Future fish distributions constrained by depth in warming seas

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European continental shelf seas have experienced intense warming over the last 30 years[1]. In the North Sea, fishes 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[2,3]. We use these data to demonstrate the remarkable power of Generalised 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[4,5], 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.

While the temperature of the world's oceans has gradually risen through the 20th 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 last 30 years[1], a rate four times faster than the global average[6]. Predictions for the North Sea suggest a further 1.8°C rise in sea-surface temperatures during the next five decades[7] (Fig. 1). Impacts of recent warming on northeast Atlantic marine ecosystems have been diverse, including reorganisation of the plankton community[8], modification to the phenology of fish spawning[9,10], and alterations of ecosystem interactions[11,12]. Due to its longstanding economic importance to fisheries (reported landings in 2007 valued at $1.2 billion[1]) 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[13], population redistributions to higher latitudes[2] and deeper water[14], and widespread changes in local abundance associated with warming, with impacts on community structure[3]. 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 2.5 times since the 1980s[3]; a pattern also identified in other marine ecosystems[15]. With a uniquely rich fish abundance time-series from the period of warming, it is possible to split these 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[16]. Existing studies have used survey data to describe past changes[2,3,13,14], or adopted process-based climate envelope models to predict future abundance without validation[17]. 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[18] and has been used to assess the importance of different environmental drivers on patterns of distributions and relative abundance in marine ecosystems[19-21]. Here we developed GAMs to predict changes in the distribution and abundance of the 10 most abundant North Sea demersal (bottom-dwelling) fish species, which accounted for 68% of commercial landings by the North Sea fishery between 1980 and 2010 (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 [e.g. 2,3,14,22]). For each species we calculated from summer and winter monitoring surveys the mean annual abundance per grid cell in a 10 year time-slice (2000–2009, inclusive) and used these data to train GAM models based on different combinations of variable 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 Figure 1, Supplementary 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 since 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. 2), thus we used 10-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 8 of the 10 species using both survey datasets (Fig. 2c and Supplementary Fig. 2).

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 forecasted with the Hadley Centre *QUMP_ens_00* model (Fig. 3 and Supplementary Fig. 2). 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 fishes 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. 3) suggesting that expected climate change may force the species into less optimal habitats.

Seasonal temperatures, depth and salinity and likely co-varying habitat variables, appear 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[17]. A recent study demonstrated that 1.6°C of warming across the European continental shelf over the last 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[3]. Dependence of species on specific non-thermal habitat, together with spatially-contrasting local changes in responses to warming[3], may explain why mean latitudinal range shifts are only apparent in some species[2], 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[23]. Indeed a dominant driver of changes in the central distributions of cod in the North Sea appears to have been intense fishing pressure over the last 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[22]. 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 fishes that had preferences for cooler water increased by approximately 5m during the warming of the 1980s but tended to slow or stabilise thereafter[14]. Based on 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 capacity to remain in cooler water by changing their depth distribution has 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[24]. 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[25]. Capacity to tolerate warming will thus depend on scope for thermal acclimation[26] and adaptation[27], 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 acclimatise 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[28] 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

Fish surveys. We used two long-term monitoring surveys that give detailed descriptions of the distribution and abundance of demersal (bottom-dwelling) fishes 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 encompassing 69 1x1° latitude-longitude cells. 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 encompassing 84 1x1° cells. (We only considered cells that had been surveyed at least three times 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 4th-root transformed to reduce skew that is inherent in ecological abundance data.

Our study focused on the 10 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). For both surveys, we grouped data into three 10-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 only used for testing predictions from the GAMs. To ensure a balanced design,

mean values for each 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 4th root transformed before being subject to GAM modelling, and predictions were back transformed before calculation of correlation coefficients.

Depth. We used mean 1x1° cell *in situ* measures of depth taken during the hauls for each survey (Supplementary Fig. 4), which closely matched data from the 1x1^{o} resolution GEBCO Digital Atlas (summer survey, r = 0.91; winter survey, r = 0.90; www.gebco.net/data_and_products/gebco_digital_atlas/)[3].

Temperature and salinity. We calculated Sea-Surface Temperature (SST), Near-Bottom Temperature (NBT) and salinity (Supplementary Fig. 4) 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/). Data from the *QUMP_ens_00* model were provided as monthly means for 1x1° 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 10-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)[3] with mean otter and beam trawling effort for each 1x1° cell based on hours of fishing[29] (Supplementary Fig. 4). 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 *gam* package in *R* (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 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 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, while 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 characterise 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 i) the strength of correlation *r* between observed and predicted data, ii) weighted AIC[30] using data from the AIC function in *R*, and iii) using generalised 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. 1).

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 (Fig. 2a, Supplementary Table 1). Since 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 10 years into the future (Supplementary Fig. 2), 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. 2). We compared predicted with known abundance data for each species for each forecasting period (0–30 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 & 6) using environmental variables (Supplementary Figs. 4 & 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. 3). For the widespread species in this study it is therefore likely that at least parts of the population have experienced future conditions. However we recognise that in future projected conditions the climate in some areas of the North Sea will depart from existing variability in the model training period. Since it is not possible to test the model beyond current thermal conditions using know data, some caution should be taken interpreting projections for cells as they begin to experience temperatures beyond those currently in the region (Supplementary Fig. 3).

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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.

AUTHOR INFORMATION

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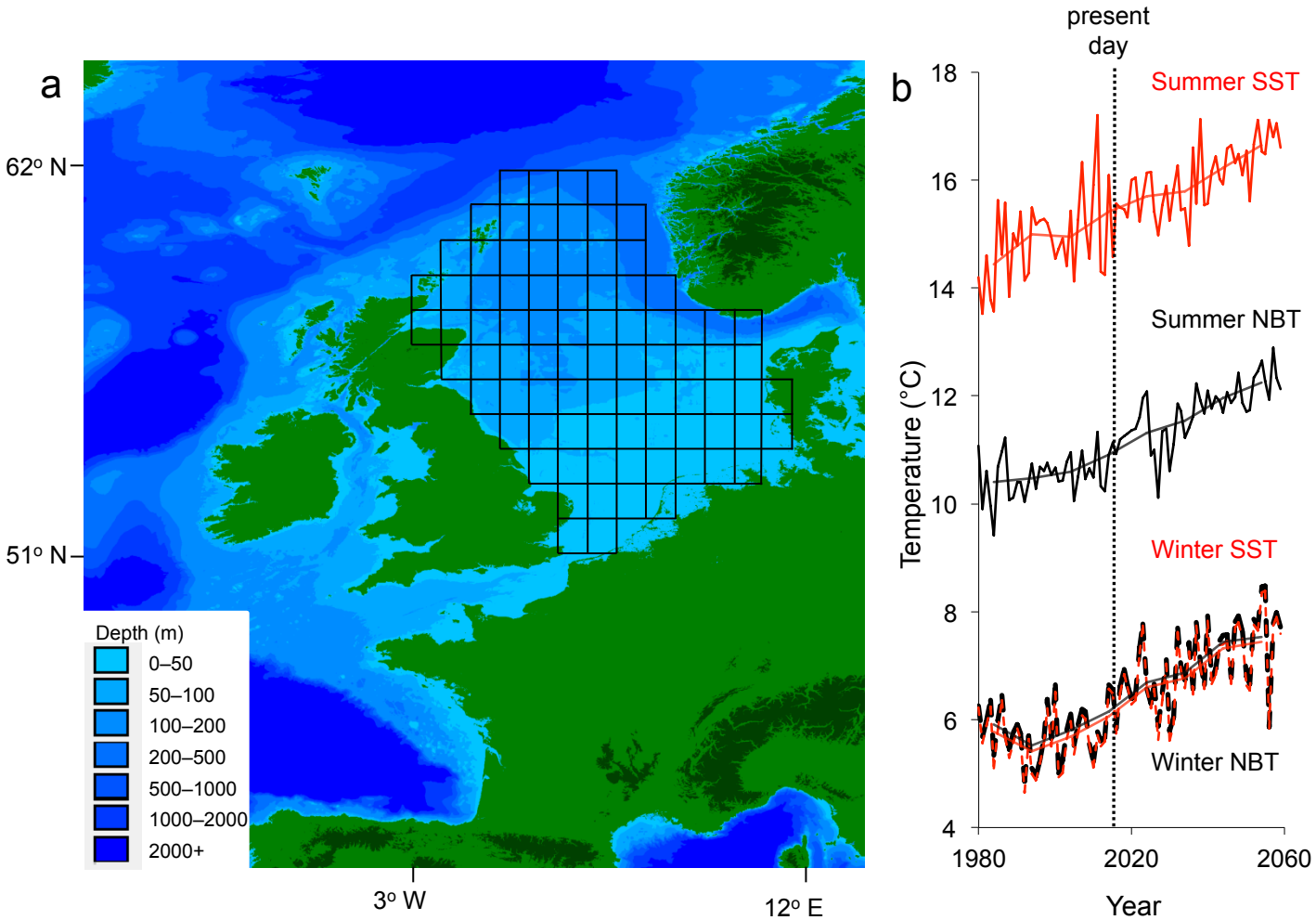
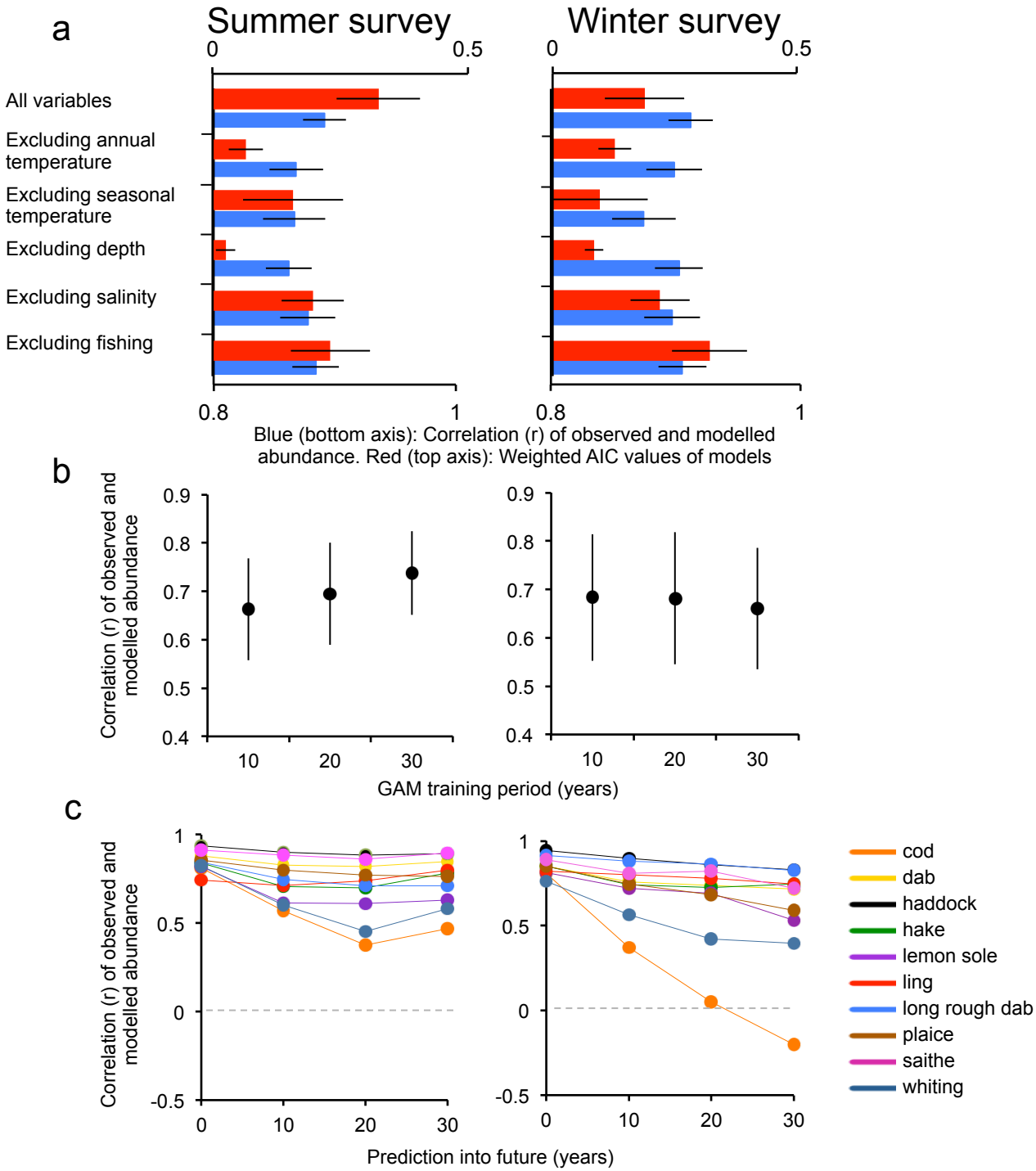
FIGURE LEGENDS

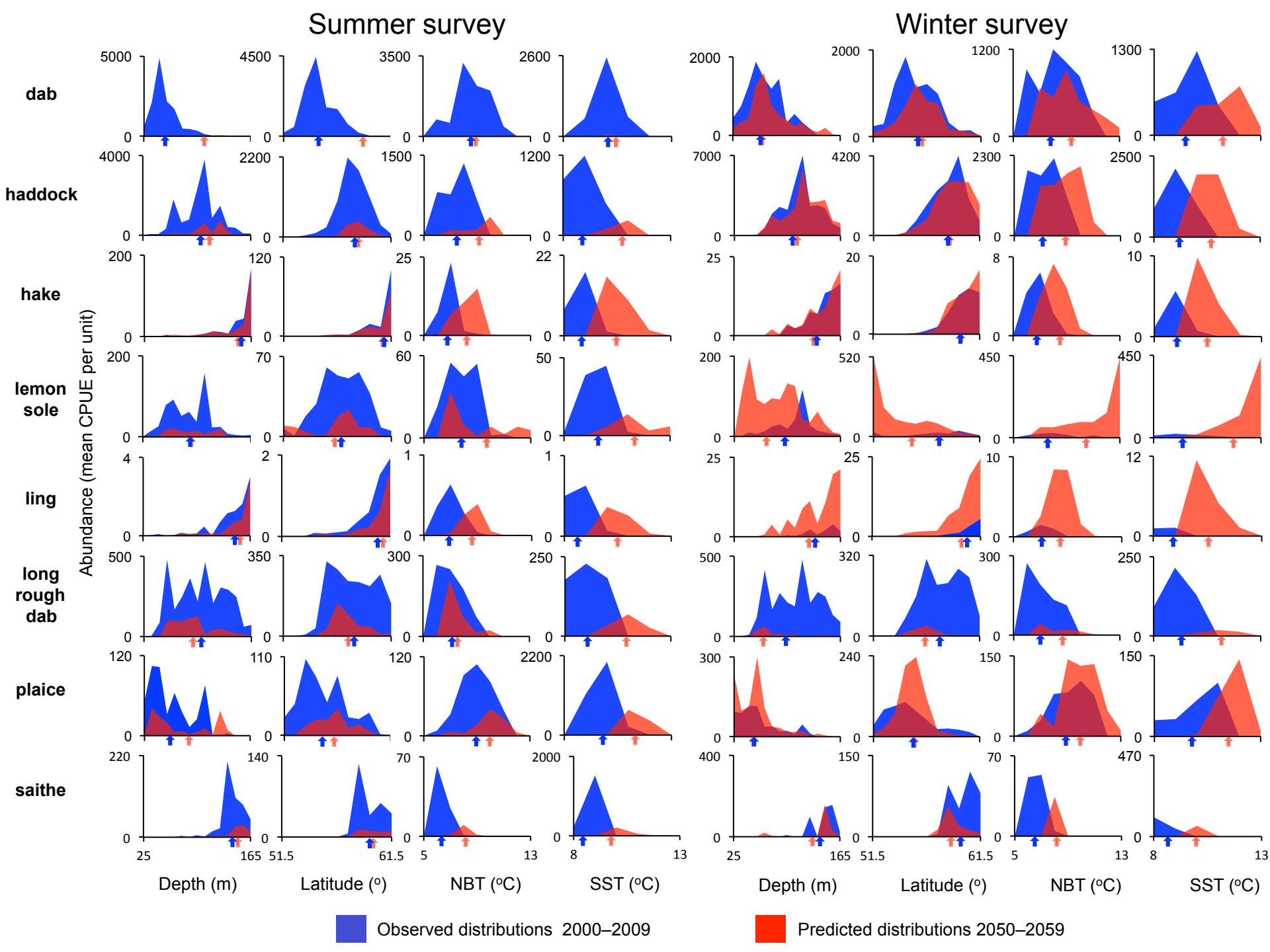
Figure 1. Physical environment of the North Sea. (a) Bathymetry with an overlay showing locations of the 84 1x1° latitude-longitude cells in which fish abundance, distribution and sea temperature were reported and predicted; (b) mean Sea-Surface Temperature (SST, red) and Near-Bottom Temperature (NBT, 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.

Figure 2. Predictive ability of Generalised 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 ± SE Pearson's *r* coefficient across species) and weighted Akaike Information Criterion (AIC: mean ± SE across species). (b) Duration of training data and predictive performance of GAMs using depth and seasonal temperatures. Correlations (mean ± SE 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 GAM training period.

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 datasets. Weighted means are shown for each time period using arrows of corresponding colours along the x axis.


a
62° N
51° N
3° W
12° E
Depth (m)
0–50
50–100
100–200
200–500
500–1000
1000–2000
2000+
b
present day
Summer SST
Summer NBT
Winter SST
Winter NBT
Temperature (°C)
18
16
14
12
10
8
6
4
1980
2020
2060
Year


a
Summer survey
Winter survey
0
0.5
All variables
Excluding annual temperature
Excluding seasonal temperature
Excluding depth
Excluding salinity
Excluding fishing
0.8
1
Blue (bottom axis): Correlation (r) of observed and modelled abundance. Red (top axis): Weighted AIC values of models
b
Correlation (r) of observed and modelled abundance
0.9
0.8
0.7
0.6
0.5
0.4
10
20
30
GAM training period (years)
c
1
0.5
0
-0.5
0
10
20
30
Prediction into future (years)
cod
dab
haddock
hake
lemon sole
ling
long rough dab
plaice
saithe
whiting


Summer survey
Winter survey
dab
haddock
hake
lemon sole
ling
long rough dab
plaice
saithe
Abundance (mean CPUE per unit)
Depth (m)
Latitude (°)
NBT (°C)
SST (°C)
Observed distributions 2000–2009
Predicted distributions 2050–2059