

# Future fish distributions constrained by depth in warming seas

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**European continental shelf seas have experienced intense warming over the past 30 years<sup>1</sup>. In the North Sea, fish have been comprehensively monitored throughout this period and resulting data provide a unique record of changes in distribution and abundance in response to climate change<sup>2,3</sup>. We use these data to demonstrate the remarkable power of generalized additive models (GAMs), trained on data earlier in the time series, to reliably predict trends in distribution and abundance in later years. Then, challenging process-based models that predict substantial and ongoing poleward shifts of cold-water species<sup>4,5</sup>, we find that GAMs coupled with climate projections predict future distributions of demersal (bottom-dwelling) fish species over the next 50 years will be strongly constrained by availability of habitat of suitable depth. This will lead to pronounced changes in community structure, species interactions and commercial fisheries, unless individual acclimation or population-level evolutionary adaptations enable fish to tolerate warmer conditions or move to previously uninhabitable locations.**

Although the temperature of the world's oceans has gradually risen through the twentieth century, the northeast Atlantic has experienced particularly intense warming, resulting in the North Sea mean annual sea surface temperature increasing by 1.3 °C over the past 30 years<sup>1</sup>, a rate four times faster than the global average<sup>6</sup>. Predictions for the North Sea suggest a further 1.8 °C rise in sea surface temperatures during the next five decades (Hadley Centre QUMP\_ens\_00 model, unpublished data supplied by J. Tinker) (Fig. 1). Impacts of recent warming on northeast Atlantic marine ecosystems have been diverse, including reorganization of the plankton community<sup>7</sup>, modification to the phenology of fish spawning<sup>8,9</sup>, and alterations of ecosystem interactions<sup>10,11</sup>. Owing to its longstanding economic importance to fisheries (reported landings in 2007 valued at \$1.2 billion<sup>1</sup>) and other industries, the ecology of the North Sea has been intensively monitored throughout this period of recent warming.

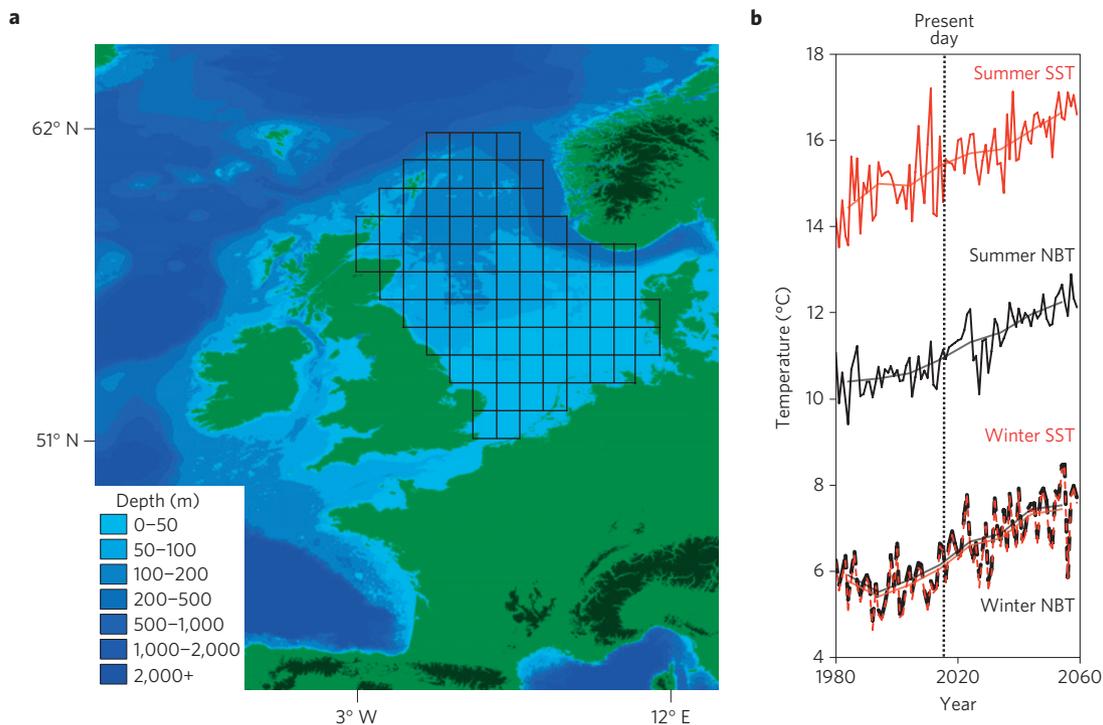
Analyses of North Sea fish surveys have revealed northerly range expansions of warmer-water species<sup>12</sup>, population redistributions to higher latitudes<sup>2</sup> and deeper water<sup>13</sup>, and widespread changes in local abundance associated with warming, with impacts on community structure<sup>3</sup>. This substantial modification to fish

community composition in the region has had an observable economic impact on fisheries, with landings of cold-adapted species halved but landings of warm-adapted species increasing by a factor of 2.5 since the 1980s<sup>3</sup>; a pattern also identified in other marine ecosystems<sup>14</sup>. With a uniquely rich fish abundance time series from the period of warming, it is possible to split the data to assess how predictions made using data from earlier years match observations from later years; a validation approach which has been promoted for terrestrial systems<sup>15</sup>. Existing studies have used survey data to describe past changes<sup>2,3,12,13</sup>, or adopted process-based climate-envelope models to predict future abundance without validation<sup>16</sup>. Thus there is a need to compare the predictions of climate-envelope models with those from more structurally complete data-driven models that have been developed and tested using spatially and temporally explicit abundance data.

The GAM approach makes no a priori assumptions about the nature of associations between predictors and response variables<sup>17</sup> and has been used to assess the importance of different environmental drivers on patterns of distributions and relative abundance in marine ecosystems<sup>18–20</sup>. Here we developed GAMs to predict changes in the distribution and abundance of the ten most abundant North Sea demersal (bottom-dwelling) fish species, which accounted for 68% of commercial landings by North Sea fisheries between 1980 and 2010 ([www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx](http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx)). We used a two-step approach. First, predictive models with different sets of variables were compared using data earlier in the time series to train the models and predict known distributions and abundances later in the time series. Second, models were used to predict changes in species distributions over the next 50 years.

Predictors of species' abundance were identified from a wider array of potential variables (annual sea surface and near-bottom temperatures; seasonal sea surface and near-bottom temperatures; depth; salinity; fishing pressure: all of which are expected to influence fish abundance and distribution—see, for example, refs 2,3,13,21). For each species we calculated from summer and winter monitoring surveys the mean annual abundance per grid cell in a ten-year time slice (2000–2009, inclusive) and used these data to train GAM models based on different combinations of variable

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**Figure 1 | Physical environment of the North Sea.** **a**, Bathymetry with an overlay showing locations of the  $84\ 1^\circ \times 1^\circ$  latitude–longitude cells in which fish abundance, distribution and sea temperature were reported and predicted. **b**, Mean sea surface temperature (SST, red) and near-bottom temperature (NBT, black) in the study cells from 1980–2060 in summer (July–September, solid line) and winter (January–March, dashed line) from the *QUMP\_ens\_00* northwest European shelf seas climate model. Mean decadal values (as used in the model) are overlaid in the corresponding colours for SST and NBT for each season.

sets to predict the same data. We then analysed associations between the predictions and original observations. All model combinations performed well with predictions against known data, all exceeding correlation coefficients of 0.67 and only marginal changes with the loss of each variable for each species (Supplementary Table 1). Following an assessment of the performance of alternate GAMs (Supplementary Fig. 4 and Tables 1 and 2), a model that included temperature, depth and salinity variables was applied to each species (Fig. 2a and Supplementary Table 1). The selected models excluded the metric for fishing pressure as this was a relatively poor predictor variable in the majority of cases (Fig. 2a and Supplementary Table 1).

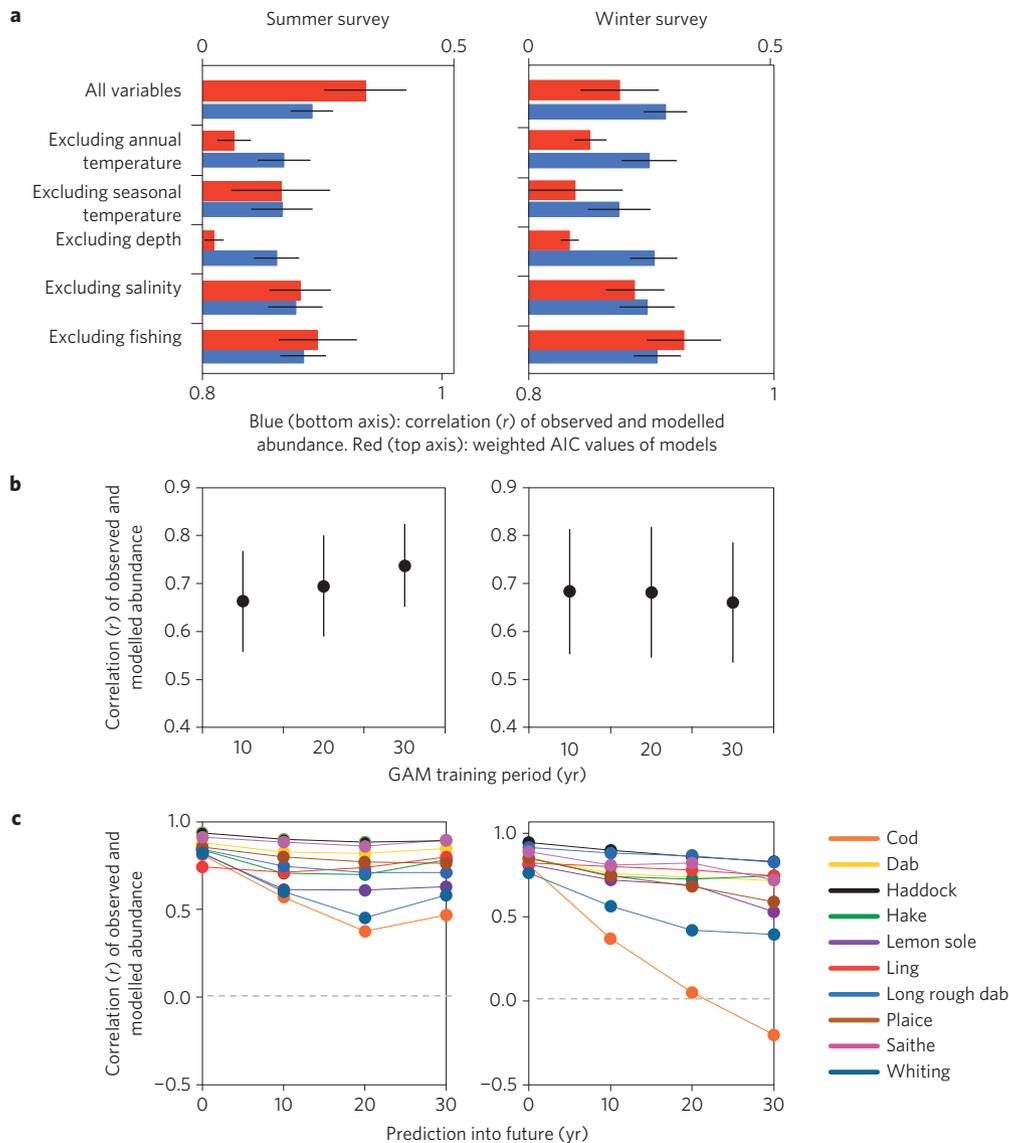
To assess the most appropriate length of time series to use for future projections, we developed models to predict the abundance of species across the region in a decade using annual and seasonal temperature, salinity and depth data from the periods 10, 20 and 30 years beforehand. There was no consistent improvement in model fit with increasing periods of training data (Fig. 2b and Supplementary Fig. 1), thus we used ten-year training periods for all subsequent projections. The final stage of the model development stage was to assess the ability of GAMs, using an effective set of variables, to predict distributions for 10, 20 and 30 year periods into the future and compare with observations. Predictions closely matched observations for eight of the ten species using both survey data sets (Fig. 2c and Supplementary Fig. 1).

Following model development and testing, models trained on data from 2000–2009 were used to predict future distributions, abundance and thermal occupancy of the eight species for which the models were effective, based on environmental conditions forecast with the Hadley Centre *QUMP\_ens\_00* model (Fig. 3 and Supplementary Fig. 1). Predictions based on independent winter and summer fish surveys showed congruent temperature occupancy patterns, with species predicted to experience warmer conditions and maintain existing distributions, rather than maintaining

their preferred temperature ranges by redistributing to other locations (Fig. 3).

We quantified latitudinal ranges, a commonly used estimator of distributions, which showed considerable overlap between present and future conditions, with no consistent pattern among species in predicted changes in distributions (Fig. 3). This indicates that poleward advances of North Sea demersal fish following preferences for colder waters are unlikely to be commonplace, and highlights how process-based models that predict northward shifts may underestimate dependence on non-thermal habitat. Importantly, predicted depth ranges were also similar for present and future conditions (Fig. 3), implying that depth-associated niches are the primary drivers and constraints of the distributions of demersal species. One species predicted here to have the most marked reduction in abundance alongside a proportionate increase in individuals in deeper water was dab (Fig. 3). As a shallow water species predominantly found in the southern North Sea their current thermal experience is expected to be exceeded through the projection period (Supplementary Fig. 2), suggesting that expected climate change may force the species into less optimal habitats.

Seasonal temperatures, depth and salinity and likely co-varying habitat variables, seem to be major determinants of current species distributions of commercially important demersal species in the North Sea, and were good predictors of past changes in distribution for many species. Looking to the future, our results suggest that the strong associations of species with specific habitats may ultimately prevent further poleward movement of species in response to warming as previously predicted<sup>16</sup>. A recent study demonstrated that  $1.6^\circ\text{C}$  of warming across the European continental shelf over the past 30 years locally favoured some demersal species suited to warmer waters, but drove local declines in cold-adapted species, despite long-term stability in spatial patterns of species presence–absence<sup>3</sup>. Dependence of species on specific non-thermal habitat,



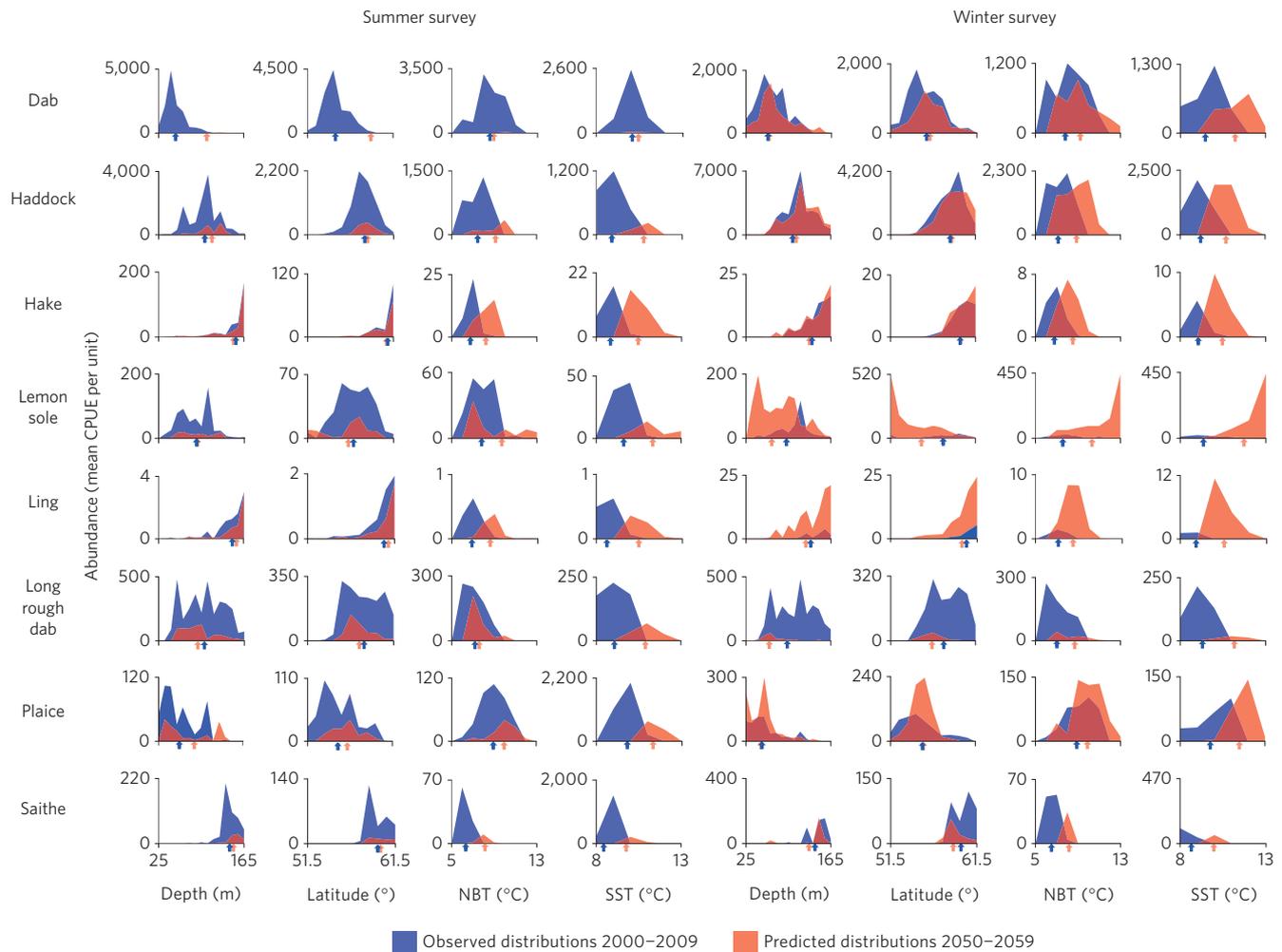
**Figure 2 | Predictive ability of generalized additive models (GAMs).** **a**, Fits of predicted to observed species abundance using 2000–2009 data. Variables were sequentially removed. Model fits were evaluated using correlation (mean  $\pm$  s.e.m. Pearson’s  $r$  coefficient across species) and weighted Akaike information criterion (AIC: mean  $\pm$  s.e.m. across species). **b**, Duration of training data and predictive performance of GAMs using depth and seasonal temperatures. Correlations (mean  $\pm$  s.e.m. Pearson’s  $r$  coefficient across species) indicate no improvement in performance with longer time series. **c**, Relationship between known data and GAM predictions using depth, salinity and seasonal and annual temperature, for decades beyond the GAM training period.

together with spatially contrasting local changes in responses to warming<sup>3</sup>, may explain why mean latitudinal range shifts are apparent only in some species<sup>2</sup>, and are not detected in others despite sharing similar temperature preferences. Dependence on specific non-thermal habitat has been observed in tagged Atlantic cod (*Gadus morhua*), where fish occupied suboptimal thermal habitat for extended periods with likely costs to metabolism and somatic growth<sup>22</sup>. Indeed a dominant driver of changes in the central distributions of cod in the North Sea seems to have been intense fishing pressure over the past century rather than warming, which has depleted former strongholds in the western North Sea, driving an eastward longitudinal shift in relative population abundance but no apparent poleward shift<sup>21</sup>. These factors, together with potential indirect effects of warming potentially not captured in our models (for example, from changes to prey abundance), may explain why models based on depth and temperature were not effective for longer-term projections for Atlantic cod and

whiting (*Merlangius merlangus*). It is necessary to evaluate the performance of alternate predictor variables for data-driven models of these species.

Mean depth distributions of North Sea fish that had preferences for cooler water increased by approximately 5 m during the warming of the 1980s, but tended to slow or stabilize thereafter<sup>13</sup>. On the basis of the GAM results we do not expect or predict substantial further deepening for cooler water species, because depth is such a strong predictor of distribution. Collectively, the studies imply that the capacity of fish to remain in cooler water by changing their depth distribution had been largely exhausted in the 1980s and that fish with preferences for cooler water are being increasingly exposed to higher temperatures, with expected physiological, life history and population consequences.

In the absence of substantial distributional shifts that would allow fish to occupy different habitats and depths, North Sea populations are likely to experience 3.2 °C of warming over the coming century



**Figure 3 | Observed and predicted abundances of eight focal species along depth, latitude and mean annual near-bottom temperature (NBT) and sea surface temperature (SST) gradients.** Analyses were based on both the summer and winter survey data sets. Distribution averages for each time period are shown using arrows of corresponding colours along the x-axis.

(J. Tinker, Hadley Centre). Although such temperature increases are within observed thermal limits for these species, the ecological consequences are unknown, especially when warmer conditions are closer to thermal preferences of other species using the same habitats. Furthermore, physiological theory suggests that responses of species to projected warming will eventually reach thermal thresholds. As species' Pejus temperatures are reached, increased metabolic costs will compromise growth, with associated declines in population productivity<sup>23</sup>. Capacity to tolerate warming will thus depend on scope for thermal acclimation<sup>24</sup> and adaptation<sup>25</sup>, with the degree of connectivity between thermally adapted sub-populations across the geographic range of species influencing the rate of adaptation to future warming. Unless adaptation or acclimation can track the rate of warming, it is likely that stocks will be affected, both directly through individual physiological tolerances, and indirectly through climate-related changes to the abundance of prey, predators, competitors and pathogens.

Our study demonstrates the power of data-driven GAM models for predicting future fish distributions. In contrast to process-based models that attempt to integrate discrete ecological mechanisms such as dispersal and density dependence, GAMs are grounded by past net responses of populations to all these processes, in addition to interspecific interactions and habitat associations that are not typically considered in process-based modelling, perhaps explaining the strong predictive power of our GAM approach

for predicting known future conditions. The results of this study suggest that we should be cautious when interpreting process-based model projections of distributional shifts, and that interpretations should be informed by data-driven modelling approaches, especially when using predictions for policy and management planning. Our projections suggest that if populations fail to adapt or acclimatize to a warmer environment, warming will change fishing opportunities for currently targeted species in the North Sea over the next century. Historically, fishing pressure has substantially modified the North Sea<sup>26</sup>, and ongoing changes in management will play an important role in shaping future fisheries resources. Species responses to temperature should be considered when planning future fisheries management strategies to ensure that anticipated long-term benefits of management are ecologically feasible in this period of intense warming.

## Methods

Methods and any associated references are available in the [online version of the paper](#).

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### Author contributions

M.J.G. and M.P.J. conceived the research; S.J., J.L.B. and D.W.S. contributed to project development; S.D.S. and S.J. pre-processed fisheries agency data; L.A.R. and J.T. pre-processed climate data; S.D.S., M.J.G., L.A.R., M.P.J. and S.J. designed the analysis; L.A.R. and S.D.S. conducted the analysis; S.D.S., L.A.R. and M.J.G. prepared the initial manuscript and all authors contributed to revisions.

### Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at [www.nature.com/reprints](http://www.nature.com/reprints). Correspondence and requests for materials should be addressed to S.D.S.

### Competing financial interests

The authors declare no competing financial interests.

## Methods

**Fish surveys.** We used two long-term monitoring surveys that give detailed descriptions of the distribution and abundance of demersal (bottom-dwelling) fish in the North Sea. The Centre for Environment, Fisheries and Aquaculture Science UK (Cefas) time series is a summer survey (August–September) conducted since 1980. The survey encompasses  $69\ 1^\circ \times 1^\circ$  latitude–longitude cells with at least three hauls conducted in each decade. The International Council for the Exploration of the Sea (ICES) International Bottom Trawl Survey (IBTS) time series is a winter survey (January–March) conducted since 1980. The survey encompasses  $84\ 1^\circ \times 1^\circ$  cells with at least three hauls conducted in each decade. Both surveys are conducted using otter trawling gear (Granton trawl for pre-1992 Cefas surveys, otherwise Grande Ouverture Verticale (GOV) trawls). Raw catch data were fourth-root transformed to reduce skewness that is inherent in ecological abundance data.

Our study focused on the ten most abundant demersal species targeted by commercial fisheries or taken as bycatch (Fig. 2c), which together accounted for 68% of commercial landings (by weight) in the North Sea fishery from 1980–2010 ([www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx](http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx)). For both surveys, we grouped data into three ten-year time slices and one three-year time slice for the analyses: 1980–1989, 1990–1999, 2000–2009 and 2010–2012. The limited 2010–2012 time slice was used only for testing predictions from the GAMs. To ensure a balanced design, mean values for each decadal time period were used. This method controls for the variable numbers of survey hauls taken in each cell and ensures that longer-term responses to climate change are identified rather than year-on-year variability. All data were fourth root transformed before being subject to GAM modelling, and individual cell predictions were back-transformed before calculation of correlation coefficients.

**Depth.** We used mean  $1^\circ \times 1^\circ$  cell *in situ* measures of depth taken during the hauls for each survey (Supplementary Fig. 3), which closely matched data from the  $1^\circ \times 1^\circ$  resolution GEBCO Digital Atlas (summer survey,  $r = 0.91$ ; winter survey,  $r = 0.90$ ; [www.gebco.net/data\\_and\\_products/gebco\\_digital\\_atlas](http://www.gebco.net/data_and_products/gebco_digital_atlas))<sup>3</sup>.

**Temperature and salinity.** We calculated sea surface temperature (SST), near-bottom temperature (NBT) and salinity (Supplementary Fig. 3) for the period 1980–2012 using the UK Meteorological Office Hadley Centre QUMP\_ens\_00 standard model for the northwest European shelf seas. Modelled temperatures closely matched data from the Hadley Centre global ocean surface temperature database (*HadISST1.1*; 92 cells, Pearson's  $r = 0.84$ ; [www.metoffice.gov.uk/hadobs/hadisst](http://www.metoffice.gov.uk/hadobs/hadisst)). Data from the QUMP\_ens\_00 model were provided as monthly means for  $1^\circ \times 1^\circ$  cells, enabling mean winter (January–March), summer (July–September) and mean annual values to be calculated (Fig. 1).

**Fishing pressure.** We calculated a spatially explicit metric of fishing pressure for each ten-year time slice by combining annual multispecies fishing mortality ( $F$ ) estimates for North Sea demersal species (mean estimates of regional  $F$  for cod, dab, haddock, hake, lemon sole, ling, long rough dab, plaice, saithe and whiting, weighted by spawning-stock biomass, from ICES stock assessments; [www.ices.dk/datacentre/StdGraphDB.asp](http://www.ices.dk/datacentre/StdGraphDB.asp))<sup>3</sup> with mean otter and beam trawling effort for each  $1^\circ \times 1^\circ$  cell based on hours of fishing<sup>27</sup> (Supplementary Fig. 3). This integrated metric, combining temporal trends in fishing mortality and spatial distribution of fishing effort, enabled us to test the importance of fishing pressure as a predictor of abundance.

**Identifying key predictors.** We used GAM models, coded using the *mgcv* package in R ([www.r-project.org](http://www.r-project.org)), to test the performance of GAMs for predicting changes in fish species' distribution and identify the importance of different variables to these predictions. The  $s$  smooth was used with  $k = 7$  for all variables to limit the degrees of freedom in line with the number of data points. The Gaussian model was used. Assessment of the plots for each variable using the *gam.plot* function showed that increasing the  $k$  value did not improve the model fit to each variable. The *gam.check* function was used to check the  $k$  index was above or close to 1, with non-significant  $p$  values. Analysis of the residuals showed no obvious

deviations from normal distributions, and the response to fitted values relationship was close to linear.

Data from 2000–2009 were used to test sets of variables, as this period had the greatest survey intensity. To identify variables that most strongly influenced prediction we first developed a model with all variables (annual temperatures, seasonal temperatures, depth, salinity and fishing), and a subsequent five models each excluding one set of variables (Supplementary Table 1). Sea surface and near-bottom temperatures from both the summer and winter were grouped together to characterize seasonal fluctuations. This suite of potentially correlated variables captured the extremes of temperatures that all species may experience at different life stages, and ensured that thermal conditions with and without the seasonal thermocline, annually varying ocean currents and land mass effects are all included. We compared the performance of models based on: the strength of correlation  $r$  between observed and predicted data, weighted AIC (ref. 28) using data from the AIC function in R, and using generalized cross validation (GCV, through *summary.gam* in R). Inclusion of interaction terms between depth and seasonal temperature extremes either reduced or had little influence on model performance (Supplementary Table 2 and summaries based on Akaike weights in Supplementary Fig. 4).

**Model development.** We developed predictive GAMs with a set of variables that were effective across all species. The correlation coefficient  $r$ , AIC values and GCV values of modelled and observed data were compared. Across-species inclusion of depth, seasonal temperature, annual temperature, salinity and fishing effort all improved the predictions (Fig. 2a). A key finding from this model development stage is that variables that are readily measured and projected in climate models effectively predict species distributions. On average, models that excluded fishing effort were most similar to the all-variable models (Supplementary Table 1 and Fig. 2a). As this metric had little predictive value, and we have no robust models of future fishing effort, we excluded it when making future predictions.

**Training period and predictive performance.** To assess the influence of the duration of training data on predictive power, GAMs trained on sets of one, two and three decades of data for each species were used to predict ten years into the future (Supplementary Fig. 1), and the associations between predicted and known data compared. We also assessed the performance of the model to predict further into the future within the historic records available (Supplementary Fig. 1). We compared predictions with known abundance data for each species for each forecasting period (0 to 30 years).

**Forecasting future distributions.** We used surface and near-bottom annual and seasonal temperature projections from the QUMP\_ens\_00 model, surface and near-bottom salinity, and average depths from surveys between 1980–2012 as the environmental variables for our predictions. We predicted fish abundances for sequential decades from 2000–2009 to 2050–2059 (Supplementary Figs 5 and 6) using environmental variables (Supplementary Figs 3 and 7), and observed fish abundances from 2000–2009. Throughout the projection period many cells do not experience temperatures outside of the range used to train the model (Supplementary Fig. 2). For the widespread species in this study it is therefore likely that at least parts of the population have experienced future conditions. However, we recognize that in future projected conditions the climate in some areas of the North Sea will depart from existing variability in the model training period. As it is not possible to test the model beyond present thermal conditions using known data, some caution should be taken in interpreting projections for cells as they begin to experience temperatures beyond those at present in the region (Supplementary Fig. 2).

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