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Original Article

Spawning grounds of Atlantic cod (*Gadus morhua*) in the North Sea

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The protection of spawning fish from anthropogenic impacts requires information on the location, timing, and interannual persistence of spawning aggregations. In this study, generalized additive models were used to predict the spawning habitat of North Sea cod, based on the abundance of spawning fish within three population subareas and nine environmental layers. The length of spawning cod differed among population subareas, consistent with published evidence of maturation differences. In the northeast North Sea (Viking), the peak in the spawning season was estimated to occur after the survey which made the prediction of spawning grounds for this area less certain. Cod were found to prefer areas with temperatures around 5–7°C for spawning and there was a general preference for high salinity waters. Persistence of cod spawning grounds over the study period was related to interannual stability in temperature, with high variability in the use of Southern Bight spawning grounds. As such, cod appear to minimize interannual variability in the initial environmental conditions affecting offspring survival by selecting suitable cold spawning grounds. Seabed conditions also affected spawning distribution with cod selecting coarse sand and avoiding areas of very high tidal flow. The model prediction was compared with the distribution of cod aggregations during the spawning season reported by fishing boats. Seventy per cent of the aggregations was located in areas classified as occasional or recurrent spawning grounds. The predicted distribution confirmed the widespread occurrence of spawning in the North Sea and showed good agreement with recent and past studies of cod egg distribution, suggesting that nearly all major historical areas of spawning still appear in use today. However, the study also found that the recent recovery of spawning-stock biomass was not uniform across the stock, being centred in the northwest subarea.

Keywords: *Gadus morhua*, GAM, SDM, spawning grounds, thermal preference.

Introduction

Knowledge of the occurrence and persistence of spawning grounds is becoming increasingly important to help minimize human impacts on fish stocks. Species, which aggregate to spawn in specific areas and return there over many years, can be vulnerable to excessive fishing pressure (Van Overzee and Rinsdorp, 2014) and other types of human activity ranging from seismic surveys to marine developments (Stelzenmüller *et al.*, 2010). Loss of spawning grounds may impact recruitment since having multiple sites where eggs are released should help mitigate the effects of local mortality and promote favourable egg and larval transport (Smedbol and Stephenson, 2001). Re-colonization of extirpated spawning grounds may take many generations, as inexperienced recruits appear to learn the routes to grounds by following older experienced individuals (Ames, 2004). Consequently, many countries have introduced legislation to reduce anthropogenic impacts during the spawning season and avoid the destruction of such essential fish habitat, e.g. the US Magnuson-Stevens Act and EU Marine Strategy Framework Directive. To comply with this legislation, managers need advice on the location, timing, and interannual persistence of spawning aggregations.

Understanding where and when spawning takes place requires consideration of both the environmental and population processes affecting reproductive development and choice of spawning location. Spatial distribution models (SDMs) have been widely used to consider environmental influences on species distribution (Elith and Leathwick, 2009). However, population conditions, such as demographic structure, migratory tendency, and historical expiration, are also important in understanding fish spawning distribution (Marteinsdottir *et al.*, 2000; Ames, 2004). Indeed, many studies have ignored potentially important evolutionary constraints on spawning distribution by focusing on the distribution of managed stocks, rather than the populations that comprise them. These evolutionary constraints relate to life-cycle connectivity, social structure, and reproductive and larval physiology (Ciannelli *et al.*, 2015), which ultimately will determine the relevant scale of environmental influence on the choice of spawning habitat.

Atlantic cod (*Gadus morhua*) is a species known to aggregate over specific grounds to spawn (Nordeide and Folstad, 2000; Windle and Rose, 2007; Dean *et al.*, 2014). Cod aggregate on a spawning arena where males hold small territories in a lek-like mating system (Windle and Rose, 2007; Dean *et al.*, 2014). This aggregative behaviour together with seasonal site fidelity (Skjæraasen *et al.*, 2011) makes cod, especially vulnerable to anthropogenic impacts. Impacts that alter the nature of spawning ground, such as aggregate extraction and marine developments, pose a permanent threat to cod spawning areas (Stelzenmüller *et al.*, 2010). Fishing has also been shown to impact spawning cod in several ways. Catch rates on spawning cod are typically substantially greater during spawning than at other times of year leading to high fishing mortality (Hislop, 1986). Fishing disrupts shoals of spawning cod with the passage of a single trawl being detectable for more than an hour after it has passed (Morgan *et al.*, 1999), and spawning shoals can be trawled on hundreds of occasions during a season (Kulka *et al.*, 1995). Disturbance within the male arenas may interfere with mate choice because hierarchies break-up and dominant males may be selectively removed (Rowe and Hutchings, 2003) and stressed males initiate fewer courtships (Morgan *et al.*, 1999). Noise might interfere with male courtship calls, affecting female mating decisions and reproductive success (Slabbekoorn *et al.*, 2010). This sensitivity to anthropogenic impacts has led to a range of measures to protect spawning cod including permanent, seasonal, and rolling closures (Needle and Catarino, 2011; Armstrong *et al.*, 2013).

Spawning fidelity in Atlantic cod has been linked with both resident and migratory populations. In the North Sea, there is clear evidence of two populations, one inhabiting the deep northeast North Sea and the other shallower waters, based on genetic differentiation (Heath *et al.*, 2014) and the limited movements among life stages of cod (Wright *et al.*, 2006a, b; Heath *et al.*, 2008; Neat *et al.*, 2014). In addition, the scale of juvenile and adult fidelity indicated from non-genetic methods suggests an even finer scale of population structuring (Figure 1), with little exchange between the southern and northwest North Sea (Wright *et al.*, 2006a, b; Righton *et al.*, 2007). Cod from these regions exhibit different maturation schedules with the northeast North Sea (centred on Viking Bank) cod currently maturing at older ages and larger size (Yoneda and Wright, 2004; Wright *et al.*, 2011). Due to differences in geographical distribution, the annual temperature and depth range that individuals experience differ substantially among these populations (Righton *et al.*, 2010; Neat *et al.*, 2014).

Cod spawning areas in the North Sea have mainly been identified from the distribution of eggs (Brander, 1994; Heath *et al.*, 1994; Fox *et al.*, 2008; Lelievre *et al.*, 2014), whereas the presence of "running" adults (i.e. fish with a gonad maturity stage classified as "spawning") has rarely been used (Graham, 1934). However, as eggs can be rapidly dispersed away from spawning grounds, there is a problem in obtaining precise estimates of spawning location based on this life-stage as grounds are discrete, often being just a few square kilometres in area (Grabowski *et al.*, 2012; Dean *et al.*, 2014). Hence, the ability to relate the precise location of spawning with environmental variables is an important constraint on developing reliable SDMs. Therefore, SDMs based on spawning adult distribution are likely to more fully account for environmental influences on distribution than those based on eggs, and for this reason we consider the distribution of "running" adults. Cod spawning times can generally be linked to the onset of primary production, favouring a match between larval hatching and prey availability (Brander, 1994). Across the North Sea spawning has been reported to extend from January to April (Brander, 1994; Morgan *et al.*, 2013). Annual ICES international bottom trawl surveys (IBTS) conducted in the earlier part of this period sample for age and maturity in many species, including cod (ICES, 2012). A synoptic North Sea egg survey in 2004 found that the highest density of eggs did not correspond to the main concentration of mature cod in the IBTS (Fox *et al.*, 2008), which may have been linked to regional differences in spawning time.

In this study, we use a general additive model (GAM) framework to model the spatio-temporal spawning distribution of North Sea cod in relation to possible physical constraints and to consider interannual persistence in the period 2009–2014. The ability of the model to predict spawning distribution was considered by comparing estimates of spawning persistence with the location of real time cod closures. Possible differences in the fish size and timing of spawning among populations were examined by assigning all data records to population subarea. By this means, we determine the environmental constraints in the three subareas and examine whether there have been differences in the recent rate of recovery.

Material and methods

Biological data

The abundance of cod in spawning stage (CSS) was derived from ICES DATRAS (DAtabase of TRAwl Surveys, http://ices.dk/marine-data/data-portals/Pages/DATRAS.aspx) data from the North Sea International Bottom Trawl Survey (NS-IBTS) for quarter 1. The timing of this survey covers much of the spawning period of cod (Brander, 1994; Morgan *et al.*, 2013). The NS-IBTS survey is based on a stratified random design in which the North Sea is divided into statistical rectangles of size 1° longitude × 0.5° latitude. This survey involves eight different countries (France, Germany, Scotland, England, Netherlands, Sweden, Denmark, and Norway), and ideally for each statistical rectangle two hauls are taken by different countries and separated by at least 10 Nm (Figure 1; ICES, 2012). The study period was restricted to 2009–2014 as years before 2008 had a different maturity staging protocol for gadoids (ICES, 2007), which had an effect on the abundance of cod in stage III (spawning) in some countries and CTD coverage in 2008 was incomplete. According to the last updated ICES protocol, the maturity stage was defined using external signs (like gonad colour or texture) and the presence of semen in the spermatoduct for males (ICES, 2012). Length stratified samples of at least 10 individuals per 1 cm length class were routinely taken for age and maturity analysis from all ICES demersal areas. However, during the period of this study, >90% of the total catch of cod was sampled for maturity which allowed us to estimate the percentage of each maturity stage for each length and haul, then calculate the abundance of CSS with a high level of confidence. Once the percentage of each maturity stage for each length class in each haul was estimated, the abundance of CSS by haul (CSS_r) was calculated according to:

$$\mathrm{CSS}_r = \sum_{\mathrm{Length}(i)=1}^{\mathrm{Length}(n)} (\text{Proportion of CSS}\quad\text{of length } (i) \times \text{Abundance of cod of length } (i)). \qquad (1)$$

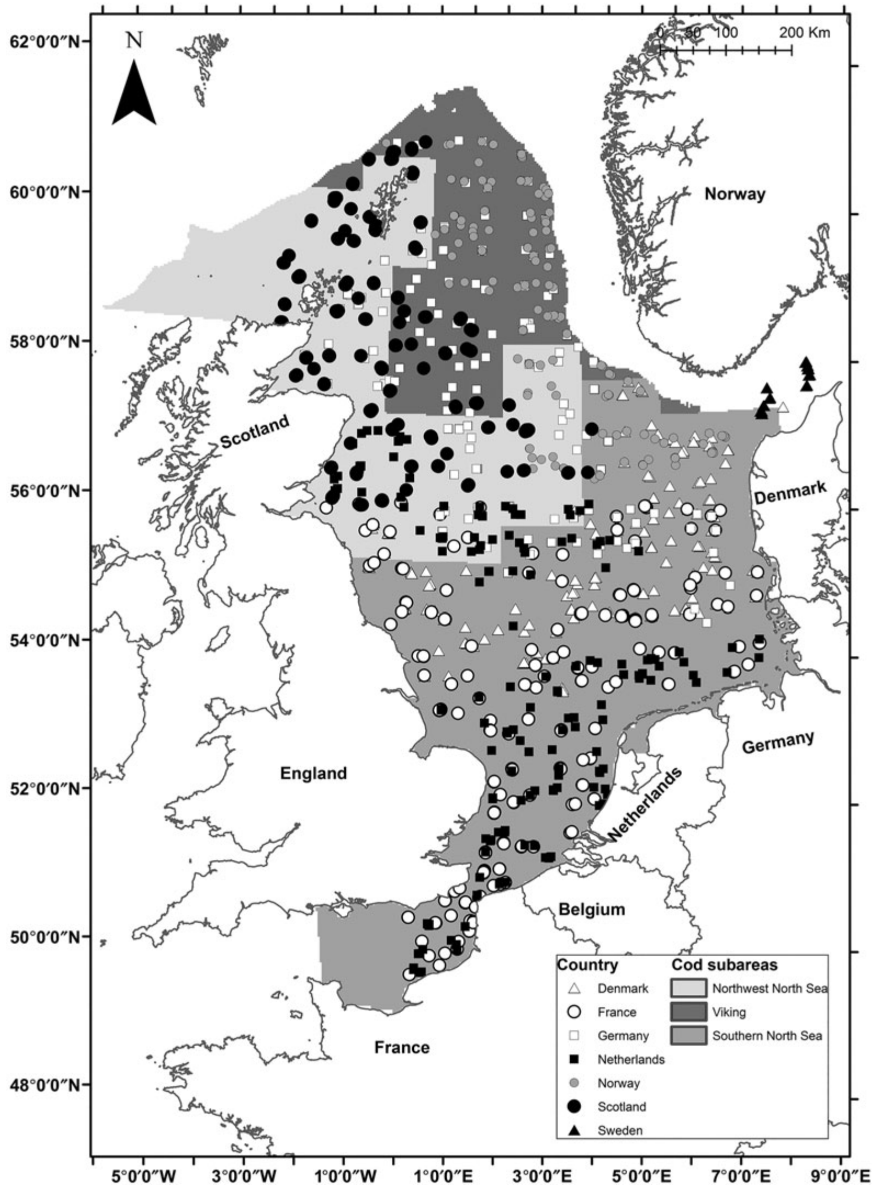

Figure 1. Distribution of hauls by country across the North Sea during the study period (2009–2014). The three studied cod subareas are shown in the figure.

The location of the hauls was estimated using the mean point between the shoot and haul position. This mean point was later used to extract the value of the environmental layers used for analysis. As hauls covered ~2 Nm (30 min average haul duration at an average speed of 4 knots), we can infer that the incidence of spawning can be estimated within a precision of one nautical mile (1.852 km). Only hauls with at least one cod caught were included.

Environmental layers

The temporally invariant environmental data layers were constructed in ArcGIS 10.0 for bathymetry, slope, distance to coast, springtide, sediment type, and cod spawning subareas. Annual layers for near bottom temperature and salinity were constructed in R 3.0.3. (R Development Core Team, 2014; Supplementary Figure S1). Taking into consideration the resolution of all the contributing variables and the location errors inherent in the abundance data, all layers were calculated for a final resolution of 3 × 3 km or resampled to this resolution using the bilinear resampling algorithm. To construct the bathymetry layer, we used data from the General Bathymetric Chart of the Oceans (GEBCO, http://www.gebco.net) and data supplied to Marine Scotland Science (OceanWise, 2014). The processed bathymetry layer was then used to produce the slope layer using the ArcGIS Spatial Analyst tool "slope". Distance to coast was computed using the ArcGIS Spatial Analyst tool, "Euclidean distance". This variable was included in the analysis to consider the preference of cod for coastal waters regardless of salinity or depth. Temperature and salinity near bottom were calculated using CTD data downloaded from the ICES Oceanographic database. This database covers all the North Sea with a minimum of 364 CTD stations in any year. For each CTD profile, the deepest value of temperature and salinity was extracted. The near bottom temperature and salinity values were then interpolated using drift kriging (with depth as a covariate) using the implementation fit.gstatModel from the "GSIF" package (Hengl, 2014). The sediment data were downloaded from the European Marine Observation and Data Network (EMODNET, www.emodnet-geology.eu). Springtide was calculated by combining the tidal current east-velocity and north-velocity components. This variable was included since it reflects the dispersal potential for eggs and is a key factor determining seabed characteristics (e.g. sediment type and oxygenation). The original tidal constituent data were from the Oregon State University Tidal Prediction model (Egbert *et al.*, 1994). For the seabed sediments, the existing substrate classifications were translated to a scheme that was supported by EUNIS, the European Nature Information System (EMODNET, 2012). The EMODNET reclassification scheme consists of four substrate classes defined on the basis of the modified Folk triangle; mud and sandy mud (e.g. <1% of the sediment was coarser than 2 mm, and at least 20.1% of the sediment was finer than 0.0625 mm) sand and muddy sand, coarse sediment, mixed sediment, and two additional substrate classes; diamicton and rock. As diamicton contains particles ranging from clay to boulders, suspended in a matrix of mud or sand, this sediment was reclassified as mixed sediment. Hard substrate areas were not included in the model since this kind of bottom is unavailable for the gears used in the surveys (otter trawl). Finally, given the evidence of cod populations—northeast (Viking), south and northwest—a new layer was generated with the borders used by Holmes *et al.* (2014) to define subareas of the North Sea. As the environmental conditions of the three subareas that these population inhabit differs (Righton *et al.*, 2010; Neat *et al.*, 2014), we considered whether distributional responses to environmental constraints were common to all populations or differed, which might suggest local adaptation.

Data analysis

The analysis of the abundance of CSS in the North Sea was especially complex as a consequence of the observed differences in the spawning timing and abundance among the three cod subareas. Differences among subareas in spawning fish length (stratified into 10 cm classes) and proportion of CSS by calendar day (pooled into fortnightly intervals) were analysed using a Kruskal–Wallis test and the Nemenyi *post hoc* test (Zar, 1999). Proportion rather than abundance of CSS was used since it is independent of the total number of cod (in any maturity stage) and therefore allows a clearer comparison of any maturity differences among subareas. The abundance of CSS across the North Sea was modelled using GAMs, using the implementation gam in the package "mgcv" (Wood, 2011). This technique is particularly suited for these analyses since the responses were not normally distributed and there are not necessarily linear or monotonic relationships between the response and the explanatory variables. Moreover, GAMs have been successfully used in similar studies (Hedger *et al.*, 2004; Loots *et al.*, 2011; Höffle *et al.*, 2014) and performed well when compared with other available techniques (González-Irusta *et al.*, 2015). The abundance of CSS was calculated for 30 min of trawling rounded to the nearest integer and modelled using a Poisson GAM with log-link function. Before starting the analysis, the correlation between the explanatory variables was checked for colinearity using Spearman rank correlations and variance inflation factors (VIFs; Zuur *et al.*, 2009). Spearman rank values were lower than 0.5 and the VIFs lower than 3, so all the variables were included in the model. There was evidence of slight overdispersion in the standard errors, which was corrected by applying a quasi-Poisson model, where variance is given by the dispersion parameter multiplied by the mean (Zuur *et al.*, 2009). To avoid overfitting, all the smoothers were constrained to 4 knots. Moreover, to avoid edge effects, the analysed range of some of the variables has been reduced by removing extreme values (Supplementary Table S1). The full model was:

$$\begin{aligned}\mathrm{CSS}_p = {} & \beta 1 + s1(\text{springtide}) + s2(\text{calendar day, by} = f\,(\text{cod subareas}))\\ & + s3(\text{depth}) + f\,(\text{year}) * f\,(\text{cod subareas}) + f\,(\text{sediment type})\\ & + s4(\text{temperature}) + s5(\text{salinity}) + s6(\text{distance to coast})\\ & + s7(\text{slope}) + \varepsilon,\end{aligned}$$

where CSS_p is the predicted abundance of CSS, $\beta 1$ is the intercept, s is an isotropic smoothing function (thin plate regression splines), f indicates the variables which were included as factors in the formula and ε is the error term. The observed differences among cod subareas in the spawning season were analysed in the model testing the adequacy of fitting a different smooth for each subarea. Moreover, differences in the annual evolution of CSS_p between cod subareas were investigated by testing the adequacy of including the interaction term between year and cod subareas. The inclusion of variables (or interactions) in the model was analysed using a backwards/forwards stepwise process. Since the Akaike Information Criterion and Bayesian Information Criterion were not available for quasi-Poisson models, the generalized cross validation (GCV) values and model deviances (using ANOVA F-test) were used. The different tested models, GCV scores, explained deviance, residual deviance, and the p-values of the ANOVA F-test are given in Supplementary Table S1. The relative importance of each variable was tested by removing the targeted variable from the final model and computing the deviance variation.

The spatial autocorrelation of residuals was analysed for each year separately using the variogram implementation in the gstat package (Pebesma, 2004) and the Moran's I test, computed using the R implementation Moran.I in the package "ape" (Paradis *et al.*, 2004). The semi-variance of the residuals did not show any trend with distance in any year and, although the Moran's I statistic was significantly different ($p < 0.01$) from the expected value in 2010 and 2013, it was close to 0 in both cases (0.06 and 0.04, respectively), indicating that the level of spatial autocorrelation was practically nil. The statistical model was then applied to the GIS layers to generate maps for each year of CSS_p. Each map was computed using the median survey date (7 February) about the annual temperature and salinity layer (Supplementary Figure S1) and applying year and subarea-specific coefficients. To analyse the year-to-year persistence of the different spawning grounds, we applied the methodology used by Lelievre *et al.* (2014). These authors set egg density predictions within the range between 0 and 1 (for four different years) and calculated the mean and standard deviation in each pixel for all years combined. Finally, they combined both these metrics to identify four categories of spawning areas: (i) *recurrent* (high mean abundance values but low standard deviation), (ii) *occasional* (high mean abundance values and high standard deviation), (iii) *rare* (low mean abundance values but high standard deviation), and (iv) *unfavourable* (low mean abundance values and low standard deviation). As CSS_p was fixed for a given date, differences in spawning times among subareas will influence this estimate. Similarly, interannual variation in total cod abundance will also influence this estimate. Therefore, to reduce the effect of these sources of temporal bias for identifying key spawning locations, we also ranged each annual map to values between 0 and 1 separately for each cod subarea.

To evaluate the model, we have used independent data from the distribution of real time closures [RTCs; see Needle and Catarino

(2011)]. Unfortunately, due to the restricted region where these were applied, data were only available for two of the three subareas modelled (northwest North Sea and Viking subareas). The distribution of past RTCs, chosen on the basis of substantial cod aggregations located by fishing boats, reflects the distribution of important cod aggregations. The distribution of the RTCs (based on centroids) during the spawning period (January–March) for the years 2009–2014 was compared with the model prediction. The percentage of these centroids in each category of spawning area (unfavourable, rare, occasional, and recurrent) was then calculated.

Results

Differences in the length of spawning cod among subareas was apparent, especially among Viking and the other two subareas (Figure 2a). Viking cod spawned at a larger length than in the other two subareas. The proportion of CSS in Viking was therefore significantly less than in the other two subareas (northwest North Sea and southern North Sea; $\chi^2 = 1124.9$, d.f. $= 2$, $p < 0.001$) and for all length classes except the largest (>90 cm). Indeed, the proportion of CSS only exceeded 0.1 at lengths $\geq$70 cm in Viking, whereas in the other two subareas this threshold was exceeded at $\geq$40 cm. The proportion of CSS also differed significantly with time when categorized into fortnightly intervals ($\chi^2 = 48.0$, d.f. $= 3$, $p < 0.001$; Figure 2b). CSS was present in the southern North Sea earlier than in the other two subareas. From 20 January, the proportion of CSS increased in all three subareas, but peaked earlier in the southern North Sea than the northwest. The proportion of CSS then declined from 20 February to 7 March in the southern North Sea while that in Viking increased.

Of the 10 variables analysed, only slope was not subsequently included in the final model. Calendar day was nested by subarea, and the interaction between year and cod subarea was included in the model since that significantly improved the deviance explained by the model (Supplementary Table S1). Differences in the spawning cycle among subareas led to a significant effect of calendar day on CSS_p in the northwest and southern North Sea, but not in Viking (Table 1), consistent with the observed changes described from Figure 2b. There was a positive influence of salinity (Figure 3b) and very strong tidal currents (i.e. >1.1 m s^{-1}) were a significant constraint on CSS_p (Figure 3c). CSS_p tended to decline at depths >125 m, but was practically constant over the range 20–125 m (Figure 3d). Distance to coast had a negative and linear effect on CSS_p, with highest abundance of CSS in areas close to the coast (Figure 3e). Finally, the relationship between temperature and the CSS_p was negative for values >5°C (Figure 3f).

Sediment type had a significant effect on CSS_p (Table 1), with coarse sand being a preferred spawning substrate compared with mud or sand (Figure 4a). There was significant interannual variation of CSS_p for all the subareas combined, with the lowest abundance in 2009 and a peak in the last 3 years of the study (Figure 4b). However, this trend was significantly different between the southern and northwest North Sea, generating significant differences in the interaction between year and subareas in 2012 and 2013 (Figure 4d).

Year was the most important variable in the final model (Table 2), especially when the interaction with cod subareas was included. Calendar day explained the second most deviance, but only when it was included in the model nested within cod subarea. Salinity and springtide were the third and fourth most important variables respectively (with a similar impact on the deviance), and after this sediment type, temperature, and depth (the last two explained similar levels of deviance). Distance to coast had the least effect.

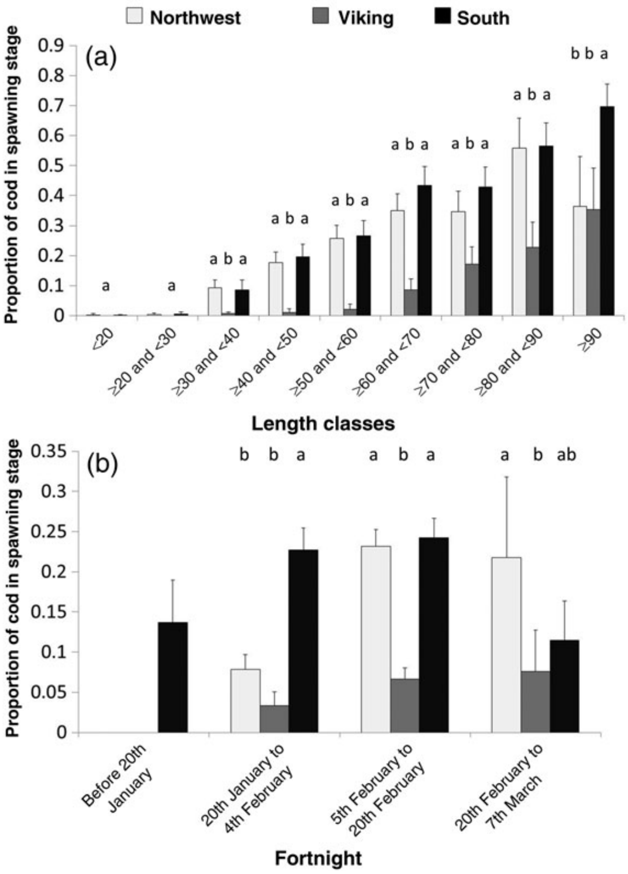

Figure 2. Variation in the proportion of CSS in the three studied cod subareas. (a) Proportion of CSS by length class. (b) Proportion of CSS by fortnight. The differences between cod subareas were analysed inside each group using the Nemenyi *post hoc* test and significant differences between them labelled with a letter, a (higher value), b or c in a decreasing order. The label ab was used in levels with no significant difference with any of the other two levels (which were significantly different between them).

The abundance of CSS by haul (CSS_r) showed a different distribution in the North Sea across the studied period. During the first year, most hauls with higher abundance were located in the southern North Sea, whereas by the end of the studied period (especially in 2012 and 2013), most were located in the northwest (Supplementary Figure S2). This change in the distribution of CSS_r (which is responsible for the significant differences in the interaction between year and subarea) is also apparent in the maps of predicted abundance (CSS_p, Figure 5a). In the first year, the highest values of CSS_p were located mainly in the southern North Sea (Dogger Bank, Norfolk Bank, Southern Bight, and coastal waters of Netherlands and Denmark), whereas the abundance in the other two areas was lower (except the coastal waters southwest of Shetland). During 2010 and 2011 the predicted abundance in the southern and northwest North Sea was similar and, as a consequence, the border between these subareas was not evident. Finally, in 2012 and 2013, the predicted abundance in the northwest North Sea was higher than in the other two subareas, and the spawning grounds with the highest CSS_p values were all located in this subarea. After ranging the CSS_p values within subareas, it appears that Viking contains extensive spawning areas, except in the northern part and the Fladen grounds. This had an important effect in the mean reclassification values

Table 1. GAM results.

		N	Spearman coefficient	Explained deviance
Model: abundance $\sim \beta_1 + s_1$(springtide) $+ s_2$(calendar day, by $= f$(cod subareas)) $+ s_3$(depth) $+ f$(year) $* f$(cod subareas) $+ f$(sediment type) $+ s_4$(temperature) $+ s_5$(salinity) $+ s_6$(distance to coast) $+ \varepsilon$		1189	0.36	29.6%
Parametric terms		d.f.	F	p-value
Sediment type		3	7.87	<0.001
Year		5	6.27	<0.001
Cod areas		2	2.72	0.06
Year * cod areas		10	2.2	0.016
Approximate significance of smooth terms	e.d.f.	Ref. d.f.	F	p-value
Springtide	2.86	2.98	6.87	<0.001
Salinity near bottom	1.38	1.66	13.02	<0.001
Distance to coast	1	1	7.68	0.006
Temperature near bottom	1.79	2.20	7.03	<0.001
Calendar day for northwest North Sea	2.11	2.53	13.83	<0.001
Calendar day for Viking	1.49	1.81	1.27	0.27
Calendar day for southern North Sea	1.97	2.38	3.19	0.03
Depth	2.91	2.99	4.95	0.002

Summary result from the final model selected using a backward/forward stepwise process and Spearman correlation coefficient between CSS_r and CSS_p. e.d.f., estimated degrees of freedom.

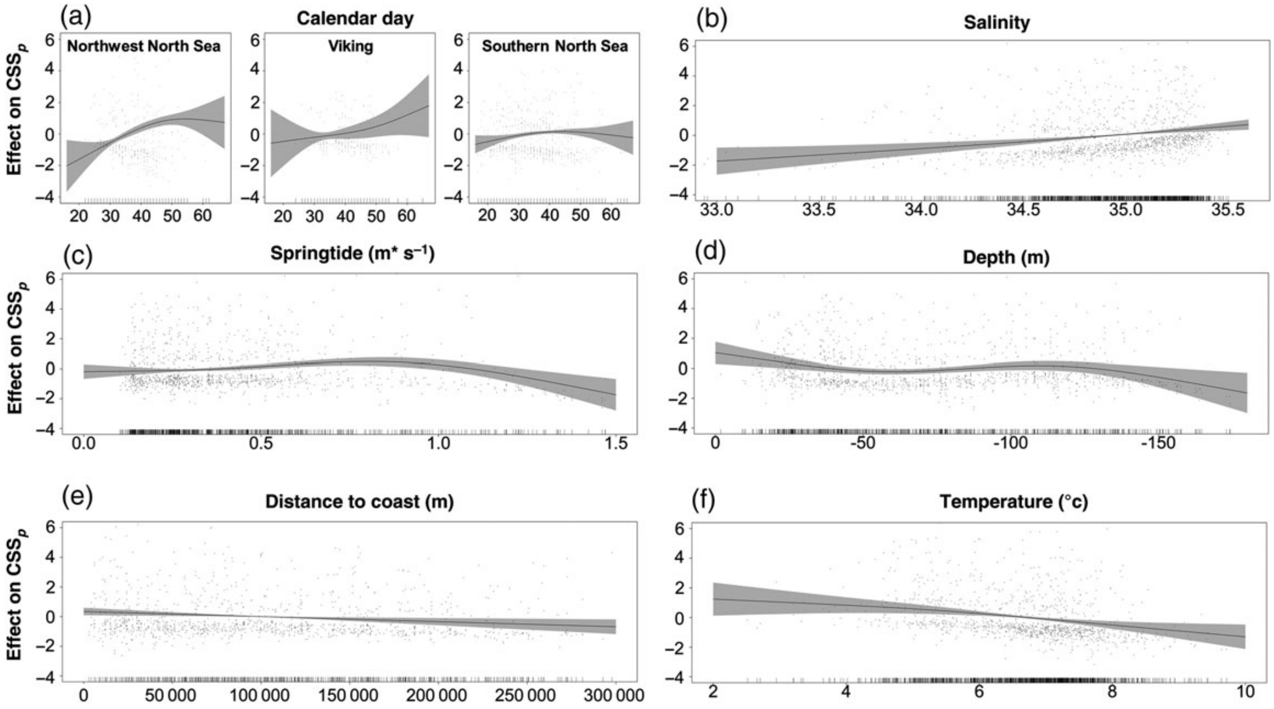

Figure 3. Effect on the predicted abundance of CSS (CSS_p) of the continuous explanatory variables. (a) Calendar day, (b) salinity near bottom, (c) springtide (m s^{-1}), (d) Depth (m), (e) distance to coast (m), and (f) temperature (°C). The smooth terms were calculated separately for each cod subarea for calendar day. The shaded area represents the nominal confidence intervals (95%). The points are the residuals.

(Figure 6a), which are also high in a large part of Viking subarea. In general, mean values were high in all coarse sand and mix sediment areas (Supplementary Figure S1), such as in the waters between Orkney and Shetland or Norfolk Bank. The standard deviation (Figure 6b) was also high in the coarse sand and mix sediment areas, as well as near the Fladen ground, areas of the English Channel and Southern Bight, and in the coastal waters of German and south of Denmark. The spawning area classification map (Figure 6c) shows an extensive area of the central North Sea as unfavourable. The deeper part of the Fladen grounds, some areas in the English Channel and the northern part of the study area, also appeared unfavourable. There were few areas classified as rare, such as in parts of the Fladen ground, east of Dogger Bank, and German Bight. The largest recurrent areas were located in the northern North Sea and Viking, with some small patches in the southern North Sea. Practically, all the coastal waters of the continental Europe and Britain (except German Bight

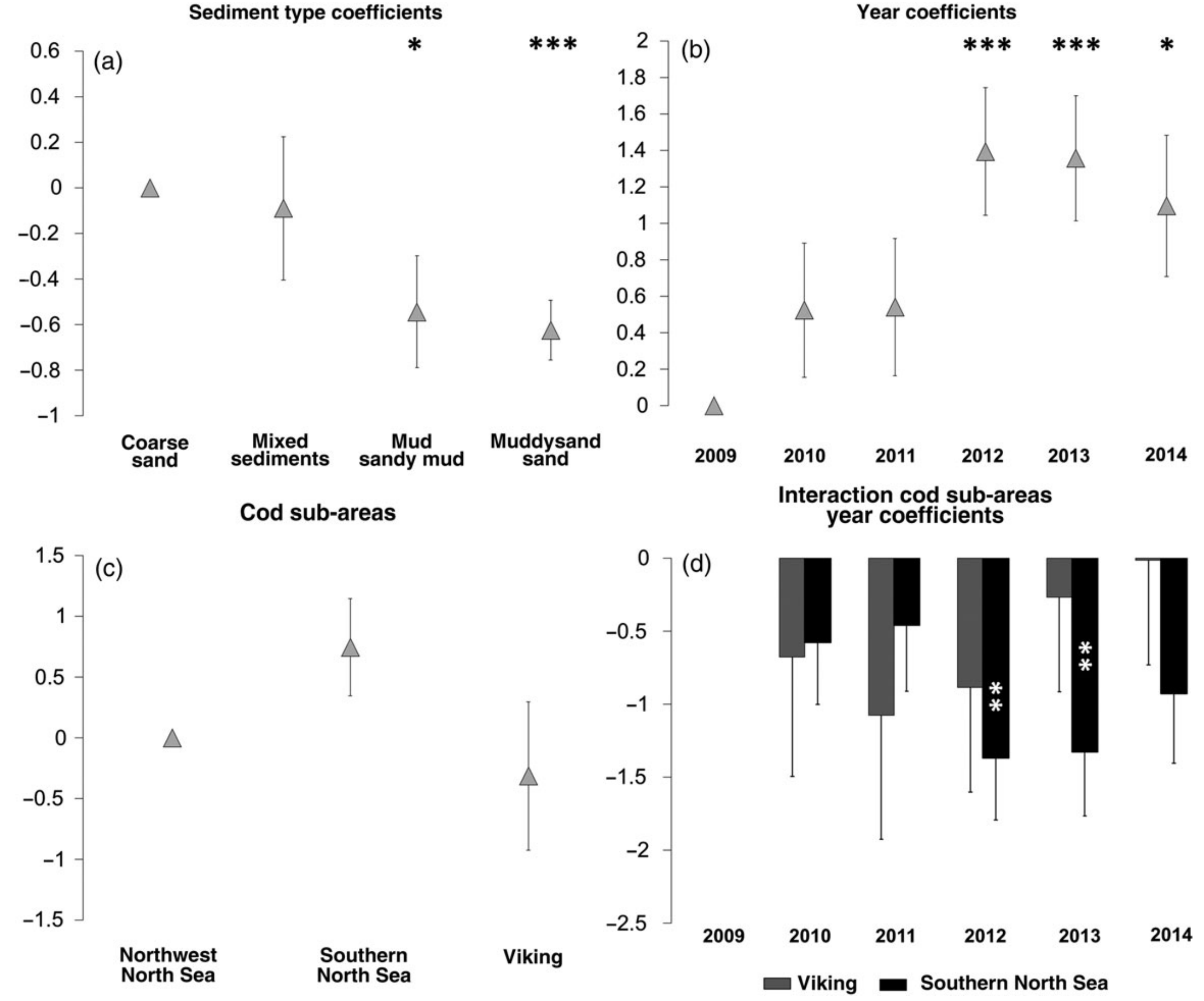

Figure 4. Coefficients values for the different levels of the explanatory variables included as factors in the model: (a) sediment type, (b) year, (c) cod subareas, and (d) interaction between year and cod subareas. The value of the interaction coefficient compared CSS_p trend in Viking and the southern North Sea with an observed trend in the northwest. Since we are comparing a trend, there were no data in the first year. The error bars show the standard deviation for each coefficient. *$p < 0.05$, **$p < 0.001$, ***$p < 0.0001$.

Table 2. Variable importance.

Variable	Δ Deviance
Year * cod subarea	147.51
Day in the year by cod subarea	120.09
Year	119.67
Salinity	58.11
Springtide	57.94
Day in the year	51.35
Sediment type	48.29
Temperature	36.70
Depth	36.15
Distance to coast	20.34

Deviance variation in the final model after eliminate the variable. The explanatory variables are sorted in a decreasing order.

and east of Dogger Bank) were classified as occasional spawning grounds as well as the shallower parts of the Norwegian trench and a large part of Viking.

The GAM model explained 29.6% of the total deviance and the value of the Spearman coefficient used to measure the correlation between the predicted and the observed values was 0.36 (Table 1). The distribution of the centroids of the RTCs and the spawning habitat type map showed good agreement (Figure 7), with most of the centroids located in areas classified as recurrent (17%) or occasional (53%). Only a 30% of the centroids were located in areas classified as rare (8%) or unfavourable (22%).

Discussion

The present study used GAMs to define the spawning habitat of cod, based on cod spawning abundance (CSS_r) and a set of environmental variables and population differences. This allowed us to examine the annual fluctuations in habitat use and identify areas that are likely to be important to protect. Moreover, we were able to identify the main environmental conditions influencing spawning habitat selection in the three subareas. The two most important variables (year and calendar day) exhibited population differences,

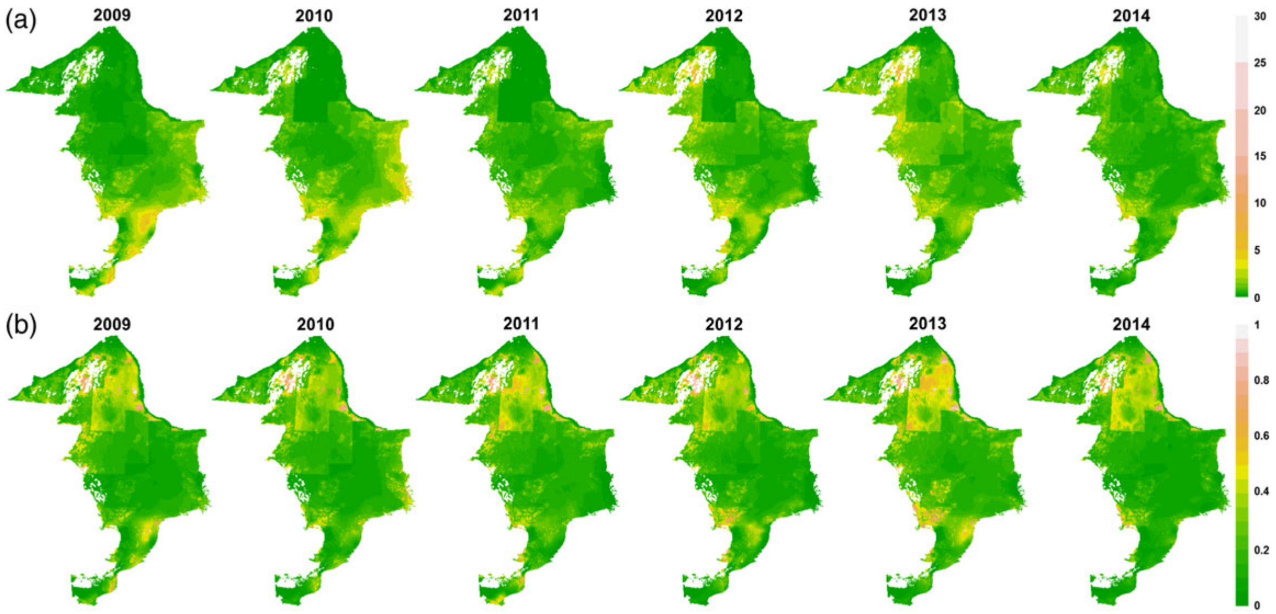

Figure 5. Annual maps from 2009 to 2014 with (a) CSS$_p$ and (b) ranged CSS$_p$ values. The CSS$_p$ inside each subarea were ranged to values between 0 and 1. This was done separately for each subarea every year.

highlighting the importance of including population structure in the distribution models. The model performance was compared with two recent studies which used a range of GLMs and GAMs to predict cod spawning distribution from early stage eggs. While not large, the deviance explained by our model (29.6%) was higher than a similar analysis of early cod egg distribution reported by Höffle *et al.* (2014). In addition, the Spearman rank's correlation in our model ($\rho = 0.36$) was also slightly higher than the value obtained by Lelievre *et al.* (2014) in their delta model describing cod egg distribution. While the present study made no account of possible density-dependent effects that might be expected to affect cod distribution (Tamdrari *et al.*, 2010), the North Sea spawning-stock biomass has only just recovered to B_{lim} (ICES, 2015) and so such effects are unlikely to have been significant during the study period.

Differences in length and timing of spawning among subareas were important to the calculation of CSS$_r$ and, therefore, for CSS$_p$ as well. Although fish length was not included in the model as an explanatory variable, the proportion of CSS by length was used in the estimation of CSS$_r$ [see Equation (1)]. The difference in length at spawning among population subareas was consistent with previous evidence of changing maturation schedules in some North Sea regions (Wright *et al.*, 2011). The downward shift in the maturation reaction norm of northwest and southern cod between the 1980s and 2000s explains why such small spawning individuals were found in these subareas in recent years when compared with both historical records and present day Viking cod (Yoneda and Wright, 2004; Wright *et al.*, 2011). This subarea difference in length at spawning has important consequences to management both in the estimation of spawning biomass for the North Sea stock (ICES, 2015) and the identification of a size threshold relevant to seasonal spawning closures.

The relationship between CSS$_p$ and calendar day differed among subareas. The latitudinal difference in the onset of spawning found in this study is consistent with that previously reported by Brander (1994). Peak spawning abundance was associated with low temperatures, with the earliest spawning cod being detected in the cold southern North Sea. Because of the regional differences in cooling rates linked to depth and the influence of Atlantic water, the Viking subarea is much warmer in January and February than the southern North Sea (Berx and Hughes, 2009). The predicted abundance of CSS in Viking did not show a significant relationship with calendar day and the proportion of CSS was lower than in the other two areas during the whole study period, probably because much of the spawning season occurs after the survey. This could explain why a comparison of egg and mature cod density during the 2004 IBTS showed little correspondence in the Viking subarea, in contrast to the other subareas (Fox *et al.*, 2008). It also highlights that there is likely to be greater uncertainty over predicted spawning distribution in Viking because the subarea is not surveyed around the peak in spawning time.

According to our model, cod prefer areas with temperatures around 5–7°C for spawning, which agrees with individual results on the thermal niche of cod during the spawning season obtained using electronic tags (Righton *et al.*, 2010). However, whether this reflects a proximal response to temperature is unclear as vitellogenesis in cod begins after the autumn equinox and is positively related to temperature (Kjesbu *et al.*, 2010). Hence, the warmer autumn months experienced by cod in the southern North Sea will allow earlier spawning the following year compared with the northern North Sea. However, interannual differences in the use of the spawning grounds in the Southern Bight are suggestive of an active avoidance of waters $\geq$8°C.

Although cod eggs may develop across a salinity range of 28–36‰ (Laurence and Rogers, 1976), the present and previous studies in the North Sea have found a preference for higher salinity waters (Lelievre *et al.*, 2014). Hence, although there was a tendency to spawn close to the coast, this was only in areas without a high freshwater input. Consistent with Munk *et al.* (2002, 2009), high spawning abundance was found around recurrent salinity fronts. These fronts present favourable feeding conditions and the related physical processes may confine egg and larval dispersal and transport them towards suitable nursery habitats (Munk *et al.* 2002,

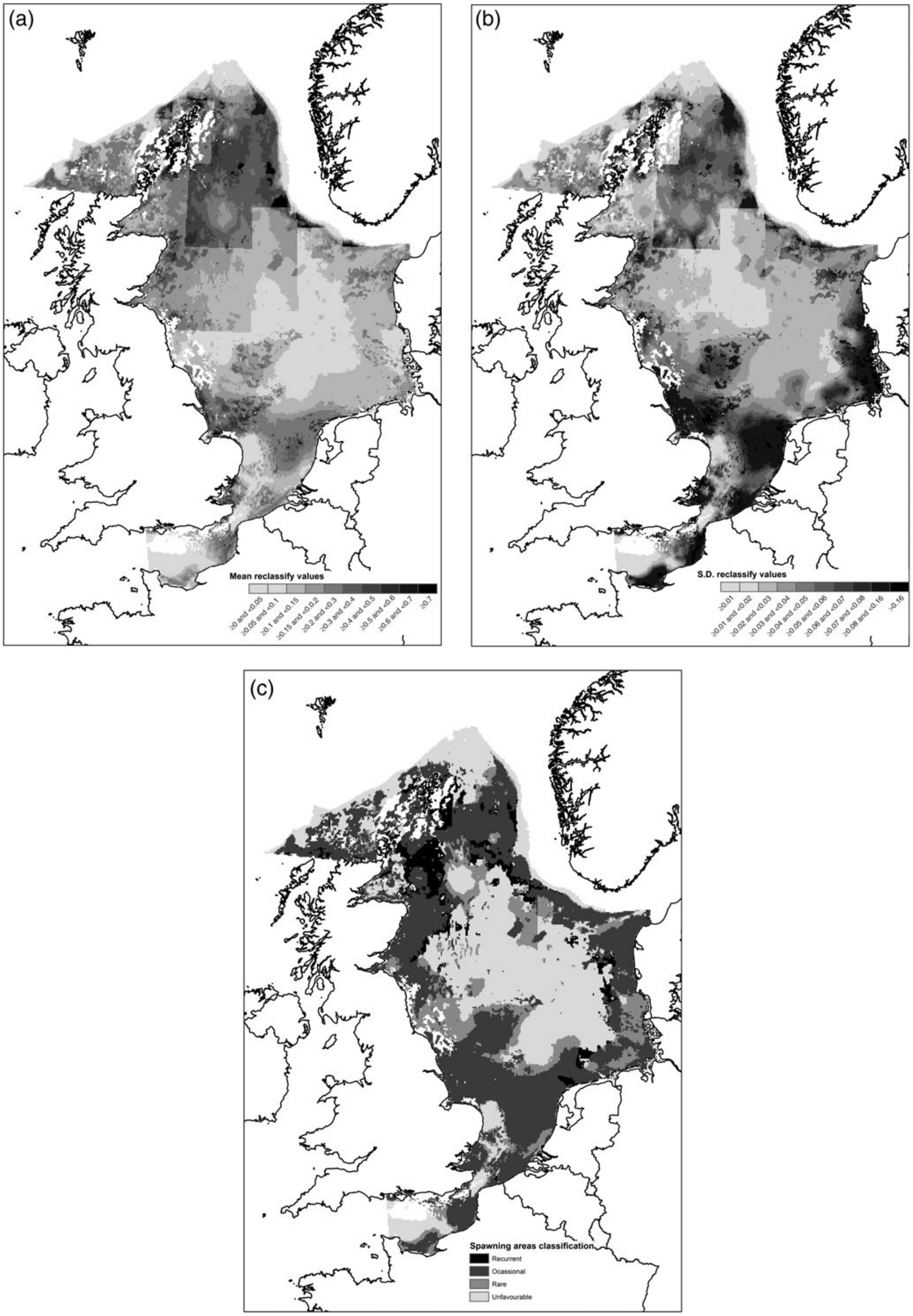

Figure 6. Maps of average (a), variability (b), and spawning habitat type (c) for the studied period.

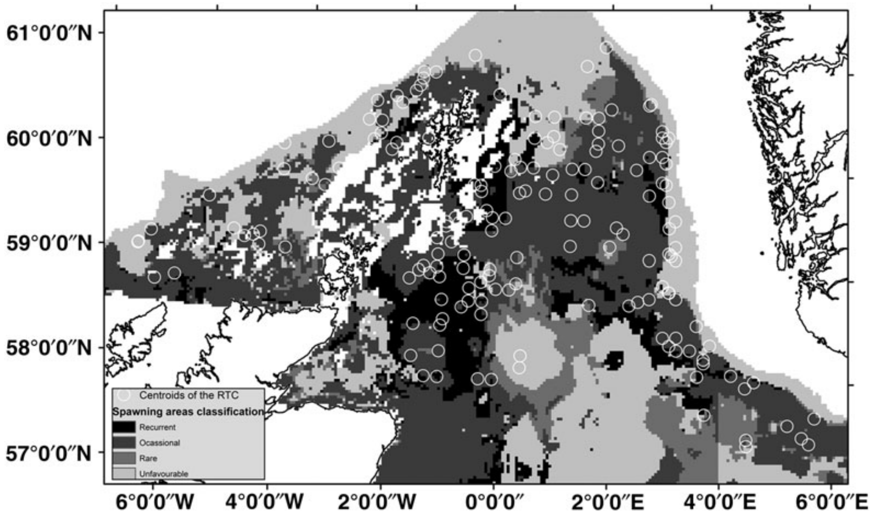

Figure 7. Comparison of the RTC centroid distribution with the spawning area classification in the northwest and Viking subareas. Of the 181 RTC areas established in the winter months between 2009 and 2014, 40 (22%) of centroids were located in unfavourable spawning areas, 14 (8%) in rare spawning areas, 97 (53%) in occasional spawning areas, and 30 (17%) in recurrent spawning areas.

2009). The limited movements of many coastal cod aggregations in the North Sea (Wright *et al.* 2006a, b; Righton *et al.*, 2007; Neat *et al.*, 2014) may explain why spawning abundance was highest close to the coast. While cod egg density has been found to be negatively related to depth in some other North Sea studies (e.g. Lelievre *et al.*, 2014), this factor had little influence over the range of 0–125 m in the present study. This difference between studies probably reflects the study area as Lelievre *et al.* (2014) only surveyed the southern and central North Sea, the latter being relatively devoid of eggs. In their analysis of mature cod across the North Sea, Hedger *et al.* (2004) found peaks in abundance in both shallow and deep areas down to 260 m. As spawning abundance was found to decline rapidly beyond 125 m in the present study, it appears that mature cod residing in deeper waters may move up onto shallower banks to spawn. Similar depth migrations looking for more suitable temperature ranges have been observed in different ecosystems for cod using electronic tags (Righton *et al.*, 2010; Neat *et al.*, 2014).

There was clear evidence that seabed conditions affected spawning cod distribution, as might be expected from a species that has a lekking-type behaviour (Nordeide and Folstad, 2000; Windle and Rose, 2007). As also found by Lelievre *et al.* (2014), areas of current flow >1.1 m s^{-1} were a constraint on spawning, leading to cod avoiding areas such as the Dover strait, off Norfolk, and waters south of Orkney. Although this effect is mainly restricted to areas with very high tidal flow, it was very clear, and springtide was the fourth most important explanatory variable. However, in contrast to Lelievre *et al.* (2014), spawning cod tended to prefer coarse sand areas. This is consistent with direct observations of spawning arenas in Icelandic and North American waters (Grabowski *et al.*, 2012; Dean *et al.* 2014). Similarly, in the North Sea, Graham (1934) did not find any spawning cod in the muddy Fladen Grounds, although there were nearby grounds to the southeast and southwest.

Subarea differences in the persistent use of cod spawning grounds could be explained by the level of interannual variability in salinity and temperature. For the northwest North Sea and Viking, these physical influences were largely stable but far greater variability was seen in the southern North Sea, especially in some areas of the English Channel and German coastal waters. In the Southern Bight, this seems to be linked to Atlantic inflow via the English Channel with years of low inflow, e.g. 2009, 2010 having near bottom temperatures of around 5°C compared with 8°C or more in years of high inflow, e.g. 2014. This increase in temperature appeared to markedly reduce the suitable area for spawning in 2014. A similar effect can be seen in the study by Lelievre *et al.* (2014) for the year 2008. Hence, spawning cod appear to avoid warm waters or some other characteristic of the warmer water mass.

The relation between temperature and predicted abundance of CSS is especially interesting in the context of climate change. In the North Sea, cod recruitment for a given spawning-stock biomass tends to be negatively related to temperature (O'Brien *et al.*, 1999). This relationship may arise both as a direct effect, since temperatures >9.6°C affect early cod survival under laboratory conditions (van der Meeren and Ivannikov, 2006) and indirectly through effects on the match of offspring with prey conditions (Cushing, 1990). However, the present study indicates that cod can minimize interannual variability in the initial environmental conditions affecting egg and possibly larval development by selecting suitably cold spawning grounds. This means that it is not accurate to infer temperature exposure of early cod life stages from the average temperature of the North Sea or even the subareas used in this study. Many studies have often made such a simplifying assumption in trying to correlate early survival with environmental conditions (e.g. Nicolas *et al.*, 2014). The present study therefore identifies the need to more accurately model the environmental conditions that early stages are exposed too. Indeed, by changing spawning location in response to temperature, this response to warm waters may have a greater effect on early dispersal than on developmental rate.

The predicted distribution of spawning cod confirmed the widespread occurrence of spawning in the North Sea as reported by a recent North Sea wide egg survey (Fox *et al.*, 2008) and showed good agreement with past studies of cod egg distribution (Brander, 1994; Heath *et al.*, 1994). Brander's (1994) study of cod egg distribution around Britain included the three subareas considered in our model. In all these subareas, there was good agreement between high egg density in surveys back to 1968 and the areas with high mean values in our model. Similarly, there was good agreement with the model of average cod egg distribution for the southern North Sea by Lelievre *et al.* (2014), especially in the English Channel. Both models showed similar distribution of mean values except for the two mud areas located in the German Bight and for the central North Sea. Historical areas of spawning cod reported by Graham (1934) west and north of Dogger Bank, and to the southeast and west of the Fladen Ground also largely match the present model. Hence, despite the near collapse of North Sea cod stock, all major historical areas of spawning still appear in use today.

The rapid increase in the abundance of CSS in the northwest North Sea since 2011, at a time when little change was seen in the southern North Sea, indicates that the rate of recovery of SSB is not homogenous across the North Sea. This finding is consistent with longer term trends in SSB among the three subareas (Holmes *et al.*, 2014). Such spatial variability in population dynamics is important to management because the imposition of measures, such as closed areas, varies regionally (Needle and Catarino, 2011) and there is considerable spatial variation in environmental conditions to which cod are exposed (Neat *et al.*, 2014). Consequently, the North Sea management unit is an inappropriate scale for considering the effectiveness of local scale measures and anthropogenic impacts.

The utility of the present study for spatial management measures will depend on the accuracy of predicted maps and the persistence of spawning grounds. The distribution of past RTCs, that were chosen based on substantial cod aggregations (Needle and Catarino, 2011), do indicate important aggregations during spawning time, although will include non-spawning cod. Importantly, our model identifies most areas which do not have substantial cod aggregations and conversely finds a high degree of overlap between RTCs and predicted persistent and occasional spawning grounds. Consequently, the present model does provide managers with a tool to consider whether spawning cod should be a key concern for further investigation at a proposed site for development and similarly be a starting point for considering whether regular seasonal closures may be appropriate.

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Supplementary data

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

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