting modelled projections (Freer et al., 2018). An SRES ensemble allowed exploration of the consequences on projected species responses of climate-model parameter uncertainty within a single climate scenario (Tinker et al., 2015, 2016). Resulting uncertainties, captured by the spread of ensemble projections, implied that we should have high confidence in the direction of changes for most species, but the magnitude of change was more uncertain. Agreement among abundance projections was especially strong for cold adapted species with narrow thermal ranges, such as anglerfish and megrim, indicating high confidence that the fishing industry will have to adapt to declining catching opportunities. For other species, there was greater variability among projections that also increased towards 2090, which may be due to these species having wider thermal ranges or tolerances. Using different climate scenarios did not result in substantially different species responses, with RCP-based projections often within the range of those produced from the SRES ensemble. There has been little change in the median temperature (and its uncertainty range) between CMIP3 (generated SRES projections) and CMIP5 (generated RCP projections) global climate projections (e.g. Kumar, Kodra, & Ganguly, 2014), and Tinker et al. (2016) showed that the median of their SRES ensemble is likely to be consistent with an ensemble downscaled from RCP8.5. Consequently, downscaled shelf sea climate projections are relatively similar, helping explain why limited differences between SRES- and RCP-based species projections were found. Given the uncertainty in future emission trajectories, projecting species responses using multiple climate projections provides the opportunity to examine the spread of all possible future outcomes, which are critical for allowing fisheries stakeholders to make climate-informed decisions.

In summary, our analyses suggest that climate change will continue to modify the abundance and distribution of commercially important fishes in the Celtic Sea, English Channel and southern North Sea. For species likely constrained by the coolest and warmest conditions, the projected directions of change in abundance are consistent among climate projections. Results suggest implications not only for the wider ecosystem (e.g. predator–prey dynamics or community composition) but also that the fishing industry and management systems will likely have to adjust their operations to address changes in availability, catchability and composition of catches. For declining species, fisheries managers may need to consider options that can reduce the vulnerability of stocks to warming temperatures, such as reducing fishing mortality rates or imposing stricter catch limits. For species not currently regulated, as a first step, species may need to be closely monitored for increasing fishing pressure, with future regulations or measures such as quotas potentially necessary. Fishers 'on-the-ground' experiences should be incorporated with scientific information to inform future management decisions to enable sustainable exploitation while supporting fishers' adaptation to changes in species' relative abundance.

ACKNOWLEDGEMENTS

We thank Simon Jennings for his invaluable advice and comments throughout this work, and for assistance sourcing survey data. This work was funded by a NERC GW4+ studentship with Cefas CASE Industrial support awarded to K.M.M. J.T. was supported by the UK Met Office Hadley Centre Climate Programme funded by BEIS and Defra.

AUTHORS' CONTRIBUTIONS

K.M.M., S.D.S. and M.J.G. conceived the ideas; all designed methodology and contributed to project development; K.M.M. and J.T. collected and/or obtained the data; K.M.M., L.A.R., J.T. and M.J.G. pre-processed all data; K.M.M. analysed the data; K.M.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.8cz8w9gmz (Maltby, Rutterford, Tinker, Genner, & Simpson, 2020).

ORCID

Katherine M. Maltby https://orcid.org/0000-0001-7570-5257

REFERENCES

Barange, M., Bahri, T., Beveridge, M. C. M., Cochrane, K. L., Funge-Smith, S., & Poulain, F. (Eds.). (2018). *Impacts of climate change on fisheries and aquaculture: Synthesis of current knowledge, adaptation and mitigation options*. FAO Fisheries and Aquaculture Technical Paper No. 627. Rome: FAO. 628 pp.

Barange, M., Merino, G., Blanchard, J. L., Scholtens, J., Harle, J., Allison, E. H., … Jennings, S. (2014). Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Climate Change*, *4*, 211–216. https://doi.org/10.1038/nclimate2119

Beare, D. J., Burns, F., Grieg, A., Jones, E. G., Peach, K., Kienzle, M., … Reid, D. G. (2004). Long-term increases in the prevalence of North Sea fishes having southern biogeographic affinities. *Marine Ecology Progress Series*, *282*, 269–278. https://doi.org/10.3354/meps284269

Blanchard, J. L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., … Barange, M. (2012). Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical Transactions of Royal Society B: Biological Sciences*, *367*, 2979–2989. https://doi.org/10.1098/rstb.2012.0231

Brander, K. M. (2007). Global fish production and climate change. *Proceedings of National Academy of Sciences of the United States of America*, *104*(50), 19709–19714. https://doi.org/10.1073/pnas.0702059104

Cheung, W. W. L., Dunne, J., Sarmiento, J. L., & Pauly, D. (2011). Integrating ecophysiology and plankton dynamics into projected maximum series catch potential under climate change in the Northeast Atlantic. *ICES Journal of Marine Science*, *68*(6), 1008–1018. https://doi.org/10.1093/icesjms/fsr012

Cheung, W. W. L., Frölicher, T. L., Asch, R. G., Jones, M. C., Pinsky, M. L., Reygondeau, G., … Watson, J. R. (2016). Building confidence in projections of the responses of living marine resources to climate change. *ICES Journal of Marine Science*, *73*(5), 1283–1296. https://doi.org/10.1093/icesjms/fsv250

Cheung, W. W. L., Jones, M. C., Reygondeau, G., Stock, C. A., Lam, V. W. Y., & Frölicher, T. L. (2016). Structural uncertainty in projecting global fisheries catches under climate change. *Ecological Modelling*, *325*, 57–66. https://doi.org/10.1016/j.ecolmodel.2015.12.018

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., … Lautenbach, S. (2012). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmller, V., Dye, S. R., & Skjoldal, H. R. (2008). Climate change and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. *Journal of Applied Ecology*, *45*(4), 1029–1039. https://doi.org/10.1111/j.1365-2664.2008.01488.x

Engelhard, G. H., Pinnegar, J. K., Kell, L. T., & Rijnsdorp, A. D. (2011). Nine decades of North Sea sole and plaice distribution. *ICES Journal of Marine Science*, *68*(6), 1090–1104. https://doi.org/10.1093/icesjms/fsr031

Fisher, J. A. D., & Frank, K. T. (2004). Abundance–distribution relationships and conservation of exploited marine fishes. *Marine Ecology Progress Series*, *279*, 201–213. https://doi.org/10.3354/meps279201

Freer, J. J., Partridge, J. C., Tarling, G. A., Collins, M. A., & Genner, M. J. (2018). Predicting ecological responses in a changing ocean: The effects of future climate uncertainty. *Marine Biology*, *165*, 7. https://doi.org/10.1007/s00227-017-3239-1

Gårdmark, A., Lindegren, M., Neuenfeldt, S., Blenckner, T., Heikinheimo, O., Müller-Karulis, B., … Möllmann, C. (2013). Biological ensemble modeling to evaluate potential futures of living marine resources. *Ecological Applications*, *23*, 742–754. https://doi.org/10.1890/12-0267.1

Haynie, A. C., & Pfeiffer, L. (2012). Why economics matters for understanding the effects of climate change on fisheries. *ICES Journal of Marine Science*, *69*, 1160–1167. https://doi.org/10.1093/icesjms/fss021

Hermans, T. H. J., Tinker, J., Palmer, M. D., Katsman, C. A., Vermeersen, B. L. A., & Slangen, A. B. A. (2020). Improving sea-level projections on the Northwestern European shelf using dynamical downscaling. *Climate Dynamics*, *54*, 1987–2011. https://doi.org/10.1007/s00382-019-05104-5

Hinz, H., Capasso, E., Lilley, M., Frost, M., & Jenkins, S. R. (2011). Temporal differences across a bio-geographical boundary reveal slow response of sub-littoral benthos to climate change. *Marine Ecology Progress Series*, *423*, 6–829. https://doi.org/10.3354/meps08963

Holsman, K. K., Hazen, E. L., Haynie, A., Gourguet, S., Hollowed, A., Bograd, S. J., … Aydin, K. (2019). Towards climate resiliency in fisheries management. *ICES Journal of Marine Science*. https://doi.org/10.1093/icesjms/fsz031

Hughes, S. L., Tinker, J., Dye, S., Andres, O., Berry, D. I., Hermanson, L., … Symth, T. (2017). Temperature. *MCCIP Science Reviews*, *2017*, 22–41. https://doi.org/10.14465/2017.arc10.003-tem

ICES. (2012). *ICES implementation of advice for data-limited stocks in 2012 in its 2012 advice*. ICES CM 2012/ACOM 68. Copenhagen, Denmark: International Council for the Exploration of the Sea, 42 pp.

ICES. (2017). *Catch statistics*. Obtained 14th June 2020. Retrieved from http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx

Ingleby, B., & Huddleston, M. (2007). Quality control of ocean temperature and salinity profiles – Historical and real-time data. *Journal of Marine Systems*, *65*, 158–175. https://doi.org/10.1016/j.jmarsys.2005.11.019

Jennings, S., Stentiford, G. D., Leocadio, A. M., Jeffery, K. R., Metcalfe, J. D., Katsiadaki, I., … Verner-Jeffreys, D. W. (2016). Aquatic food security: Insights into challenges and solutions from an analysis of interactions between fisheries, aquaculture, food safety, human health, fish and human welfare, economy and environment. *Fish and Fisheries*, *17*(4), 893–938. https://doi.org/10.1111/faf.12152

Johnson, A. F., Jenkins, S. R., Hiddink, J. G., & Hinz, H. (2013). Linking temperate demersal fish species to habitat: Scales, patterns and future directions. *Fish and Fisheries*, *14*(3), 256–280. https://doi.org/10.1111/j.1467-2979.2012.00466.x

Jones, M. C., Dye, S. R., Fernandes, J. A., Frölicher, T. L., Pinnegar, J. K., Warren, R., & Cheung, W. W. L. (2013). Projecting the impact of climate change on threatened species in UK waters. *PLoS ONE*, *8*(1), e54216. https://doi.org/10.1371/journal.pone.0054216

Kumar, D., Kodra, E., & Ganguly, A. R. (2014). Regional and seasonal intercomparison of CMIP3 and CMIP5 climate model ensembles for temperature and precipitation. *Climate Dynamics*. https://doi.org/10.1007/s00382-014-2070-3

Lam, V. W. Y., Cheung, W. W. L., Reygondeau, G., & Sumaila, U. R. (2016). Projected change in global fisheries revenues under climate change. *Scientific Reports*, *6*, 32607. https://doi.org/10.1038/srep32607

Lenth, R. M. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, *69*, 1–33. https://doi.org/10.18637/jss.v069.i01

Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. W. L., Galbraith, E. D., … Worm, B. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 12907–12912. https://doi.org/10.1073/pnas.1900194116

Maltby, K. M., Rutterford, L. A., Tinker, J., Genner, M. J., & Simpson, S. D. (2020). Data from: Projected impacts of warming seas on commercially fished species at a biogeographic boundary of the European continental shelf. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.8cz8w9gmz

Mateo, M., Pawlowski, L., & Robert, M. (2016). Highly mixed fisheries: Fine-scale spatial patterns in retained catches of French fisheries in the Celtic Sea. *ICES Journal of Marine Science*, *74*, 91–101. https://doi.org/10.1093/icesjms/fsw129

Melnychuk, M. C., Banobi, J. A., & Hilborn, R. (2013). The adaptive capacity of fishery management systems for confronting climate change impacts on marine populations. *Reviews in Fish Biology and Fisheries*, *24*(2), 561–575. https://doi.org/10.1007/s11160-013-9307-9

Montero-Serra, I., Edwards, M., & Genner, M. J. (2015). Warming shelf seas drive the subtropicalization of European pelagic fish communities. *Global Change Biology*, *21*(1), 144–153. https://doi.org/10.1111/gcb.12747

Payne, M. R., Barange, M., Cheung, W. W. L., MacKenzie, B. R., Batchelder, H. P., Cormon, X., … Paula, J. R. (2015). Uncertainties in projecting climate-change impacts in marine ecosystems. *ICES Journal of Marine Science*, *73*(5), 1272–1282. https://doi.org/10.1093/icesjms/fsv231

Perry, A., Low, P., Ellis, J., & Reynolds, J. (2005). Climate change and distribution shifts in marine fishes. *Science*, *308*(5730), 1912–1915. https://doi.org/10.1126/science.1111322

Perry, R. I., Barange, M., & Ommer, R. E. (2010). Global changes in marine systems: A social–ecological approach. *Progress in Oceanography*, *87*, 331–337. https://doi.org/10.1016/j.pocean.2010.09.010

Pinnegar, J. K., Cheung, W. W. L., Jones, M., Merino, G., Turrell, B., & Reid, D. (2013). Impacts of climate change on fisheries. *MCCIP Science Review*, *2013*, 302–317. https://doi.org/10.1371/journal.pone.0054216

Pinnegar, J. K., Garrett, A., Simpson, S. D., Engelhard, G. H., & van der Kooij, J. (2017). Fisheries. *MCCIP Science Review*, *2017*, 73–99. https://doi.org/10.14465/2017.arc10.007-fis

Pinsky, M. L., & Mantua, N. J. (2014). Emerging adaptation approaches for climate ready fisheries management. *Oceanography*, *27*, 146–159. https://doi.org/10.5670/oceanog.2014.93

Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., … Sydeman, W. J. (2016). Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science*, *3*, 62. https://doi.org/10.3389/fmars.2016.00062

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Roberts-Jones, J., Fiedler, E., & Martin, M. J. (2012). Daily, global, high-resolution SST and sea ice reanalysis for 1985–2007 using the OSTIA system. *Journal of Climate*, *25*, 6215–6232. https://doi.org/10.1175/JCLI-D-11-00648.1

Rutterford, L. A., Simpson, S. D., Jennings, S., Johnson, M. P., Blanchard, J. L., Schön, P.-J., … Genner, M. J. (2015). Future fish distributions constrained by depth in warming seas. *Nature Climate Change*, *5*, 569–573. https://doi.org/10.1038/nclimate2607

Searle, S. R., Speed, F. M., & Milliken, G. A. (1980). Population marginal means in the linear model: An alternative to least squares means. *The American Statistician*, *34*, 216–221.

Sguotti, C., Otto, S. A., Cormon, X., Werner, K. M., Deyle, E., Sugihara, G., & Möllmann, C. (2019). Non-linearity in stock–recruitment relationships of Atlantic cod: Insights from a multi-model approach. *ICES Journal of Marine Science*, *77*(4), 1492–1502. https://doi.org/10.1093/icesjms/fsz113

Simpson, S. D., Jennings, S., Johnson, M. P., Blanchard, J. L., Schön, P. J., Sims, D. W., & Genner, M. J. (2011). Continental shelf–wide response of a fish assemblage to rapid warming of the sea. *Current Biology*, *21*(18), 1565–1570. https://doi.org/10.1016/j.cub.2011.08.016

Skern-Mauritzen, M., Ottersen, G., Handegard, N. O., Huse, G., Dingsør, G. E., Stenseth, N. C., & Kjesbu, O. S. (2016). Ecosystem processes are rarely included in tactical fisheries management. *Fish and Fisheries*, *17*, 165–175. https://doi.org/10.1111/faf.12111

STECF. (2014). *Evaluation of fishing effort regimes in European waters – Part 2 (STECF-14-20)* (p. 844). Luxembourg: Publications Office of the European Union.

STECF. (2017). *The 2017 annual economic report on the EU fishing fleet (STECF-17-12)*. Luxembourg: Publications Office of the European Union. https://doi.org/10.2760/36154

ter Hofstede, R., Hiddink, J. G., & Rijnsdorp, A. D. (2010). Regional warming changes fish species richness in the eastern North Atlantic Ocean. *Marine Ecology Progress Series*, *414*, 1–9. https://doi.org/10.3354/meps08753

Tinker, J. P., & Howes, E. L. (2020). The impacts of climate change on temperature (air and sea), relevant to the coastal and marine environment around the UK. *MCCIP Science Reviews*, *2020*, 1–3. https://doi.org/10.14465/2020.arc01.tem

Tinker, J., Lowe, J., Holt, J., Pardaens, A., & Wiltshire, A. (2015). Validation of an ensemble modelling system for climate projections for the northwest European shelf seas. *Progress in Oceanography*, *138*(A), 211–237. https://doi.org/10.1016/j.pocean.2015.07.002

Tinker, J., Lowe, J., Pardarns, A., Holt, J., & Barciela, R. (2016). Uncertainty in climate projections for the 21st century northwest European shelf seas. *Progress in Oceanography*, *148*, 56–73. https://doi.org/10.1016/j.pocean.2016.09.003

van Hal, R., van Kooten, T., & Rijnsdorp, A. D. (2016). Temperature-induced changes in size dependent distributions of two boreal and three Lusitanian flatfish species: A comparative study. *Journal of Sea Research*, *107*, 14–22. https://doi.org/10.1016/j.seares.2015.06.020

Wilson, R. J., Spiers, D. C., Sabatino, A., & Heath, M. R. (2018). A synthetic map of the north-west European Shelf sedimentary environment for applications in marine science. *Earth System Science Data*, *10*, 109–130. https://doi.org/10.5194/essd-10-109-2018

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society B*, *73*(1), 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

SUPPORTING INFORMATION

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

How to cite this article: Maltby KM, Rutterford LA, Tinker J, Genner MJ, Simpson SD. Projected impacts of warming seas on commercially fished species at a biogeographic boundary of the European continental shelf. *J Appl Ecol*. 2020;00:1–12. https://doi.org/10.1111/1365-2664.13724