

1 **Future fish distributions constrained by depth in warming seas**

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32

33 **European continental shelf seas have experienced intense warming over the last 30**
34 **years¹. In the North Sea, fishes have been comprehensively monitored throughout**
35 **this period and resulting data provide a unique record of changes in distribution and**
36 **abundance in response to climate change^{2,3}. We use these data to demonstrate the**
37 **remarkable power of Generalised Additive Models (GAMs), trained on data earlier in**
38 **the time-series, to reliably predict trends in distribution and abundance in later years.**
39 **Then, challenging process-based models that predict substantial and ongoing**
40 **poleward shifts of cold-water species^{4,5}, we find that GAMs coupled with climate**
41 **projections predict future distributions of demersal (bottom-dwelling) fish species**
42 **over the next 50 years will be strongly constrained by availability of habitat of suitable**
43 **depth. This will lead to pronounced changes in community structure, species**
44 **interactions and commercial fisheries, unless individual acclimation or population-**
45 **level evolutionary adaptations enable fish to tolerate warmer conditions or move to**
46 **previously uninhabitable locations.**

47

48 While the temperature of the world's oceans has gradually risen through the 20th Century,
49 the northeast Atlantic has experienced particularly intense warming, resulting in the North
50 Sea mean annual sea-surface temperature increasing by 1.3°C over the last 30 years¹, a
51 rate four times faster than the global average⁶. Predictions for the North Sea suggest a
52 further 1.8°C rise in sea-surface temperatures during the next five decades (Hadley Centre
53 *QUMP_ens_00* model, unpublished data supplied by J. Tinker) (Fig. 1). Impacts of recent
54 warming on northeast Atlantic marine ecosystems have been diverse, including
55 reorganisation of the plankton community⁷, modification to the phenology of fish spawning^{8,9},
56 and alterations of ecosystem interactions^{10,11}. Due to its longstanding economic importance
57 to fisheries (reported landings in 2007 valued at \$1.2 billion¹) and other industries, the
58 ecology of the North Sea has been intensively monitored throughout this period of recent
59 warming.

60

61 Analyses of North Sea fish surveys have revealed northerly range expansions of warmer-
62 water species¹², population redistributions to higher latitudes² and deeper water¹³, and
63 widespread changes in local abundance associated with warming, with impacts on
64 community structure³. This substantial modification to fish community composition in the
65 region has had an observable economic impact on fisheries, with landings of cold-adapted
66 species halved but landings of warm-adapted species increasing 2.5 times since the 1980s³;
67 a pattern also identified in other marine ecosystems¹⁴. With a uniquely rich fish abundance
68 time-series from the period of warming, it is possible to split these data to assess how
69 predictions made using data from earlier years match observations from later years; a
70 validation approach which has been promoted for terrestrial systems¹⁵. Existing studies have
71 used survey data to describe past changes^{2,3,12,13}, or adopted process-based climate
72 envelope models to predict future abundance without validation¹⁶. Thus there is a need to
73 compare the predictions of climate-envelope models with those from more structurally-
74 complete data-driven models that have been developed and tested using spatially and
75 temporally explicit abundance data.

76

77 The GAM approach makes no *a-priori* assumptions about the nature of associations
78 between predictors and response variables¹⁷ and has been used to assess the importance
79 of different environmental drivers on patterns of distributions and relative abundance in
80 marine ecosystems¹⁸⁻²⁰. Here we developed GAMs to predict changes in the distribution and
81 abundance of the 10 most abundant North Sea demersal (bottom-dwelling) fish species,
82 which accounted for 68% of commercial landings by the North Sea fishery between 1980
83 and 2010 ([www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-](http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx)
84 [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
85 of variables were compared using data earlier in the time-series to train the models and
86 predict known distributions and abundances later in the time-series. Second, models were
87 used to predict changes in species distributions over the next 50 years.

88

89 Predictors of species' abundance were identified from a wider array of potential variables
90 (annual sea-surface and near-bottom temperatures; seasonal sea-surface and near-bottom
91 temperatures; depth; salinity; fishing pressure: all of which are expected to influence fish
92 abundance and distribution ^{e.g. 2,3,13,21}). For each species we calculated from summer and
93 winter monitoring surveys the mean annual abundance per grid cell in a 10 year time-slice
94 (2000–2009, inclusive) and used these data to train GAM models based on different
95 combinations of variable sets to predict the same data. We then analysed associations
96 between the predictions and original observations. All model combinations performed well
97 with predictions against known data all exceeding correlation coefficients of 0.67 and only
98 marginal changes with the loss of each variable for each species (Supplementary Table 1).
99 Following an assessment of the performance of alternate GAMs (Supplementary Figure 4,
100 Supplementary Tables 1 and 2), a model that included temperature, depth and salinity
101 variables was applied to each species (Fig. 2a and Supplementary Table 1). The selected
102 models excluded the metric for fishing pressure since this was a relatively poor predictor
103 variable in the majority of cases (Fig. 2a and Supplementary Table 1).

104

105 To assess the most appropriate length of time-series to use for future projections, we
106 developed models to predict the abundance of species across the region in a decade using
107 annual and seasonal temperature, salinity and depth data from the periods 10, 20 and 30
108 years beforehand. There was no consistent improvement in model fit with increasing periods
109 of training data (Fig. 2b and Supplementary Fig. 1), thus we used 10-year training periods
110 for all subsequent projections. The final stage of the model development stage was to
111 assess the ability of GAMs, using an effective set of variables, to predict distributions for 10,
112 20 and 30 year periods into the future and compare with observations. Predictions closely
113 matched observations for 8 of the 10 species using both survey datasets (Fig. 2c and
114 Supplementary Fig. 1).

115

116 Following model development and testing, models trained on data from 2000–2009 were
117 used to predict future distributions, abundance and thermal occupancy of the eight species
118 for which the models were effective, based on environmental conditions forecasted with the
119 Hadley Centre *QUMP_ens_00* model (Fig. 3 and Supplementary Fig. 1). Predictions based
120 on independent winter and summer fish surveys showed congruent temperature occupancy
121 patterns, with species predicted to experience warmer conditions and maintain existing
122 distributions, rather than maintaining their preferred temperature ranges by redistributing to
123 other locations (Fig. 3).

124

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

138

139 Seasonal temperatures, depth and salinity and likely co-varying habitat variables, appear to
140 be major determinants of current species distributions of commercially-important demersal
141 species in the North Sea, and were good predictors of past changes in distribution for many
142 species. Looking to the future, our results suggest that the strong associations of species
143 with specific habitats may ultimately prevent further poleward movement of species in

144 response to warming as previously predicted¹⁶. A recent study demonstrated that 1.6°C of
145 warming across the European continental shelf over the last 30 years locally favoured some
146 demersal species suited to warmer waters, but drove local declines in cold-adapted species,
147 despite long-term stability in spatial patterns of species presence-absence³. Dependence of
148 species on specific non-thermal habitat, together with spatially-contrasting local changes in
149 responses to warming³, may explain why mean latitudinal range shifts are only apparent in
150 some species², and are not detected in others despite sharing similar temperature
151 preferences. Dependence on specific non-thermal habitat has been observed in tagged
152 Atlantic cod (*Gadus morhua*), where fish occupied suboptimal thermal habitat for extended
153 periods with likely costs to metabolism and somatic growth²². Indeed a dominant driver of
154 changes in the central distributions of cod in the North Sea appears to have been intense
155 fishing pressure over the last century rather than warming, which has depleted former
156 strongholds in the western North Sea, driving an eastward longitudinal shift in relative
157 population abundance but no apparent poleward shift²¹. These factors, together with
158 potential indirect effects of warming potentially not captured in our models, for example from
159 changes to prey abundance, may explain why models based on depth and temperature
160 were not effective for longer term projections for Atlantic cod and whiting (*Merlangius*
161 *merlangus*). It is necessary to evaluate the performance of alternate predictor variables for
162 data-driven models of these species.

163

164 Mean depth distributions of North Sea fishes that had preferences for cooler water increased
165 by approximately 5m during the warming of the 1980s but tended to slow or stabilise
166 thereafter¹³. Based on the GAM results we do not expect or predict substantial further
167 deepening for cooler water species because depth is such a strong predictor of distribution.
168 Collectively, the studies imply that capacity to remain in cooler water by changing their depth
169 distribution has been largely exhausted in the 1980s and that fish with preferences for cooler
170 water are being increasingly exposed to higher temperatures, with expected physiological,
171 life history and population consequences.

172

173 In the absence of substantial distributional shifts that would allow fish to occupy different
174 habitats and depths, North Sea populations are likely to experience 3.2°C of warming over
175 the coming century (J. Tinker, Hadley Centre). Although such temperature increases are
176 within observed thermal limits for these species the ecological consequences are unknown,
177 especially when warmer conditions are closer to thermal preferences of other species using
178 the same habitats. Furthermore, physiological theory suggests that responses of species to
179 projected warming will eventually reach thermal thresholds. As species' *Pejus* temperatures
180 are reached, increased metabolic costs will compromise growth with associated declines in
181 population productivity²³. Capacity to tolerate warming will thus depend on scope for thermal
182 acclimation²⁴ and adaptation²⁵, with the degree of connectivity between thermally-adapted
183 sub-populations across the geographic range of species influencing the rate of adaptation to
184 future warming. Unless adaptation or acclimation can track the rate of warming, it is likely
185 that stocks will be affected, both directly through individual physiological tolerances, and
186 indirectly through climate-related changes to the abundance of prey, predators, competitors
187 and pathogens.

188

189 Our study demonstrates the power of data-driven GAM models for predicting future fish
190 distributions. In contrast to process-based models that attempt to integrate discrete
191 ecological mechanisms such as dispersal and density dependence, GAMs are grounded by
192 past net responses of populations to all these processes, in addition to interspecific
193 interactions and habitat associations that are not typically considered in process-based
194 modelling, perhaps explaining the strong predictive power of our GAM approach for
195 predicting known future conditions. The results of this study suggest that we should be
196 cautious when interpreting process-based model projections of distributional shifts, and that
197 interpretations should be informed by data-driven modelling approaches, especially when
198 using predictions for policy and management planning. Our projections suggest that if
199 populations fail to adapt or acclimatise to a warmer environment, warming will change

200 fishing opportunities for currently-targeted species in the North Sea over the next century.
201 Historically, fishing pressure has substantially modified the North Sea²⁶ and ongoing
202 changes in management will play an important role in shaping future fisheries resources.
203 Species responses to temperature should be considered when planning future fisheries
204 management strategies to ensure that anticipated long-term benefits of management are
205 ecologically feasible in this period of intense warming.

206

207 **METHODS**

208 ***Fish surveys.*** We used two long-term monitoring surveys that give detailed descriptions of
209 the distribution and abundance of demersal (bottom-dwelling) fishes in the North Sea. The
210 Centre for Environment, Fisheries and Aquaculture Science UK (Cefas) time-series is a
211 summer survey (August–September) conducted since 1980. The survey encompasses 69
212 1x1° latitude-longitude cells with at least three hauls conducted in each decade. The
213 International Council for the Exploration of the Sea (ICES) International Bottom Trawl Survey
214 (IBTS) time-series is a winter survey (January–March) conducted since 1980. The survey
215 encompasses 84 1x1° cells with at least three hauls conducted in each decade. Both
216 surveys are conducted using otter trawling gear (Granton trawl for pre-1992 Cefas surveys,
217 otherwise Grande Ouverture Verticale (GOV) trawls). Raw catch data were 4th-root
218 transformed to reduce skewness that is inherent in ecological abundance data.

219

220 Our study focused on the 10 most abundant demersal species targeted by commercial
221 fisheries or taken as bycatch (Fig. 2c), which together accounted for 68% of commercial
222 landings (by weight) in the North Sea fishery from 1980–2010 ([www.ices.dk/marine-
223 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,
224 we grouped data into three 10-year time slices and one three-year time slice for the
225 analyses: 1980–1989, 1990–1999, 2000–2009 and 2010–2012. The limited 2010–2012 time
226 slice was only used for testing predictions from the GAMs. To ensure a balanced design,

227 mean values for each for each decadal time period were used. This method controls for the
228 variable numbers of survey hauls taken in each cell and ensures that longer-term responses
229 to climate change are identified rather than year on year variability. All data were 4th root
230 transformed before being subject to GAM modelling, and individual cell predictions were
231 back transformed before calculation of correlation coefficients.

232

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

237

238 **Temperature and salinity.** We calculated Sea-Surface Temperature (SST), Near-Bottom
239 Temperature (NBT) and salinity (Supplementary Fig. 3) for the period 1980–2012 using the
240 UK Meteorological Office Hadley Centre *QUMP_ens_00* standard model for the northwest
241 European shelf seas. Modelled temperatures closely matched data from the Hadley Centre
242 global ocean surface temperature database (*HadISST1.1*; 92 cells, Pearson's $r = 0.84$;
243 www.metoffice.gov.uk/hadobs/hadisst/). Data from the *QUMP_ens_00* model were provided
244 as monthly means for 1x1° cells, enabling mean winter (January–March), summer (July–
245 September) and mean annual values to be calculated (Fig. 1).

246

247 **Fishing pressure.** We calculated a spatially-explicit metric of fishing pressure for each 10-
248 year time-slice by combining annual multispecies fishing mortality (F) estimates for North
249 Sea demersal species (mean estimates of regional F for cod, dab, haddock, hake, lemon
250 sole, ling, long rough dab, plaice, saithe and whiting, weighted by spawning-stock biomass,
251 from ICES stock assessments; www.ices.dk/datacentre/StdGraphDB.asp)³ with mean otter
252 and beam trawling effort for each 1x1° cell based on hours of fishing²⁷ (Supplementary Fig.
253 3). This integrated metric combining temporal trends in fishing mortality and spatial

254 distribution of fishing effort enabled us to test the importance of fishing pressure as a
255 predictor of abundance.

256

257 **Identifying key predictors.** We used GAM models, coded using the *mgcv* package in R
258 (www.r-project.org), to test the performance of GAMs for predicting changes in fish species'
259 distribution and identify the importance of different variables to these predictions. The *s*
260 smooth was used with $k = 7$ for all variables to limit the degrees freedom in-line with the
261 number of data points. The Gaussian model was used. Assessment of the plots for each
262 variable using the *gam.plot* function showed that increasing the *k* value did not improve
263 model fit to each variable. The *gam.check* function was used to check the *k* index was above
264 or close to 1 with non-significant *p* values. Analysis of the residuals showed no obvious
265 deviations from normal distributions, while the response to fitted values relationship was
266 close to linear.

267

268 Data from 2000–2009 were used to test sets of variables as this period had the greatest
269 survey intensity. To identify variables that most strongly influenced prediction we first
270 developed a model with all variables (annual temperatures, seasonal temperatures, depth,
271 salinity and fishing), and a subsequent five models each excluding one set of variables
272 (Supplementary Table 1). Sea surface and near bottom temperatures from both the summer
273 and winter were grouped together to characterise seasonal fluctuations. This suite of
274 potentially correlated variables captured the extremes of temperatures that all species may
275 experience at different life stages, and ensured that thermal conditions with and without the
276 seasonal thermocline, annually varying ocean currents and land mass effects are all
277 included. We compared the performance of models based on i) the strength of correlation *r*
278 between observed and predicted data, ii) weighted AIC²⁸ using data from the AIC function in
279 R, and iii) using generalised cross validation (GCV, through *summary.gam* in R). Inclusion of
280 interaction terms between depth and seasonal temperature extremes either reduced or had
281 little influence on model performance (Supplementary Table 2 and summaries based on

282 Akaike weights in Supplementary Fig. 4).

283

284 ***Model development***

285 We developed predictive GAMs with a set of variables that were effective across all species.

286 The correlation coefficient r , AIC values and GCV values of modelled and observed data

287 were compared. Across-species inclusion of depth, seasonal temperature, annual

288 temperature, salinity and fishing effort all improved the predictions (Fig. 2a). A key finding

289 from this model development stage is that variables that are readily measured and projected

290 in climate models effectively predict species distributions. On average models that excluded

291 fishing effort were most similar to the all-variable models (Supplementary Table. 1, Fig. 2a).

292 Since this metric had little predictive value, and we have no robust models of future fishing

293 effort, we excluded it when making future predictions.

294

295 ***Training period and predictive performance.*** To assess the influence of the duration of

296 training data on predictive power, GAMs trained on sets of one, two and three decades of

297 data for each species were used to predict 10 years into the future (Supplementary Fig. 1),

298 and the associations between predicted and known data compared. We also assessed the

299 performance of the model to predict further into the future within the historic records

300 available (Supplementary Fig. 1). We compared predicted with known abundance data for

301 each species for each forecasting period (0 to 30 years).

302

303 ***Forecasting future distributions.*** We used surface and near bottom annual and seasonal

304 temperature projections from the *QUMP_ens_00* model, surface and near bottom salinity,

305 and average depths from surveys between 1980–2012 as the environmental variables for

306 our predictions. We predicted fish abundances for sequential decades from 2000–2009 to

307 2050–2059 (Supplementary Figs. 5 & 6) using environmental variables (Supplementary

308 Figs. 3 & 7), and observed fish abundances from 2000–2009. Throughout the projection

309 period many cells do not experience temperatures outside of the range used to train the

310 model (Supplementary Fig. 2). For the widespread species in this study it is therefore likely
311 that at least parts of the population have experienced future conditions. However we
312 recognise that in future projected conditions the climate in some areas of the North Sea will
313 depart from existing variability in the model training period. Since it is not possible to test the
314 model beyond current thermal conditions using know data, some caution should be taken
315 interpreting projections for cells as they begin to experience temperatures beyond those
316 currently in the region (Supplementary Fig. 2).

317

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392 **ACKNOWLEDGEMENTS**

393 We thank staff of the Centre for Environment, Fisheries and Aquaculture Science UK
394 (Cefas) and all contributors to the International Council for the Exploration of the Sea (ICES)
395 International Bottom Trawl Survey (IBTS) for collecting and providing survey data. We thank
396 Sandrine Vaz for training in GAM modeling in R and David Maxwell for statistical guidance.
397 This work was supported by a Natural Environment Research Council (NERC) / Department
398 for Environment Food and Rural Affairs (Defra) Sustainable Marine Bioresources award
399 (NE/F001878/1), with additional support from a NERC KE Fellowship (S.D.S;
400 NE/J500616/2), NERC-Cefas CASE PhD Studentship (L.A.R; NE/L501669/1), Great
401 Western Research (M.J.G.), Defra (S.J. and J.L.B.), NERC Oceans 2025 (M.J.G. and
402 D.W.S), The Worshipful Company of Fishmongers (D.W.S.), and a Marine Biological
403 Association Senior Research Fellowship (D.W.S.).

404

405 **AUTHOR CONTRIBUTIONS**

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

411

412 **COMPETING FINANCIAL INTERESTS STATEMENT**

413 The authors declare no competing financial interests.

414

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416 **FIGURE LEGENDS**

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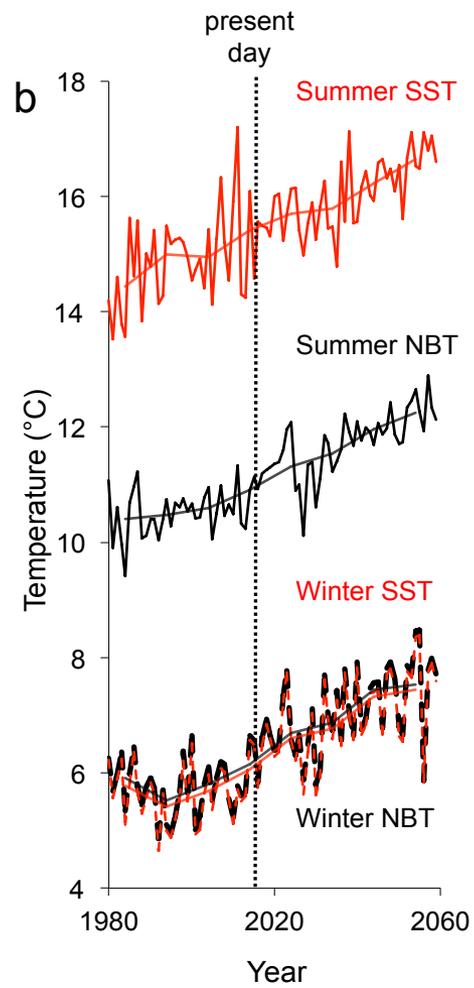
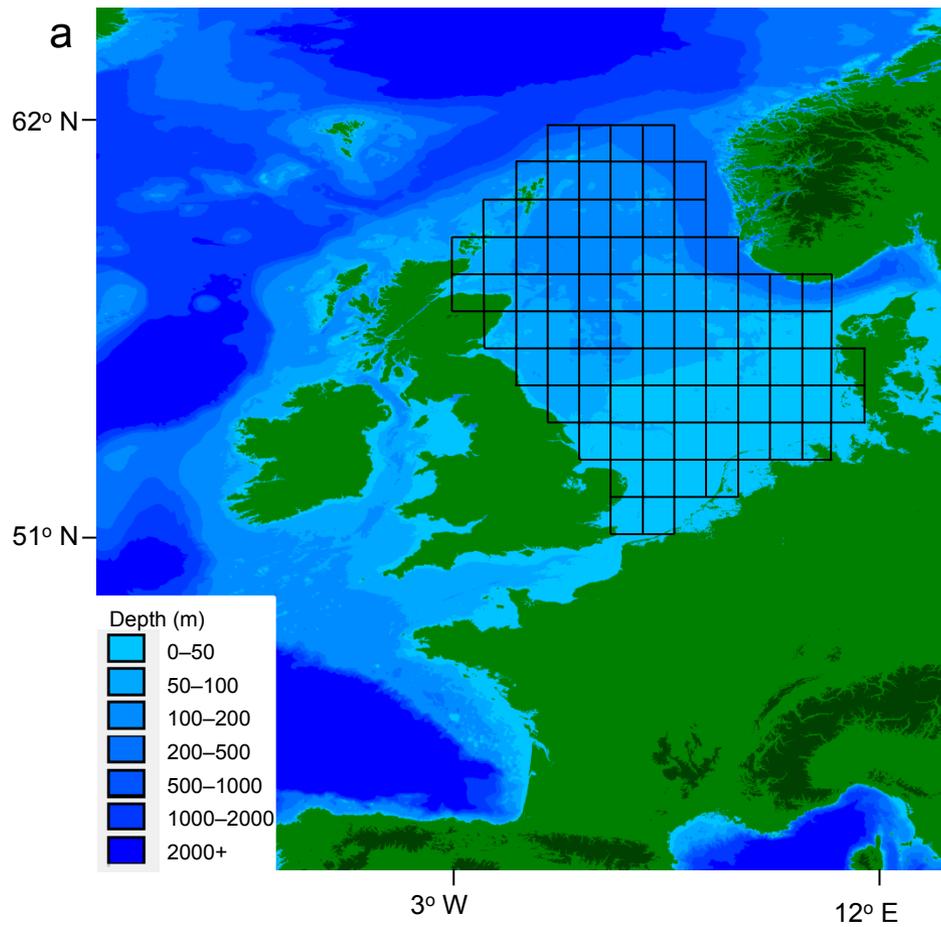
418 **Figure 1.** Physical environment of the North Sea. (a) Bathymetry with an overlay showing
419 locations of the 84 1x1° latitude-longitude cells in which fish abundance, distribution and sea
420 temperature were reported and predicted; (b) mean Sea-Surface Temperature (SST, red)
421 and Near-Bottom Temperature (NBT, black) in the study cells from 1980–2060 in summer
422 (July–September, solid line) and winter (January–March, dashed line) from the
423 *QUMP_ens_00* northwest European shelf seas climate model. Mean decadal values (as
424 used in the model) are overlaid in the corresponding colours for SST and NBT for each
425 season.

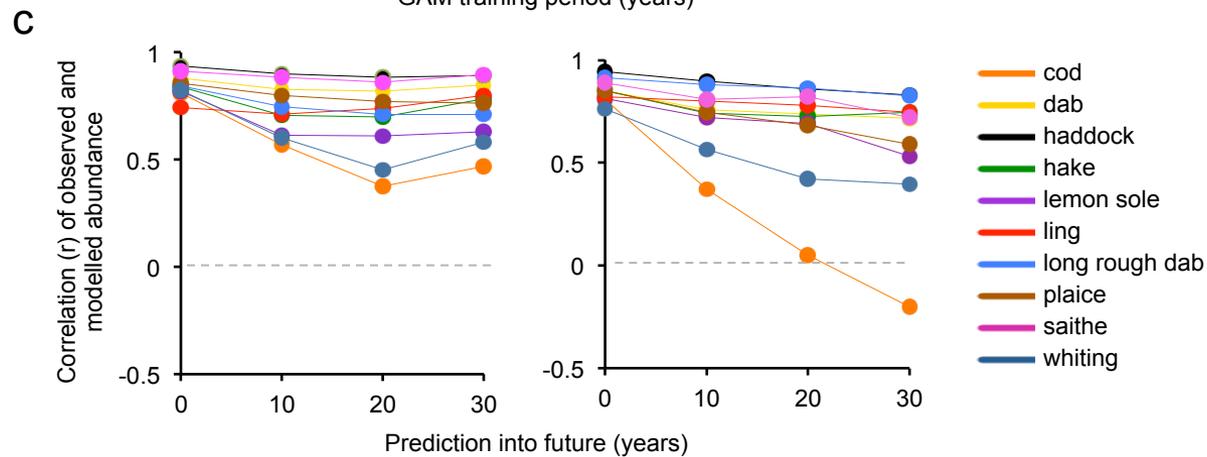
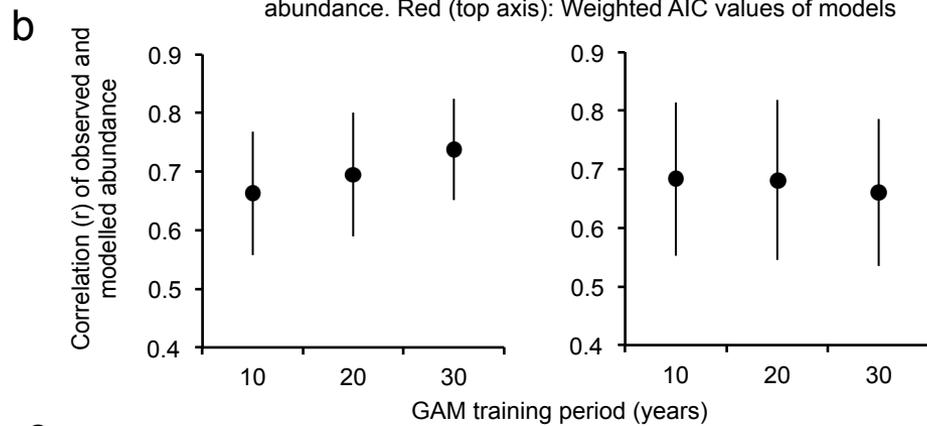
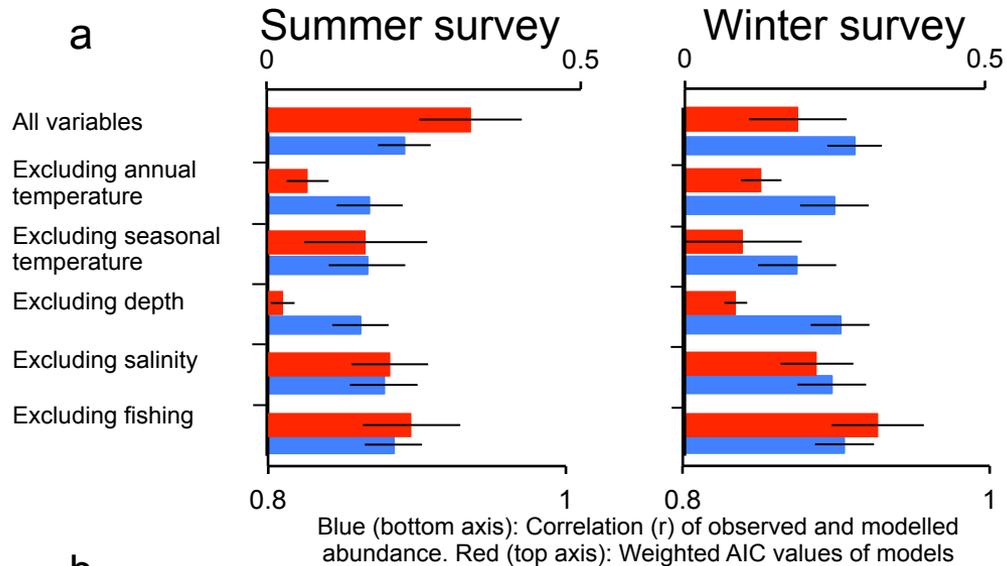
426

427 **Figure 2.** Predictive ability of Generalised Additive Models (GAMs). (a) Fits of predicted to
428 observed species abundance using 2000–2009 data. Variables were sequentially removed.
429 Model fits were evaluated using correlation (mean \pm SE Pearson's *r* coefficient across
430 species) and weighted Akaike Information Criterion (AIC: mean \pm SE across species). (b)
431 Duration of training data and predictive performance of GAMs using depth and seasonal
432 temperatures. Correlations (mean \pm SE Pearson's *r* coefficient across species) indicate no
433 improvement in performance with longer time-series. (c) Relationship between known data
434 and GAM predictions using depth, salinity and seasonal and annual temperature, for
435 decades beyond GAM training period.

436

437 **Figure 3.** Observed and predicted abundances of eight focal species along depth, latitude
438 and mean annual Near-Bottom Temperature (NBT) and Sea-Surface Temperature (SST)
439 gradients. Analyses were based on both the summer and winter survey datasets.
440 Distribution averages for each time period are shown using arrows of corresponding colours
441 along the x-axis.





Summer survey

Winter survey

