



Spatially resolved past and projected changes of the suitable thermal habitat of North Sea cod (*Gadus morhua*) under climate change

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Previous studies have identified changes in habitat temperature as a major factor leading to the geographical displacement of North Sea cod in the last decades. However, the degree to which thermal suitability is presently changing in different regions of the North Sea is still unclear, or if temperature alone (or together with fishery) is responsible for this displacement. In this study, the spatial distribution of different life stages of cod was modelled from 1967 to 2015. The model is fit point-to-point, spatially resolved at scales of 20 km. The results show that suitability has decreased south of 56°N (>12% in the Southern Bight) and increased north of it (with maximum of roughly 10% in southern Skagerrak). Future changes to suitability were estimated throughout the century using temperature projections from a regional climate model under the Intergovernmental Panel on Climate Change scenario RCP8.5. The results show that southern Skagerrak, the central and northern North Sea and the edge of the Norwegian trench will remain thermally suitable for North Sea cod throughout the century. This detailed geographical representation of thermally suitable key zones for North Sea cod under climate change is revealed for the first time through the improved resolution of this analysis.

Keywords: climate change, cod, *Gadus morhua*, habitat modelling, North Sea

Introduction

Atlantic cod (*Gadus morhua*) is one of the most important and studied commercial fish species of the North Sea (Cohen *et al.*, 1990). Hedger *et al.* (2004), Engelhard *et al.* (2014), and Nicolas *et al.* (2014) have shown that over the last decades, the geographical distribution of North Sea cod has changed from the shallow south-western to deeper, north-eastern parts of the North Sea. However, none of these previous studies has quantified the impact of temperature changes on the distribution of the suitable habitat for North Sea cod, spatially resolved at both long-term temporal and high-resolution spatial scales. In addition, it remains uncertain if the past temperature trends in the North Sea imply an increase or a decrease in thermal suitability of cod in the North Sea in general (Blanchard *et al.*, 2005) and if they alone are

responsible for cod's displacement or if fishery pressure also plays a role (Engelhard *et al.*, 2014).

In this study, a species distribution model was developed for different life stages of cod based on generalized additive models (GAMs) fitted to data of the North Sea International Bottom Trawl Surveys (IBTS) spanning almost five decades (1967–2015). Modelling changes to fish habitat is not only important to understand the mechanisms influencing geographical distribution, but also allows for projecting future changes under scenarios of climate change. Such projections are important to assess the risk of local extinction of species (Thomas *et al.*, 2004; Cheung *et al.*, 2009), predicting ecological and economical variations in the fisheries and, thus, for long-term planning on mitigating climate change impact. Future projections of fish habitat under climate

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change either focus on regional (Queirós *et al.*, 2016) or global scale changes (Cheung *et al.*, 2009), although global climate model (GCM) projections are typically used as a source of future conditions in both cases. Global studies generally show that suitable habitats for many species are shifting towards the poles under climate change. However, GCMs are unable to resolve shelf sea dynamics appropriately, including the small-scale changes in temperature occurring on regional scales. Therefore, they lack some of the detail necessary for assessing impacts on marine ecosystems and it remains uncertain how exactly fish habitats are likely to be redistributed in the North Sea as a result of future climate change.

Cheung *et al.* (2009) explicitly addressed the issue of scale, and stated that future models should use a “finer resolution” in physical and biological data. Moreover, while studies treating various species are good for a general understanding of the ecosystem (Queirós *et al.*, 2016), results from studies focusing on specific individual species are also needed. The benefits from such studies are similarly to those of regional over global models, i.e. a higher degree of detail.

In this study, changes of geographical distribution of North Sea cod under climate change were projected from 2020 to 2100 by using temperature changes according to the scenario RCP8.5 (Cubasch *et al.*, 2013) of the Intergovernmental Panel on Climate Change (IPCC). The model used to simulate this temperature projection was a high-resolution, regionally coupled ocean-atmosphere climate system model. The use of a regional, instead of a global, climate model should allow for unprecedented detail for projecting the future distribution of cod in the North Sea under climate change.

Material and methods

In this study, the spatial distribution of different life stages of cod is modelled with GAMs (Hastie and Tibshirani, 1986). The fundamentals about data and analysis are given in this section. For simplicity, details about the choices relating data, model equations, and degrees of freedom are given in [Supplementary Appendix S1](#).

Fish abundance data

Fish abundance data used in this study were catch-per-unit-effort (CPUE) per fish length class per haul for cod (*G. morhua*) from the 1st quarter (Q1; January, February, March) North Sea IBTS from 1967 to 2015. Data from Q1 were chosen over the third quarter (Q3) because the time series are longer. The data were obtained from the Database of Trawl Surveys (DATRAS, 2017) of the International Council for the Exploration of the Sea (ICES).

CPUEs for each haul were added in three length classes: 0–24.9, 25–39.9, and 40–140 cm. These length classes, denoted here as LC_{0-25} , LC_{25-40} , and LC_{40-140} , are deemed to represent different life stages with potentially different habitat requirements. While cod below 25 cm mainly represents recruits of age 0 and 1, fish between 25 and 40 cm start to mature (mainly age 2) and 40 cm is around the length at which 50% of individuals are mature in recent years (Marty *et al.*, 2014). A zero CPUE was used if no fish of a certain length class were caught in a haul.

Annual abundance by age of the entire North Sea cod stock, as derived from the ICES stock assessment (ICES, 2017), was used as an explanatory variable to account for the effect of overall population size on spatial patterns (i.e. density-dependent effect).

Environmental data

Past changes (1967–2015) of bottom temperature were taken from the Adjusted Hydrography Optimal Interpolation (AHOI; Núñez-Riboni and Akimova, 2015). This physical–statistical model is based on *in situ* observations and stability of the water column. AHOI’s domain in the North Sea spans from 48 to 62°N and from 6°W to 12°E, with a spatial resolution of $0.2 \times 0.2^\circ$.

A projection of the ocean future state (2020–2100) under climate change was obtained from the dynamical downscaling of the global model MPI-ESM (Max Planck Institute Earth System Model) performed with a high-resolution version of the regionally coupled ocean-atmosphere climate system model MPIOM/REMO (Mikolajewicz *et al.*, 2005; Sein *et al.*, 2015). The model’s horizontal resolution in the North Sea ranges from ~ 5 km at the southern coast to ~ 12 km at the northern boundary. A climate scenario conforming to the IPCC, the Representative Concentration Pathway 8.5 $W\ m^{-2}$ (RCP8.5; Cubasch *et al.*, 2013) was chosen. This scenario is considered an upper limit of increasing atmospheric greenhouse gas with carbon dioxide (CO_2) concentrations in the year 2100 of about four times the preindustrial level.

By comparing model output with AHOI data for the period 1960–2005, an offset between hydrographic observations and model results was calculated for each grid cell. This offset was added to the output of RCP8.5 climate scenario to obtain a realistic future prognostic of the hydrography changes.

Annual CPUE maps

Matching of CPUE to temperature is hindered by differences in spatial and temporal scales between IBTS and AHOI data. AHOIs are smooth maps over the complete North Sea at the monthly time scale while IBTS data are point location observations, which differ from each other even when taken inside short periods of time (few hours) and small distances (few kilometres). Both temperature and fish distribution are subject to high-frequency and short-range variations which are not resolved by the available data and are, thus, aliased to the resolvable scales (Clancy, 1983). In addition, both geophysical (tides, internal waves, eddies, atmospheric low and high pressure regimes) and fishery noises (schooling and avoidance of the net) are physically unrelated and thus matching both “raw” data sets yields a large noise-to-signal ratio, making the habitat modelling difficult.

To translate the IBTS data to the time and space scales of the AHOI data, year-quarter CPUE maps similar to the AHOI maps were created on a $0.5 \times 0.5^\circ$ grid. This scale was chosen as characteristic sampling scale of the IBTS because it is roughly the average distance between the IBTS observations. Cod abundance was mapped for each year from 1967 to 2015 on our $0.5 \times 0.5^\circ$ grid by using the GAM:

$$g(\hat{y}) = s_M(\text{lon}, \text{lat}), \quad (1)$$

where the dependent variable \hat{y} is cod CPUE, $g(\cdot)$ is a link function, and s_M is a smooth function called “scatterplot smoother.” The approach of Wood (2017) (his Section 5.5.1) is followed here and s_M was chosen as a two-dimensional thin plate spline depending on longitude and latitude [Equation (5.7) of Wood, 2017 with $d = 2$ and $m = 2$]. The model parameters are found by fitting the model to the CPUE observations through iteratively re-weighted least squares. Values of the basis dimension

k for s_M were chosen ranging from roughly 20 to 100 depending on the number of data available each year (Supplementary Appendix S1).

To deal with the many zero CPUE values, a hurdle approach (Maunder and Punt, 2004) was used, expressing the model as the product of two models:

$$\hat{y} = \hat{y}_P \cdot \hat{y}_{\text{CPUE}}, \quad (2)$$

where \hat{y}_P (the sub-index ‘‘P’’ is for ‘‘presence’’) is a model describing the probability of catching (CPUE > 0) or not catching (CPUE = 0) fish, taking continuous values between 0 and 1. \hat{y}_{CPUE} represents CPUE for the regions where fish are present (i.e. for CPUE > 0).

Both \hat{y}_P and \hat{y}_{CPUE} are defined with Equation (1), but each one with a different probability distribution and link function: For \hat{y}_P a binomial distribution with canonical link logit (Maunder and Punt, 2004) was chosen, while for \hat{y}_{CPUE} , a gamma distribution with logarithmic link. These maps are direct representations of the observed CPUE and thus will be called herewith ‘‘observations.’’

Because AHOI has a resolution higher than 0.5° , it must be downsampled (IEEE, 1979) to avoid aliasing. Therefore, AHOI temperature was low-passed with a Gaussian filter with correlation scale of 0.5° in all directions and the resulting field was interpolated on the $0.5 \times 0.5^\circ$ grid of the CPUE maps.

Matching past CPUE and hydrography changes

Because they are mapped on the same grid, matching CPUE and temperature is simply performed grid-point to grid-point. However, in regions with no fish data (for instance, the Norwegian trench) CPUE obtained from Equations (1) and (2) is only poorly estimated (it can be extrapolated by s_M rather than interpolated from near-by fishery hauls). Such poor CPUE estimates should be excluded from the fit of the habitat model.

To define a region where the annual GAMs estimates are robust for each year, a geographical region containing all haul positions, but excluding regions scarce in data, was calculated with a Delaunay triangulation (Swan and Sandilands, 1995). Matching CPUE and hydrography was performed only on grid points lying inside Delaunay triangles with all three sides smaller than 1 geographical degree (see Figure 1).

While the main analysis has been performed with survey data from Q1, they were matched to bottom temperatures of the previous summer (i.e. Q3 with a negative lag of 6 months). A justification of this choice, including a discussion of the potential mechanisms involved, is given in Supplementary Appendix S1.

Habitat modelling as function of environmental variables

The relationship between cod abundance \hat{y}_T and temperature changes T was modelled with a GAM with gamma distribution consisting of smooth functions of space and a parametric part:

$$g(\hat{y}_T) = s_{R1}(\text{lon}, \text{lat}) + a(Y) \cdot s_{R2}(\text{lon}, \text{lat}) + \mathbf{X} \cdot \mathbf{B}, \quad (3)$$

where $\hat{y}_T = E(s_M(\text{lon}, \text{lat}))$, i.e. the CPUE expected value from the annual maps $s_M(\text{lon}, \text{lat})$ for Q1 [Equations (1) and (2)]. The sub-index ‘‘T’’ in \hat{y}_T is for ‘‘temperature’’ and to distinguish this from \hat{y} in Equation (2). The variable $a(Y)$ is abundance of the complete North Sea cod stock in year Y from the ICES stock

assessments (ICES, 2017) for each fish length class. \mathbf{X} is the row vector of T :

$$\mathbf{X} = (1, T, T^2) \quad (4)$$

and $\mathbf{B} = (b_0, b_1, b_2)^T$ is a column vector of coefficients to be determined. Smoothers s_{R1} and s_{R2} are similar to s_M . s_{R1} accounts for the relationship between CPUE and cod’s long-term habitat, i.e. environmental variables which do not change on the time scales of this study. This ‘‘geographical attachment’’ (Planque *et al.*, 2011) can be sediments, bathymetry, spawning grounds (for LC_{25–40} and LC_{40–140}), end points of larval drift and nursery areas (for LC_{0–25}), and the distribution of prey and predators.

Using $a(Y)$ as explaining covariate accounts for local CPUE variations due to the size of the entire fish stock following population dynamics (fishery, recruitment, etc.). Note $a(Y)$ depends only on year Y and not on lon, lat. Therefore, the scalar $a(Y)$ is matched each year to local CPUE(lon, lat), allowing the other covariates (for instance T) and model terms to explain the remaining variance. This approach is similar to Pinsky *et al.* (2013), who used annual average biomass as explaining covariate. The interaction with the spatial smooth s_{R2} through the term $a(Y) \cdot s_{R2}(\text{lon}, \text{lat})$ is intended to account for population density effects on spatial distribution of cod, i.e. displacements of fish towards less suitable regions during times of large population. In these ‘‘geographic regression models’’ (Hastie and Tibshirani, 1993; Wood, 2017), each covariate is assumed to have a linear influence on the linear predictor for the response, but the slope parameter of that linear dependence varies smoothly with geographic location. $\mathbf{X} \cdot \mathbf{B}$ accounts for regional variations of abundance due to temperature alone.

$s_{R1}(\text{lon}, \text{lat})$, $s_{R2}(\text{lon}, \text{lat})$, and \mathbf{B} are determined from $s_M(\text{lon}, \text{lat})$, the positions lon, lat of the AHOI grid points, the AHOI Q3 bottom temperatures T and annual abundance $a(Y)$. A logarithmic function for g was chosen because, in combination with the quadratic temperature term in Equation (4), it results in a Gaussian bell-shaped temperature effect (i.e. a smooth curve with a single maximum) when Equation (3) is re-arranged and g moved to the right-hand side:

$$\hat{y}_T = \alpha \cdot \exp \left(s_{R1}(\text{lon}, \text{lat}) + a(Y) \cdot s_{R2}(\text{lon}, \text{lat}) - \frac{(T - \beta_T)^2}{2 \cdot \gamma_T} \right), \quad (5)$$

where the parameters α , β_T , and γ_T depend on the parameters \mathbf{B} . Further details about the choice for Equation (5) are given in Supplementary Appendix S1.

Once the habitat model was fitted with the downsampled data, model predictions were performed in the higher resolution of AHOI, i.e. on a $0.2 \times 0.2^\circ$ grid. This approach of intentionally reducing resolution to train the model while predicting with higher-resolution has shown good performance in habitat modelling of plant distributions (Thuiller *et al.*, 2005). CPUE changes were predicted for two cases: (i) past changes 1967–2015, to reproduce the observed historical displacement of North Sea cod, and (ii) changes 2020–2100 from the RCP8.5 climate scenario, to project future changes of the habitat of cod under future climate change.

Partial effects

The partial effect of a particular covariate was calculated by evaluating all other covariates on their sample mean over all

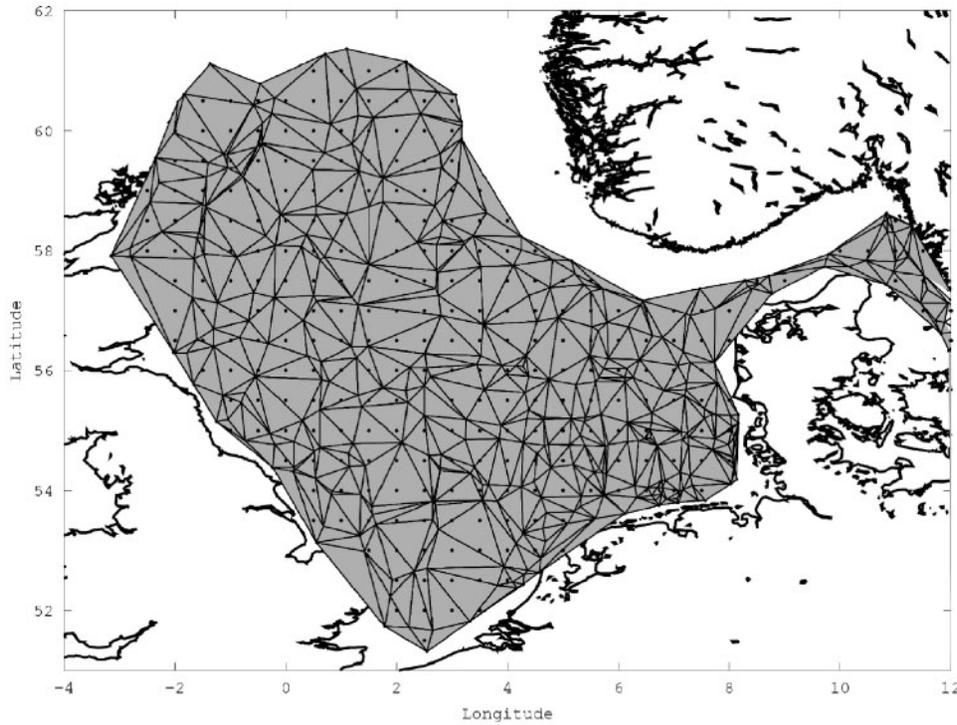


Figure 1. Study area (the North Sea), showing the positions of the fish hauls (triangle vertices) and the mapping region (grey patches) of annual CPUE maps, Equations (1) and (2), for the arbitrarily chosen year 1984. The evenly distributed black dots are the grid points of both the downsampled hydrography model AHOI and the annual CPUE maps. Lines joining the positions of the fish hauls are edges of Delaunay triangles.

observations used to fit the model. For the case of the temperature partial effect, Equation (5) becomes:

$$\hat{y}_T(T) = \alpha \cdot \exp\left(s_{R1}(\overline{\text{lon}}, \overline{\text{lat}}) + \bar{a} \cdot s_{R2}(\overline{\text{lon}}, \overline{\text{lat}}) - \frac{(T - \beta_T)^2}{2 \cdot \gamma_T}\right).$$

The overbars denote sample means, i.e. for the case of longitude:

$$\overline{\text{lon}} = \frac{1}{n} \sum_{i=1}^n \text{lon}_i,$$

with lon_i each of the n longitudinal positions used to fit the model and similar equations for lat , a and T . Model terms evaluated on the mean covariates can be expressed as amplitude of the exponential, similar to parameter α in Equation (5), giving a simple function of the single variable T :

$$\hat{y}_T(T) = A_T \cdot \exp\left(-\frac{(T - \beta_T)^2}{2 \cdot \gamma_T}\right), \quad (6)$$

with $A_T = \alpha \cdot e^{s_{R1}(\overline{\text{lon}}, \overline{\text{lat}}) + \bar{a} \cdot s_{R2}(\overline{\text{lon}}, \overline{\text{lat}})}$.

Because both smooths s_{R1} and s_{R2} depend partially on the same covariates (lon , lat), an average of model terms (instead of covariates) is needed to estimate their partial effects. Thus, the partial effect $\hat{y}_{R1}(\text{lon}, \text{lat})$ for geographical attachment is given by:

$$\hat{y}_{R1}(\text{lon}, \text{lat}) = A_R \cdot \exp(s_{R1}(\text{lon}, \text{lat})), \quad (7)$$

with $A_R = \alpha \cdot \exp\left(-\frac{(\bar{T} - \beta_T)^2}{2 \cdot \gamma_T} + \bar{a} \cdot \overline{s_{R2}}(\text{lon}, \text{lat})\right)$, with a similar equation for the density-dependent $\hat{y}_{R2}(\text{lon}, \text{lat})$.

Suitability index

Following the same reasoning of the previous section, to isolate geographically distributed cod abundance changes due to temperature alone, the population size effect was removed from Equation (5):

$$\hat{y}_T(\text{lon}, \text{lat}, T) = \alpha \cdot \exp\left(s_{R1}(\text{lon}, \text{lat}) + \bar{a} \cdot s_{R2}(\text{lon}, \text{lat}) - \frac{(T - \beta_T)^2}{2 \cdot \gamma_T}\right). \quad (8)$$

A convenient representation for $\hat{y}_T(\text{lon}, \text{lat}, T)$ was obtained by scaling α with the historical maximum (98th percentile) of $\hat{y}_T(\text{lon}, \text{lat}, T)$ for all (lon , lat , T):

$$S(\text{lon}, \text{lat}, T) = 100 \cdot \frac{\hat{y}_T(\text{lon}, \text{lat}, T)}{\max(\hat{y}_T)}. \quad (9)$$

This yielded a thermal suitability index for North Sea cod defined between 0 (completely unsuitable) to 100 (completely suitable). The few super-optimal values (those larger than the 98th percentile) were adjusted to 100.

Cross-validation

To validate our habitat model we have performed the following tenfold cross-validation: After fishery and hydrography data were matched (see ‘‘Matching past CPUE and hydrography changes’’ section), the data sets were split into ten subsets containing each randomly selected 10% of the complete data set. Afterwards, nine subsets (i.e. 90% of the data) were used to fit the model

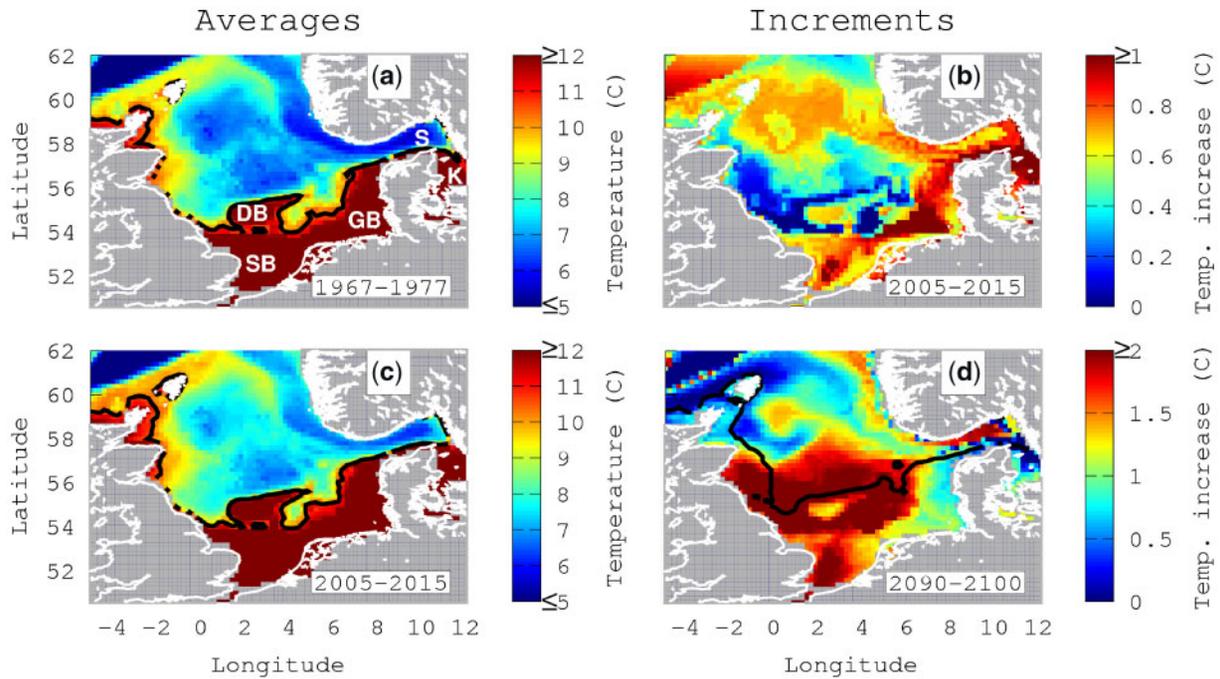


Figure 2. Average Q3 bottom temperature ($^{\circ}\text{C}$; left panels) and their increments (right panels) for selected decades: (a) 1967–1977; (b) increment between 1967–1977 and 2005–2015; (c) 2005–2015; (d) increment between 2005–2015 and 2090–2100 (RCP 8.5 scenario). The black contour is the 10.5°C isotherm. The following geographical locations referred in the text are shown in panel a: DB, Dogger Bank; SB, Southern Bight; GB, German Bight; K, Kattegat; S, Skagerrak.

[Equation (5)]. Values of the explaining co-variables in the remaining subset were used to predict CPUEs (10% of the data) which were compared to the corresponding observations to estimate residuals. The procedure was repeated with all 10 subsets. We calculated deviance residuals R_i for gamma distribution following McCullagh and Nelder (1989) (Sections 2.3.1 and 2.4.3):

$$R_i = \text{sign}(\hat{y}_T^i - \hat{y}^i) \cdot \sqrt{2 \cdot \left(-\log\left(\frac{\hat{y}^i}{\hat{y}_T^i}\right) + \frac{\hat{y}^i - \hat{y}_T^i}{\hat{y}_T^i} \right)}, \quad (10)$$

with \hat{y}^i being the i th abundance estimate from Equation (2) and \hat{y}_T^i the corresponding output estimate from the habitat model Equation (5). Note from their definitions that both \hat{y}^i and \hat{y}_T^i are always positive and, thus, the two quotients and the logarithm in Equation (10) are defined in all cases. Similarly, it can be shown that the square root is also always real. To generally validate the model and study also possible regional or temporal biases, deviance residuals have been grouped inside space, time, and temperature bins.

Results

Temperature changes

Q3 bottom temperature increment in the North Sea from 1967 to 2015 (Figure 2a and b) ranged between zero for the eastern coast of England and deep central parts of the North Sea to $>1^{\circ}\text{C}$ in the western German Bight and Skagerrak. Regions of <50 m in depth, mostly south of 56°N (the Dogger Bank, Southern and German Bights, and southern Skagerrak; see geographical locations in panel a) show the maximum temperature increase. In regions of >50 m in depth, mostly north of 56°N , the

temperature increase is moderate (0.7°C in the central North Sea), none or even slightly negative (around the Dogger Bank).

Model validation

Before describing the results of the habitat model, a brief, general validation of the model will be given. Modelled CPUE against observed values (Figure 3a–c) are roughly homogeneously distributed around the identity line. Only small CPUE values ($\text{CPUE} < 1$) seem to be somewhat overestimated by the model. The model explains 43.9% (for LC_{0-25}), 36.2% (for LC_{25-40}), and 58.6% (for LC_{40-140}) of the observed deviance (see Table 1). All model terms are highly significant, with p -values undistinguishable from zero. These notions speak of a reasonable fit and good model performance.

The model term explaining the highest amount of deviance is the population-density effect $a(Y) \cdot s_{R2}(\text{lon}, \text{lat})$ with almost 14% for LC_{0-25} and LC_{25-40} , and with 30% for LC_{40-140} (Table 1). It is followed by the spatial attachment $s_{R1}(\text{lon}, \text{lat})$ with an explained deviance ranging from 9 to 12%. The term explaining the least deviance is the temperature effect, with $<1\%$ for each of the three length class models.

Deviance residuals from the cross-validation [Equation (10)] are also roughly centred on zero and homogeneously distributed in space (Figure 3d–f), temperature (Figure 3g–i), and year bins (Figure 3j–l). There is only a bias of <0.5 (black curves in panels g–l), which is small in comparison to the amplitude of the residuals (dots). Most importantly, there are no evident residual patterns in space (panels d–f), temperature (panels g–i), or year (panels j–l) for all three length classes, indicating lack of autocorrelation in the residuals as well as a fair splitting of noise and

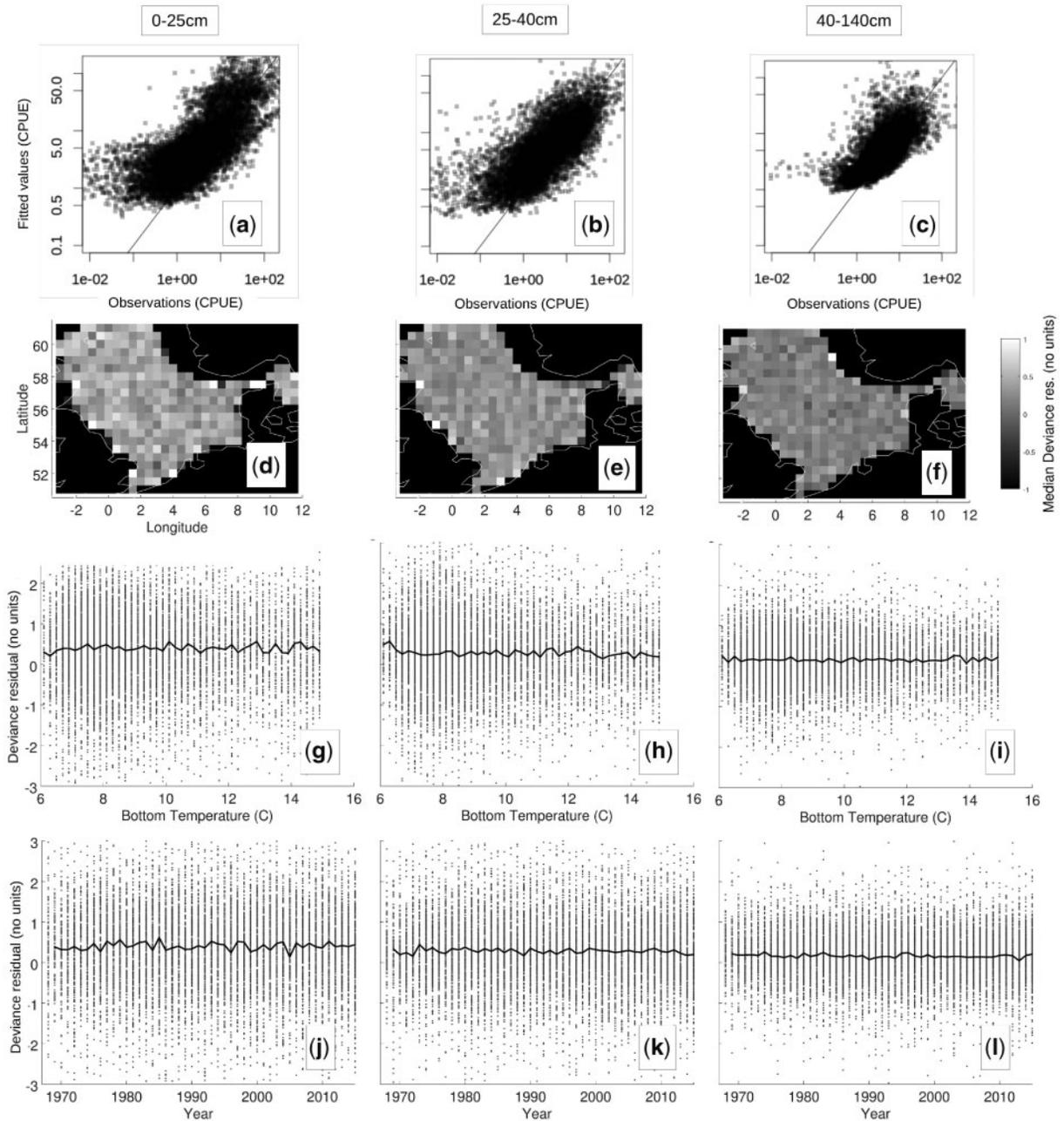


Figure 3. Validation of the habitat model for LC_{0-25} (left panels), for LC_{25-40} (central panels), and for LC_{40-140} (right panels). (a–c) Modelled CPUE [Equation (5)] against observed gridded CPUE [Equation (2)]. The straight line is the identity line. Both axes are logarithmic. Following panels: deviance residuals [Equation (10); no units] binned in space (median residuals in each bin are shown; panels d–f), temperature (dots; panels g–i), and year (dots; panels j–l) bins. The black curves in panels g–l joint the median residuals in each bin.

signal. Therefore, the cross-validation supports the notion of an adequate fit and good representation of thermal habitat.

Furthermore, more specific details relating the model validation (for instance of the temperature partial effect alone) are described for brevity in [Supplementary Appendix S1](#).

Preferred temperatures

Preferred Q3 temperatures for North Sea cod, as given by the maximum partial temperature effects [Equation (6)]; see

[Supplementary Figure S4](#), red curves), were roughly 10.0°C for LC_{0-25} and LC_{25-40} , and 11.0°C for LC_{40-140} .

Geographical attachment (\hat{y}_{R1})

Regions in the North Sea showing large geographical attachment $\hat{y}_{R1}(\text{lon}, \text{lat})$ [Equation (7)] are ([Figure 4](#), light grey areas): the Southern and German Bights, Skagerrak, and Kattegat (see [Figure 2a](#) for geographical locations) for all three length classes, the eastern coast of England, central, and eastern North Sea (east

of 5°E) for LC_{0–25}, as well as the central and north-eastern North Sea for LC_{25–40} and LC_{40–140}.

Density-dependent habitat use (\hat{y}_{R2})

Regions in the North Sea showing large density-dependent habitat use \hat{y}_{R2} (lon, lat) are (Figure 5, light grey areas): The German Bight for the three length classes, the Southern Bight for LC_{0–25}, the central North Sea (for LC_{0–25} and LC_{40–140}) and the northern North Sea (for LC_{40–140}).

Changes of suitable habitat

Suitable habitat attributed to historical temperature changes can be divided into two regions for all three fish length classes (Figure 6a–c): A region of decreased suitability south of 56°N and a region northward (excepting the eastern coast of Scotland) where suitability either remained unchanged (mostly for LC_{0–25}, panel a) or increased (for LC_{25–40}, panel b; and LC_{40–140}, panel c). The region of decreased suitability covered the Southern and German Bights and the Dogger Bank (geographical locations are in Figure 2a). A maximum decrease in suitability of 12% and lower occurred for LC_{40–140} in the Southern Bight. Increase in thermal suitability was roughly 10% in southern Skagerrak for the three length classes. In addition, LC_{25–40} (panel b) and

LC_{40–140} (panel c) showed increased suitability in the northern North Sea and the edge of the Norwegian Trench of 6% or more. In the rest of the North Sea, suitability remained unchanged for LC_{0–25} (panel a), while LC_{25–40} (panel b) and LC_{40–140} (panel c) experienced modest suitability increases in roughly 2%.

The spatial pattern of suitability changes remained almost unchanged for the future projection under climate change as represented by the climate scenario RCP8.5 (Figure 6d–f): Suitability further decreased south of 56°N and east of Scotland. For LC_{25–40} and LC_{40–140}, suitability decreased in the Southern Bight additionally 15%. Similarly, suitability further increased additional 10% in southern Skagerrak for all three length classes and in the central and northern North Sea for LC_{25–40} (panel e) and LC_{40–140} (panel f). The only prominent difference in the changes of suitability pattern in the future projection (in comparison to the historical one) is an additional increase in suitability in the central North Sea (~56°N and 3°E) for all three length classes.

Changes of the area of the most suitable thermal habitat (suitability >50%; Figure 7) indicate an increase in suitable area for North Sea cod from the 1980s until the 1990s for the three length classes (roughly 3% for LC_{0–25} and LC_{25–40} and 5% for LC_{40–140}). After the 1990s, the suitable area of LC_{0–25} (panel a) started to decrease, with LC_{25–40} (panel c) and LC_{40–140} (panel e) staying roughly steady. Similar trends for the three length classes (decrease for LC_{0–25}, panel b, and steadiness for LC_{25–40} and LC_{40–140}, panels d and f) continue for the future projection until the end of the century.

Table 1. Deviance (%) explained by each model term [Equation (5)] as calculated by refitting the model excluding each of the terms and comparing to the deviance explained by the full model.

Model term	Length class		
	0–25 cm	25–40 cm	40–140 cm
Full model	43.9	36.2	58.6
Temperature ($T - \beta_T$) ² /2 · γ_T	0.5	0.7	0.7
Spatial attachment s_{R1} (lon, lat)	11.2	8.7	12.3
Population density effect $a(Y) \cdot s_{R2}$ (lon, lat)	13.7	13.7	30.0

Deviance of the full model does not match the sum of individual deviances because the deviance of the intercept is not shown and model terms are commonly not completely independent.

Discussion

Bottom temperature increase

Though not focusing on summer temperatures and the same time period than used in this study (1967–2015), some previous studies have also shown significant temperature increases in agreement with the summer bottom temperature changes of Figure 2a and b: Hiddink and Ter Hofstede (2008) showed a trend of roughly 2°C in the average winter bottom temperature during the period of 1977–2003. Dye *et al.* (2013) showed spatially resolved trends of satellite sea surface temperature for the period of 1983–2012, indicating changes of 0.5°C in the South

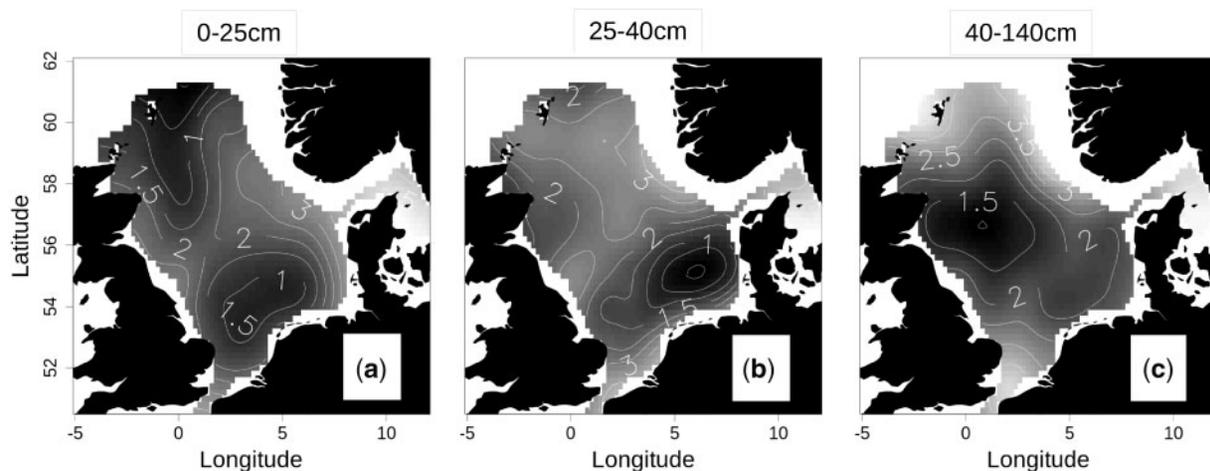


Figure 4. Geographical attachment \hat{y}_{R1} (lon, lat) [CPUE per model grid point; Equation (7)] for LC_{0–25} (a), LC_{25–40} (b), and LC_{40–140} (c). Lighter shading indicates regions with higher values for geographical attachment.

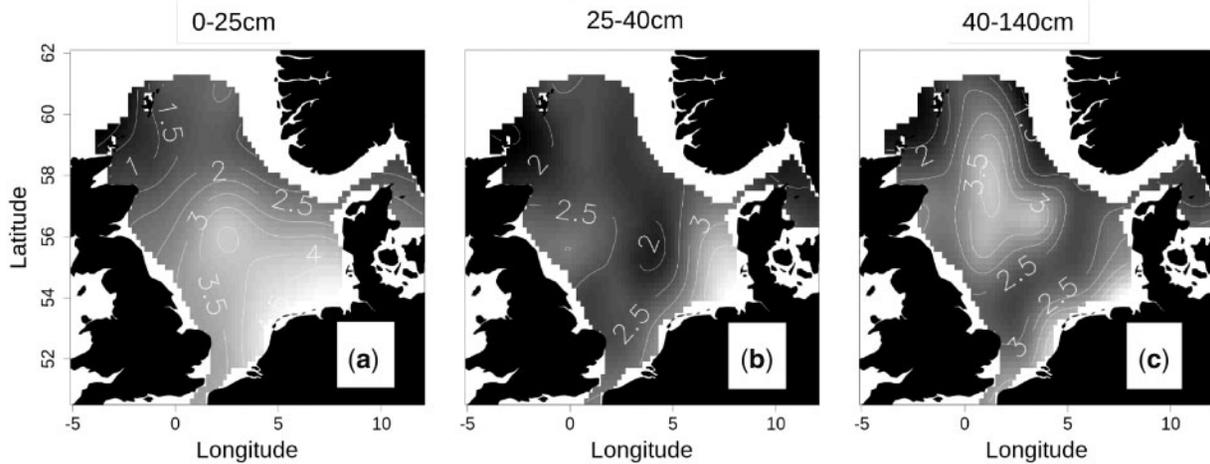


Figure 5. As Figure 4 but for density-dependent habitat use \hat{y}_{R2} (lon, lat) [calculated with an equation similar to Equation (7)] for LC_{0-25} (a), LC_{25-40} (b), and LC_{40-140} (c).

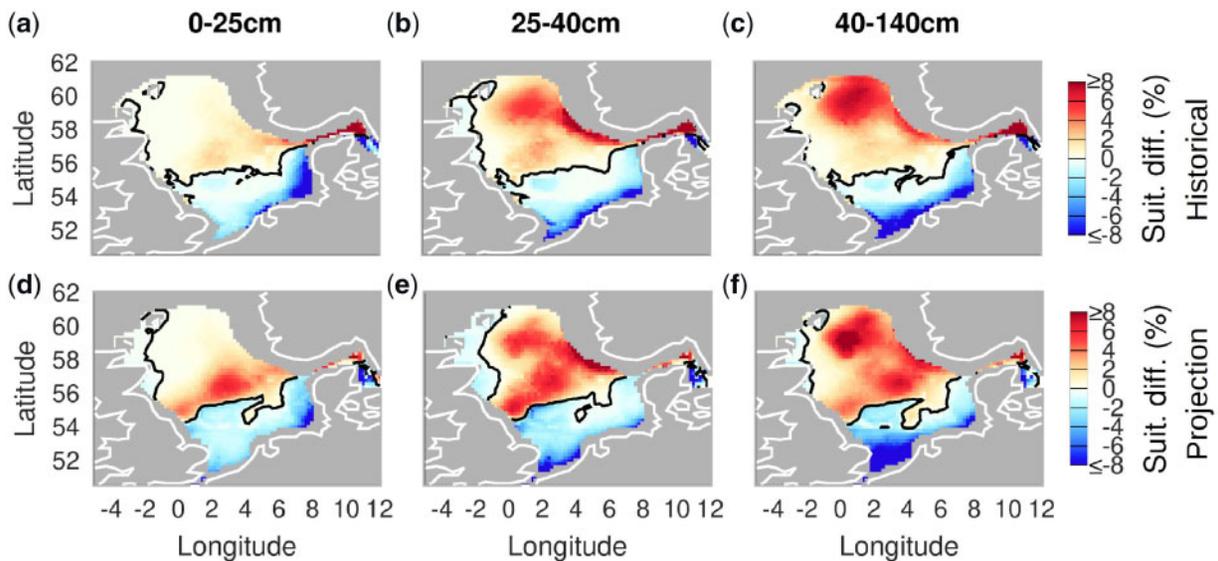


Figure 6. Changes of thermal suitability [%; Equation (9)] of North Sea cod between the decade 1967–1977 and the decade 2005–2015 (a–c) and between the decade 2005–2015 and the decade 2090–2100 (RCP8.5; d–f) for LC_{0-25} (left panels), for LC_{25-40} (central panels), and for LC_{40-140} (right panels). Red tones represent a suitability increase, blue tones a decrease. Unchanged suitability is stressed with a thick black contour.

(the coast of the Nederland), as well as of winter bottom temperature from *in situ* ICES observations of 0.5°C all over the North Sea (though trends in the south were non-significant due to large interannual variability). Using a spatially resolved model-data synthesis, Holt *et al.* (2012) showed strongest near bottom temperature changes (0.15°C year) in the shallow southern North Sea during the period of 1985–2004.

Preferred temperature

The temperature partial effect [Equation (6) and Supplementary Figure S4] reveals a preferred Q3 bottom temperature for North Sea cod of roughly 10.5°C for the three length classes. Because this preference is defined by the previous summer temperature, it

is not a direct measure of the temperature experienced by individual cod during the time of the survey sampling. However, the geographical distribution of cod abundance being similar in Q1 and Q3 (Section “Q3 vs. Q1 temperature” in Supplementary Appendix S1) would indicate a link to the 10.5°C isotherm (though not necessarily physiological). This finding is supported by previous studies, where the preferred temperatures were calculated as those for which the growth rate of cod is maximum; Pörtner *et al.* (2001) show highest growth rates for cod associated with water temperatures between 10 and 11°C (see Figure 4 therein). Brander (2003) presents a growth-temperature model based on assessment weight-at-age data, which shows that North Eastern Atlantic cod grows fastest for roughly 11°C (for fish

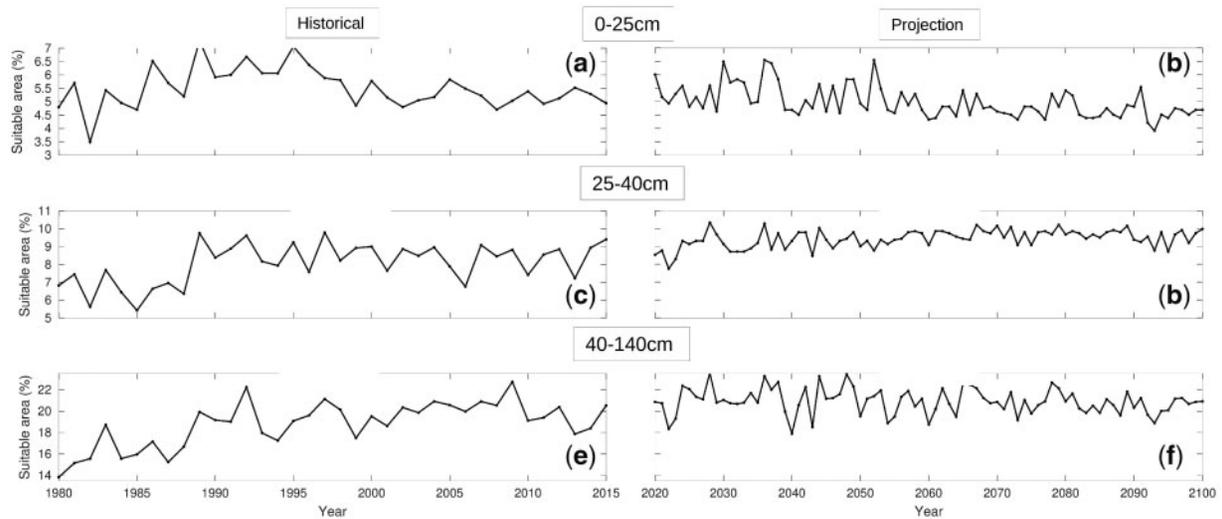


Figure 7. Changes of the suitable area [suitability Equation (9) of $>50\%$] as function of year for the historical (left panels) and projected (right panels) periods, for the 3 length classes LC_{0-25} (a, b), LC_{25-40} (c, d), and LC_{40-140} (e, f). The historical period is plotted after 1980 because before this year the IBTS grid (and thus the total area) was still not standardized (see Section “Spatial biases of IBTS data” in the Supplementary).

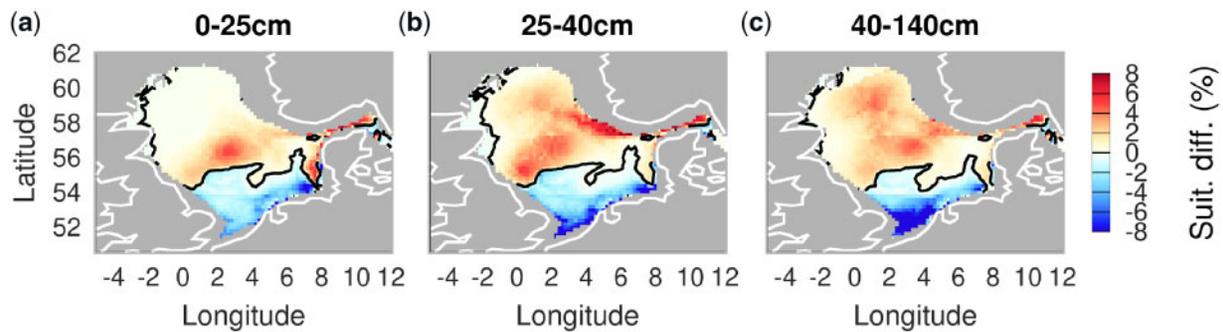


Figure 8. Similar to Figure 5d–f, i.e. changes of thermal suitable habitat of North Sea cod (%) but from 1967 to 1997 for LC_{0-25} (a), LC_{25-40} (b), and LC_{40-140} (c).

roughly 4 kg, i.e. adults; see Figure 6 therein). Butzin and Pörtner (2016) model a physiologically optimal temperature of $\sim 11^\circ\text{C}$ for Atlantic cod of roughly 1 kg (i.e. juveniles; see Figure 1a therein). Histograms of frequency of Q3 isotherms occupied by tagged cod in the northern North Sea from Neat and Righton (2007) (their Figure 4c) roughly indicate a preferred temperature of 11.8°C .

Blanchard *et al.* (2005) quantified the effect of temperature and fish spatial density on the distribution of the suitable habitat of juvenile cod from 1977 to 2002 using a model of ideal free distribution fed with abundance estimates of a virtual population analysis. Based on laboratory experiments from Björnsson and Steinarsson (2002), they support cooler optimal temperatures: 9.1°C for age-1 cod (equivalent to our LC_{0-25}) and 7.4°C for age-2 cod (partially equivalent to our LC_{25-40}). The differences with Blanchard *et al.* (2005) might lie on the preferred *in situ* temperature for cod differing from its physiological thermal optimum due to food availability or avoidance of predators. In agreement with this notion, Neat and Righton (2007) stated that thermal

optima may be inadequately described by laboratory experiments (based on observations of temperature as recorded by tagged cod), with natural variance in thermal tolerance of cod allowing residence in apparently unsuitable areas.

Geographical displacement of cod's habitat

Modelled CPUE as function of temperature alone [Equation (9); Figure 6a–c] revealed a geographical displacement of cod's suitable thermal habitat. Hedger *et al.* (2004) were the first discussing a displacement of cod from the Southern and German Bights in the 1980s to the north-eastern North Sea in the 1990s. Perry *et al.* (2005) described a long-term northward shift of latitudinal range of North Sea cod (together with other fish species), but they did not consider longitudinal shifts. Based on centre of mass calculations by Engelhard *et al.* (2014) the stock showed a northward displacement during the period of 1980–2010 based on IBTS data (their Figure 3b) and an eastward displacement during the period of 1980–2000 based on commercial data (their Figure 3a). This study agrees with those notions by reproducing a similar north-

eastward displacement until 1997, from the south-western part (the Southern Bight) onto the northern and eastern North Sea, including here part of the German Bight, the western coast of Denmark, and southern Skagerrak (Figure 8; compare panel b with Figure 4, upper panels, of Hedger et al., 2004). Maximal eastward displacement in 1997 was confirmed by calculating a mass centroid index as biomass-weighted average longitude (similar to Engelhard et al., 2014 and Pinsky et al., 2013; no figure shown). Afterwards, a subsequent northward displacement occurred until 2015 (Figure 6).

Engelhard et al. (2014) used linear models with random effect to examine the impact of temperature, fishery and abundance on the North Sea cod distribution. By correlation analysis, they concluded that the northward displacement of adult cod in the North Sea was due to temperature increase, but the eastward displacement was mostly related to fishing pressure. While the spatial effect of fishing was not included in this study, the effect of year-to-year changes of the entire fish stock (whether from recruitment or from total fishery) are included in the term $a(Y) \cdot s_{R2}(\text{lon}, \text{lat})$ [Equation (3)]. The results suggest that the eastward displacement can be explained without involving fishery (i.e. with temperature alone) because its effect is eliminated in [Equation (8)] and, yet, an eastward displacement is still evident (Figure 8).

A possible explanation of this disagreement is that the analysis of Engelhard et al. (2014) is based on a single-dimensional time series of temperature, total fishing pressure in the North Sea and longitudinal and latitudinal components of the centre of gravity of the cod stock. The lack of spatially resolved temperature changes would not have been able to identify the eastward displacement of cod; however, the possibility of differing regional fishery impacts to cod distribution cannot be disregarded. Unfortunately, data on the spatial distribution of fishing effort with sufficient coverage of the North Sea were only available from 2000 onward for the study area, which was deemed insufficient for a robust investigation of its effect on long-term changes to cod distribution. Lack of spatially resolved fishing effort is unfortunately common in fishery studies, independently of the study area (see for another example, Pinsky et al., 2013).

By comparing tag-recorded temperatures with simultaneously sampled ICES CTD data, Neat and Righton (2007) stated that individual cod had access to cooler waters than those they were observed to have occupied. Since individual cod only seldom accessed those cooler waters, Neat and Righton (2007) conclude that the northward shift of cod towards cooler waters (described then by Perry et al., 2005) could have been due to a depletion of cod in the south rather than from increased temperature. However, the time scale of the habitat displacement indicates that the cod stock only emigrated from a particular region due to warming conditions over decades and generational time scales. Therefore, it may be difficult to draw conclusions from the study due to a small sample size spanning a considerably shorter time period (1999–2005). Results from this and similar studies (Hedger et al., 2004; Perry et al., 2005; Engelhard et al., 2014; Nicolas et al., 2014), suggesting a real shift of cod habitat, are consistent with Neat and Righton (2007) only if the mechanism behind the displacement is not a physiological impairment of temperature for adult cod, but indirect links between temperature and other aspects of the cod habitat (spatial differences in recruitment and survival, prey availability, etc.; Neat and Righton, 2007; Engelhard et al., 2014).

In line with these notions, the distribution of the zooplankton species *Calanus finmarchicus* (the preferred and often dominant prey of larval North Sea cod) has displaced northwards in the last years (Olsen et al., 2011), probably as consequence of increasing temperatures. Such is inferred by a negative correlation between a plankton index (reflecting quality and quantity of plankton food available for larval cod) and sea surface temperature in the North Sea (Beaugrand et al., 2003; Beaugrand and Kirby, 2010). Furthermore, Olsen et al. (2011) pointed out, that lower larval cod survival rates would in turn lead to difficulties in stock regeneration. The implied spatial changes in survival rate of larval and success of spawning cod in different parts of the North Sea match well the changes in spatial distribution observed in this study, supporting the notion of an indirect (rather than direct) influence of temperature on the cod habitat.

The area of suitable thermal habitat for North Sea cod (Figure 7) could seem intuitively too small in absolute values (ranging from 5% for LC_{0-25} to 20% for LC_{40-140}). However, the spatial distribution of fish, and thus of the size of its suitable area, depends not only on the spatial distribution of environmental properties but also on the stock size (fish density effect). Assuming, as it seems probable, that North Sea cod was mainly underpopulated in the later years of the study period, most cod would have been concentrated only on a relatively small, highly suitable area of the North Sea (see Supplementary Figure S1). This would lead to an underestimation of the size of the thermal suitable area, explaining the small values in Figure 7. However, the relative values (i.e. the changes) of suitable area are independent of an absolute scale of suitability and, thus, provide evidence of a reduction in area of the thermal habitat for LC_{0-25} and of increase for LC_{25-40} and LC_{40-140} . This positive impact of the temperature increase on the habitat of for LC_{25-40} and for LC_{40-140} in a large region of the North Sea (Figure 6b, c, e, and f) is contrary to Blanchard et al. (2005) who concluded that the suitable cod habitat in the complete North Sea has reduced from 1977 to 2002 (their Figure 5). An explanation for this disagreement may again be due to an underestimation of preferred temperature for North Sea cod by Blanchard et al. (2005) (physiological thermal optimum based on laboratory experiments might differ from preferred *in situ* temperatures due to food availability or avoidance of predators).

The small amount of deviance explained by temperature alone (<1%) in comparison to all other terms (Table 1) should not be misunderstood as climate change having only a small influence on the spatial distribution of North Sea cod. Temperature changes at the climate scale explain so little variance because spatial variations of temperature or time variations at shorter time scales (such as daily, annual, or interannual variations) are one order of magnitude larger than climate change signals. Yet, the magnitude of those changes alone says nothing about their impact on an ecosystem. For instance, while typical variations of temperature at daily basis can be as large as 12°C and have no negative influence on an ecosystem, a much smaller increase in temperature at climate scale of 1°C can cause important well-documented changes (see for instance Table SPM.A1 in IPCC, 2014, for a summary of observed impacts attributed to climate change reported in the scientific literature in the last years). In addition, a large degree of abundance variability is associated with changes in overall historical population size and other spatial habitat preferences. Only after careful consideration of these

influences, as accounted for by the other model terms, can the residual thermal habitat signal be identified.

Even though some previous studies have considered temperature changes as the major mechanism behind the north-eastward displacement (Hedger *et al.*, 2004; Perry *et al.*, 2005; Engelhard *et al.*, 2014; Nicolas *et al.*, 2014), or as an explanation of a general decline of the cod habitat (Blanchard *et al.*, 2005), none have quantified the changes of suitability due to temperature alone, spatially resolved at scales smaller than hundreds of kilometres. Therefore, the present maps of suitability changes as function of temperature alone (Figure 6) represent a step forward in our understanding of the processes driving changes to cod habitat.

Relation to distribution of temperature and spatial smooth terms

As described above in “Material and methods” section, $\hat{y}_{R1}(\text{lon}, \text{lat})$ (Figure 4) should represent geographical preference of non-variable environmental properties such as bathymetry and sediments because it explains the geographical distribution of cod abundance only as function of space [Equation (7)]. $\hat{y}_{R2}(\text{lon}, \text{lat})$ (Figure 5) depends on an interaction with abundance which modifies the effect of total population depending on location [Equation (5)]. Therefore, $\hat{y}_{R2}(\text{lon}, \text{lat})$ should represent the use of habitat as function of population density or, alternatively, a density-dependent geographical preference. Large values of this term indicate the regions which North Sea cod inhabits during times of higher population sizes (the German Bight, for instance, see Figure 5). Such regions would be indicative of less-preferred habitats, but possibly still acceptable during periods of higher competition. The spatial pattern for these density-dependence terms generally shows higher values around the margins of the positive regions of the geographical attachment term. This result is consistent with the observation that fish stocks will often reduce their spatial distribution to a core, preferred habitat during periods of low population size when competition is low, which often results in higher fishing selectivity in terms of CPUE. Thus, the geographic attachment term is likely also identifying core habitat areas that are associated with higher abundances across the entire time period.

$\hat{y}_{R1}(\text{lon}, \text{lat})$ and $\hat{y}_{R2}(\text{lon}, \text{lat})$ have different spatial distributions, with $\hat{y}_{R1}(\text{lon}, \text{lat})$ having maximum mostly in Skagerrak and $\hat{y}_{R2}(\text{lon}, \text{lat})$ in the Southern Bight (for LC_{0–25}), the German Bight (all length classes), and the central North Sea (LC_{40–140}). In the present analysis, both terms are considered as contributing to the regional changes of thermal habitat of North Sea cod in the last decades (Figure 5a–c) as described by Equation (8). A qualitative discussion of which is the role of each term follows.

Because of the exponential function in Equation (8), temperature changes have a larger contribution to suitability in regions where $\hat{y}_{R1}(\text{lon}, \text{lat})$ and $\hat{y}_{R2}(\text{lon}, \text{lat})$ are large (for instance, the Southern Bight, the German Bight, Skagerrak, and Kattegat; see Figures 4 and 5). In agreement, these regions showed strong changes of cod abundance throughout the decades in this and previous studies, indicating they are particularly sensitive to temperature changes (Hedger *et al.*, 2004; Kempf *et al.*, 2013; Nicolas *et al.*, 2014). Those changes can be geographically divided into two groups:

- (i) *Regions of decreased suitability.* These are regions of <50 m in depth, mostly south of 56°N (the Dogger Bank, Southern

and German Bights, and southern Skagerrak) and the eastern coast of Scotland. In these regions, Q3 bottom temperature was at the identified preferred level of 10.5°C or above in 1967–1977 (Figure 2a; black contour curve) and increased by roughly 1°C during the period of 2005–2015 (Figure 2b). This increase beyond the preferred temperature reduced the thermal suitability for cod for the three length classes (see Figure 6). For the LC_{40–140} class, the Southern Bight stands out with a reduction in suitability of >12%, which is due to both a large positive increase in temperature and a high geographical attachment ($\hat{y}_{R1}(\text{lon}, \text{lat})$) for this length class (Figure 4c). In agreement with these findings, Hedger *et al.* (2004) argued that temperatures during the 2000s in the southern North Sea might have already become too warm for cod. Similar strong changes of thermal habitat in the German Bight for the three length classes (particularly LC_{0–25}) seem to be related to a large $\hat{y}_{R2}(\text{lon}, \text{lat})$ in that region (Figure 5). In this case, a reduction of cod population might be partially responsible (together with the temperature increase) for the strong abundance decrease in the German Bight. Such a reduction in population would have led to a concentration of cod in the most suitable region of Skagerrak (see Supplementary Figure S1, bottom panels).

- (ii) *Regions with increased suitability.* These are regions of >50 m in depth, mostly north of 56°N. From 1967 to 1977, these regions were considerably below cod’s preferred temperature of 10.5°C (6–9°C; Figure 2a), while temperature increased during the last decades by roughly 0.7°C (Figure 2b). The large geographical attachment ($\hat{y}_{R1}(\text{lon}, \text{lat})$) in these deep, cool regions of the central and northern North Sea for LC_{25–40} (Figure 4b) and LC_{40–140} (Figure 4c) renders the temperature increase (onto the preferred temperature) as particularly favourable for cod’s habitat. Suitability improved up to 8% in northern Skagerrak for all length classes (Figure 6a–c), the central and northern North Sea, as well as the edge of the Norwegian trench for LC_{25–40} (Figure 6b) and LC_{40–140} (Figure 6c). Therefore, these regions seem to become key zones for suitable thermal habitat for North Sea cod. This general displacement of North Sea cod habitat onto the central deep regions of the North Sea is in agreement with Dulvy *et al.* (2008), who observed distribution shifts into deeper waters by demersal fish assemblages as reaction to climate change. The temperature increase in the central and northern North Sea had virtually no impact on the thermal suitability of LC_{0–25} because this is a region of small geographical attachment ($\hat{y}_{R1}(\text{lon}, \text{lat})$) for the length class (Figure 4a).

Future projection of cod habitat suitability

The projected changes in suitability for 2020–2100 (Figure 6d–f) indicate that the geographical pattern of past changes of thermal suitability (Figure 6a–c) are likely to continue under the scenario RCP8.5, with a further decrease in suitability south of 56°N and an increase north of it. An examination of the geographical attachment $\hat{y}_{R1}(\text{lon}, \text{lat})$ (Figure 4) and temperature changes (Figure 2c and d) can again explain these patterns in suitability changes.

At the end of the present century, water temperature in the southern regions of the North Sea, shallower than 50 m in depth, are projected to increase by roughly 1.5°C as compared to present

conditions; i.e. reaching and exceeding the preferred temperature of 10.5°C (black contour in Figure 2d). As a result, these regions are projected to further decrease in suitability in the decades to come (Figure 6d–f).

The regions north of 56°N were still below the preferred temperature of 10.5°C during the period of 2005–2015 (Figure 2c). Under RCP8.5, most of these regions are projected to increase in temperature by 1.5–2.0°C in the following decades (Figure 2d); for example, increases from 7 to 8.5° in the central North Sea (56°N 5°W) are still considerably below the preferred temperature of 10.5°C. The key zones of thermal habitat remain geographically unchanged but further increase in suitability (particularly for LC_{25–40}). Roughly one half of the North Sea is projected to still be at or below the preferred temperature at the end of the century (black contour in Figure 2d). RCP8.5 represents the most pessimistic scenario regarding increase in atmospheric CO₂ (Cubasch et al., 2013) and the large range of tolerated temperatures of cod (see “Q3 vs. Q1 temperature” in Supplementary Appendix S1) suggest that the central and northern North Sea will still remain, from a thermal tolerance perspective, habitable for cod till the end of the century.

Following ideas put forward by Queirós et al. (2016), such observations render the regions of increased suitability (Figure 6) as important for planning and protection policies during the following decades. These identified regions of improved habitat for cod are consistent with the findings of Queirós et al. (2016) (their Figure 1) for the north eastern North Sea and east of Scotland. However, contrary to our findings, Queirós et al. (2016) consider the north-eastern coast of England (see Figure 6d–f) a region where the North Sea ecosystem will become more vulnerable to increasing environmental temperature. Similarly, this study identifies the German and Southern Bights as regions of strongly decreased suitability, which were not identified as vulnerable regions to climate change by Queirós et al. (2016).

Such mismatches may be explained by the fact that Queirós et al. (2016) did not focus particularly on cod, but considered the more complex North Sea ecosystem as a whole. While this approach is helpful for a general understanding of the ecosystem, generalizing the preference of various fish species does not allow drawing conclusions about a specific fish like cod. In addition, while focusing on the North Sea, Queirós et al. (2016) projections are based on outputs from GCMs. A main weakness of GCMs is the neglect of tides, known to be important in the seasonal stratification of the water column in the tidally mixed areas of the southern North Sea, which induces an artificial vertical temperature gradient (Mathis et al., 2017). The regional climate model used in this study should be better able to resolve temperature increases at the spatial scales addressed by this study due to its higher grid resolution and simulation of tidal waves (Mathis et al., 2015).

Currently it is well known that most geographical regions, species, ecosystems and countries will be harmed by climate change, while others (even if to a lesser extent) are benefitting (see IPCC, 2014). From a fisheries standpoint, fish habitat shifts have already caused losses to some countries while benefitting others, which has already led to conflicts and are expected to continue in the decades to come (Pinsky et al., 2018). The past changes and projections of thermal suitable habitat for North Sea cod has the potential for a similar outcome; for example, the Economic Exclusive Zones (EEZ) of Belgium, the Netherlands, Germany, and Denmark are completely inside regions of projected habitat

suitability decreases (Figure 6), indicating greater impacts from cod displacement in the future independent of sound management. The situation for the United Kingdom remains relatively unchanged, with a portion of its EEZ decreasing on suitability but another one increasing. Norway seems to be the only country definitively winning on North Sea cod suitability, with its complete EEZ in a region of increment. This has potential major implications for management, since relative stability in quotas (each country gets a constant share of the total allowable catch) could be questioned under such circumstances.

An increasing thermal suitability in the Skagerrak and Kattegat could support mixing between North Sea cod and local cod stocks increasing the potential competition between North Sea cod and local populations. Especially juvenile cod has been proofed to drift into the Skagerrak and Kattegat from where it currently moves back to the North Sea when becoming adults (Knutsen et al., 2004).

An interesting follow-up study relating the projected displacement of North Sea cod could be to model its geographical expansion into areas outside the present survey area. This demands expanding the domain of AHOI as well or, alternatively, integrating another hydrography product with a larger domain (for instance, an ocean reanalysis) into the habitat model. In addition, geographical attachment should be represented not with the proxy-variables longitude and latitude but with model terms depending on, for instance, bathymetry and sediments.

The influence of increasing temperatures on the biology of cod

The results of the analysis suggest that the suitable thermal habitat of cod has generally improved in the northern areas and decreased in southern areas of the North Sea, and these trends are predicted to continue in the coming decades under climate change scenarios (Figure 6). However, the overall net gain of roughly 3 and 6% area for the most suitable habitat of LC_{25–40} and LC_{40–140} (Figure 7c and e) is opposing the observed decline in North Sea cod population (Supplementary Figure S2). This apparent contradiction arises from the fact that yearly biomass changes ($a(Y) \cdot s_{R2}(\text{lon}, \text{lat})$) explain a considerably larger amount of variation than that attributable to temperature-induced regional variations ($((T - \beta_T)^2 / 2 \cdot \gamma_T$; see Table 1). Thus, the findings must be taken within the context of other factors that have strong effects to overall abundance, such as fishing mortality and recruitment. Decreased recruitment survival has also been associated with increasing temperature (ICES WGNSK, 2018). This work has taken care to remove the influence of these confounding factors on overall population size by focusing on post-recruitment dynamics in distribution as influenced by thermal habitat changes. In this section, we draw attention to the complexity of the ecosystem cod inhabits and briefly discuss how climate change directly and indirectly affects cod through aspects other than thermal suitability, such as pre-recruitment dynamics. Note, however, that this topic is beyond the scope of this study and, thus, only a short overview can be given.

Several studies (O’Brien et al., 2000; Olsen et al., 2011; Akimova et al., 2016), have shown a negative relationship between water temperature and cod recruitment in the North Sea. Cod seems to need relatively low temperatures to spawn: During a tagging experiment, Righton et al. (2010) found preferred temperatures of around 6.02°C (± 1.09) during spawning season (late

winter–early spring) in the southern North Sea and 7.56°C (± 0.48) in the northern North Sea, while a peak in abundance for spawning cod in the North Sea was identified for low temperatures, ranging between 5 and 7°C (González-Irusta and Wright, 2016). Based on the results of the Southern Bight, which showed interannual variability in the use of spawning grounds, González-Irusta and Wright (2016) imply an active avoidance of spawning grounds with winter temperatures $>8^\circ\text{C}$ for cod. In line with this notion, Nicolas *et al.* (2014) pointed out that the redistributions of adult cod in the North Sea (due to shifts of its thermal suitable habitat) could possibly lead to local failures in recruitment. They further argue that, considering that environmental temperature will continue to rise in the North Sea, the impact of temperature would further reduce the cod stock regardless of any management measure. It is important to reiterate that these observed optimal temperatures are likely to be associated with optimizing recruitment success rather than habitat suitability for the spawning cod themselves.

Climate change may evoke different responses of species, which influence their survival rate and abundance of the stock (Kingsolver *et al.*, 2009). A change of distribution in time and space may lead to a mismatch between prey and predator, which in turn affects the connectivity and therefore the ecosystem in its vulnerability and resilience (Hollowed *et al.*, 2013). Butzin and Pörtner (2016) imply that cod in the southern North Sea is already at the edge of its thermal window, limiting oxygen uptake in higher temperatures. To adapt to higher temperatures, especially in summer, cod would need to adjust their thermal window by adjusting their oxygen supply capacity and therefore their aerobic metabolism (Pörtner and Knust, 2007). Perhaps as a consequence of this limitation, and the time required for such adaptation to occur, North Sea cod has been observed over decades to be limited in its distribution by a relatively constant summer thermocline threshold, as shown by this study.

Summarizing, while the rising temperatures can have an overall positive impact on the thermal habitat of North Sea cod, they can also lead simultaneously to a general decrease in the total fish abundance because of differing physiological constraints during specific processes, such as spawning, or during specific life stages, i.e. larvae. Further modelling considering all effects of temperature on North Sea cod is needed to obtain a profound understanding of the complete consequences of climate change on cod. Such understanding is indispensable for adapting management to the effects of climate change.

Summary and conclusions

Previous studies have identified changes in habitat temperature as a major factor for a geographical displacement of North Sea cod in the last decades. However, none of those studies has quantified the impact of temperature on this displacement in a spatially resolved manner at scales smaller than 100 km (Nicolas *et al.*, 2014). In this study, the spatial distribution of different life stages of cod was modelled from 1967 to 2015. The model was fit point-to-point with realistic past temperature changes spatially resolved at scales of 20 km. The results (Figure 6a–c) show that, following observed temperature increases in the North Sea from 1967 to 2015, suitability has decreased south of 56°N ($>12\%$ in the Southern Bight) and increased north of it (with maximum of roughly 10% in southern Skagerrak). Because our study considers density-dependent effects associated with overall changes in population size [through the term $a(Y) \cdot s_{R2}(\text{lon}, \text{lat})$; see Equations

(5) and (8)], our results indicate that the decadal displacement of North Sea cod can be explained with temperature changes alone. However, the density-dependent use of habitat (Figure 5) indicates that population decline would have been perceived stronger in the Southern Bight than in Skagerrak, giving the impression of an eastward displacement of habitat. This notion is in partial agreement with Engelhard *et al.* (2014) who attribute an eastward displacement of cod mostly to fishery.

Future changes to suitability were estimated throughout the century using temperature projections from a regional climate model under the most pessimistic IPCC scenario (RCP8.5). The projection (Figure 6d–f) shows further suitability decrease south of 56°N and increase north of 56°N, with exception of east of Scotland where suitability is predicted to decrease. An additional 15% decrease in suitability is projected for the Southern Bight and an additional 10% in southern Skagerrak. Together with the latter region, the central, and northern North Sea, as well as the edge of the Norwegian trench, will most probably remain thermally suitable for North Sea cod throughout the century in spite of strong temperature increase due to climate change.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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