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Spawning grounds of haddock (*Melanogrammus aeglefinus*) in the North Sea and West of Scotland

J.M. González-Irusta*, P.J. Wright

Marine Scotland Science, Marine Laboratory, 375 Victoria Road, Aberdeen AB119DB, UK

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ABSTRACT

The importance of physical constraints on the spawning distribution of northern shelf haddock was examined using a 2 stage generalized additive model applied to 1st quarter bottom trawl survey data from the North Sea and west of Scotland. In order to consider possible effects of biomass-dependent spatial dynamics on local density, geostatistical aggregation curves and the spaces selectivity index were computed. Local changes in abundance were proportional to changes in annual abundance and therefore density did not confound the estimate of the physical habitat preference of spawning haddock. Model performance was good, with AUC and Kappa values higher than the threshold for good performance and Pearson coefficient scores higher than previous studies of fish spawning distribution. An optimum temperature for spawning of 7 °C was evident for North Sea and west of Scotland regions. Spawning haddock preferred high salinity waters in the northern North Sea and shelf edge waters to the west of Scotland. They tended not to aggregate on mud-rich sediments, which was associated with a split in the main spawning areas between the east and west North Sea. The distribution of spawning haddock from this study indicated a shift in the spawning grounds compared to historic reports. By identifying the physical characteristics and persistent use of spawning grounds, the present study provides a guide for future marine developments and an aid to discussions about the utility of spawning closures.

1. Introduction

Knowledge of fish distribution is important for the development of spatial fisheries measures and marine spatial planning. Species that regularly aggregate to spawn are vulnerable to excessive fishing pressure (Van Overzee and Rijnsdorp, 2014) and other types of human activity ranging from seismic surveys to marine developments (Stelzenmuller et al., 2010). Loss of spawning grounds may reduce the resilience of stocks since having multiple sites would be expected to help mitigate the effects of local mortality on year-class strength (Smedbol and Stephenson, 2001). Recovery of spawning grounds may take many generations as inexperienced recruits appear to learn migration routes 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, including the US Magnuson-Stevens Act and technical measures under the EU Common Fishery Policy. In order to comply with this legislation managers need advice on the location and inter-annual persistence of spawning aggregations.

In modelling the distribution of a fish population it is important to account for both external constraints, such as environmental conditions and internal constraints, such as demographic structure, site fidelity and spatial density dependent processes (Planque et al., 2011). Distribution Models (DMs) provide a framework to consider environmental influences on species distribution (Elith and Leathwick, 2009). These models relate statistically the spatial distribution of a species to environmental variables, constructing a predicted distribution related to a species niche (Guisan and Zimmermann, 2000). However, relationships between species density and environmental conditions may be partially confounded by the local response of density to a population level change in abundance. According to ideal free distribution theory, individuals adopt a foraging strategy that maximizes their net energy intake per unit of time so only the best foraging habitats are occupied at low abundance but as abundance increases individuals start to occupy less optimal habitats due to intra specific competition (Fretwell and Lucas, 1969). Therefore, if fish do exhibit an ideal free response then local density may not reflect habitat suitability at high population abundance. Petitgas (1998) categorised possible distributional responses into four models of biomass-dependent spatial dynam-

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* Corresponding author.
E-mail address: gonzalezirusta@gmail.com (J.M. González-Irusta).

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ics. In the first two models the area occupied by fish remains constant but density either varies in sub-areas in response to local environment (D1) or density at each point remains a constant proportion of population abundance (D2), the latter dynamic corresponding to the “consistent spatial pattern” of Houghton (1987). In the third model, the area occupied by fish increases with population abundance whereas fish density remains constant (D3), which corresponds to the constant density model of Hilborn and Walters (1992). In the fourth model the area occupied as well as fish density vary with population abundance (D4). Hence local density does not change at the same rate as population abundance, and maximum density increases with abundance. This latter response corresponds to the “basin theory” of MacCall (1990). From these biomass-dependent spatial dynamic models we can therefore expect that physical habitat suitability should provide a reliable and independent index of local density when the population density response corresponds to D2 model, since this implies that the density at each point remains a constant proportion of the population abundance.

In this study we examine the spawning habitat of haddock (*Melanogrammus aeglefinus*), an important component of demersal fisheries in the North Atlantic. A decrease in occupied area at low stock abundance has been reported for juvenile haddock on the south-western Scotian Shelf (Marshall and Frank, 1995), although nothing is known about the density distributional responses of spawning haddock. Haddock are known to aggregate over specific grounds to spawn (Waiwood and Buzeta, 1989) and laboratory studies indicate they spawn in arenas where males call to females and hold small territories in a lek-like mating system (Casaretto et al., 2014). This aggregative behaviour makes haddock susceptible to anthropogenic impacts and measures to minimise fishing on spawning fish have included spawning closures (Halliday, 1988; Murawski et al., 2000).

ICES (2015) recently combined haddock from the North Sea (NS) and Scottish West Coast (SWC) into the northern shelf stock since there is evidence for exchange of larvae (Heath and Gallego, 1998) and juveniles (Wright et al., 2010) and similar stock trends (Holmes et al., 2014) between these two regions. Despite the importance of this stock, there is little known about the spawning grounds. Information on the location of spawning in this stock has been inferred from the historic occurrence of mature or spawning adults (Schmidt, 1909; Thomson, 1924; Thompson, 1928; Tormosova, 1980) and egg surveys (Damas, 1909; Saville, 1959; Heath et al., 1994; Munk et al., 2009), although only in a 2004 synoptic egg survey was it possible to differentiate between newly spawned stage I haddock eggs and those from Atlantic cod and whiting (Taylor et al., 2002). Based on these studies, spawning appears to extend over much of the north and central part of the North Sea and to the west of the Hebrides (Thomson, 1924; Saville 1959; Heath et al., 1994). Based on the distribution of newly hatched eggs in 2004, depth and salinity appear to be influential factors on spawning distribution in the North Sea (Munk et al., 2009). Despite haddock mixing between the west NS and the SWC there appears to be little exchange between east and west of the Greenwich meridian based on both tag recapture evidence (Jones, 1959) and differences in transferrin allozyme frequency (Jamieson and Birley, 1989). Moreover, whilst haddock use to mostly mature at age 3 across the NS, there has been a significant reduction in the maturation reaction norm for size in the west NS over the last four decades with the result that most in that region now mature by age 2 (Wright et al., 2011). The present day difference in maturation size reaction norms of haddock between the east and west NS have been found to persist when juveniles are raised under a common environment indicating that these regional differences may reflect a local adaptation (Wright and Tobin, 2013). Whether these maturation differences and low rates of adult mixing reflect discontinuities in the spawning habitat is unknown.

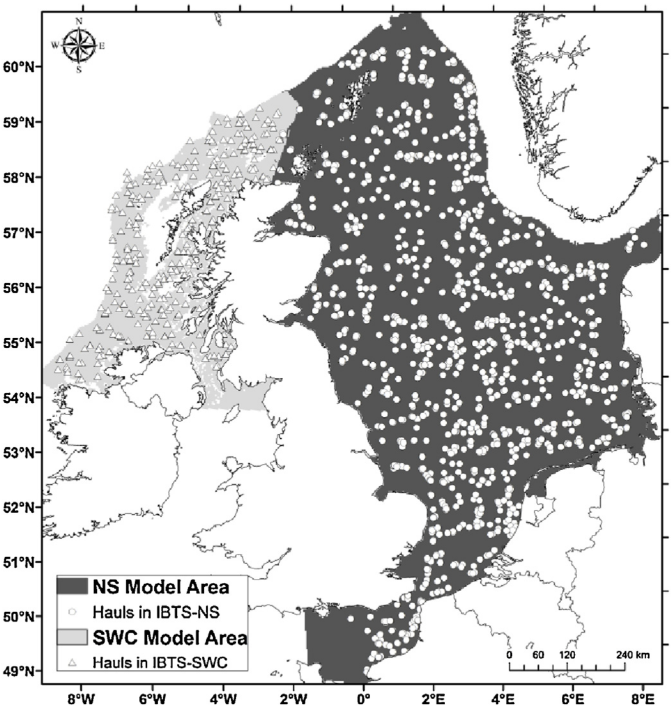

Fig. 1. Haul locations during the studied period (2009–2015) in the two surveyed regions; North Sea (NS, Dark grey) and the Scottish West Coast (SWC, Light grey).

In this study, we use a generalized additive model (GAM) framework to examine the spatio-temporal spawning distribution of northern shelf haddock in relation to possible physical constraints and to consider inter-annual persistence in the period 2009–2015. The study also examined whether there was geographical evidence for segregation of spawning grounds consistent with the apparent east–west differences in maturation in the North Sea (Wright et al., 2011; Wright and Tobin, 2013). In order to consider biomass-dependent spatial dynamics, geostatistical aggregation curves and the spaces selectivity index (Matheron, 1981; Petitgas, 1998) were used to establish the relevant dynamic model for spawning haddock.

2. Material and methods

2.1. Biological data

The abundance of Haddock in Spawning Stage (HSS) was derived from ICES DATRAS (DAtabase of TRAwl Surveys, http://ices.dk/marine-data/data-portals/Pages/DATRAS.aspx) from two surveys; the North Sea International Bottom Trawl Survey (NS-IBTS) and the Scottish West Coast Bottom Trawl Survey (SWC-IBTS). Both take place during the 1st quarter of the year and cover much of the spawning period of haddock (Wright and Gibb, 2005; Morgan et al., 2013). The NS-IBTS takes place in January-February whilst the SWC-IBTS is in February-March. Both surveys use a similar ICES rectangle (1° longitude × 0.5°latitude) based sampling strategy although the NS-IBTS involves eight different countries and includes two hauls per rectangle separated by at least 10 km for most ICES statistical rectangles (ICES, 2012), whilst only one haul per rectangle is carried out in the SWC-IBTS. The haul distribution of both surveys and the two modelled regions in the NS and the SWC are shown in Fig. 1. The study period was restricted to 2009–2015 as years prior to 2008 had a different maturity staging protocol for gadoids (ICES, 2007) and

CTD coverage in 2008 was incomplete in the NS. According to the last updated ICES protocol (ICES, 2012), the spawning stage was defined using external signs (e.g. light pressure on the abdomen releases eggs or milt). When the number of haddock caught was too high to allow an analysis of the whole sample, it was subsampled according to ICES protocols. 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. Once the percentage of each maturity stage for each length class in each haul was estimated, the abundance of HSS by haul (H_a) was calculated according to:

$$H_a = \sum_{\mathrm{Length}(i)=1}^{\mathrm{Length}(n)} (Proportion\ of\ HSS\ of\ Length\,(i) \times Abundance\ of\ haddock\ of\ Length\,(i)) \quad (1)$$

The location of the hauls was estimated using the mid-point between the shoot and haul position. This mid-point was later used to extract the parameter values for each of the environmental layers used in subsequent analysis. As hauls covered approximately 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 to within a precision of one nautical mile (1.852 km).

2.2. Density dependence

Geostatistical aggregation curves (Matheron, 1981; Petitgas, 1998), using hauls as the surface unit, and the spaces selectivity index (Ssp) were used to establish the type of spatial dynamics that haddock distribution follows for each modelled region (Tamdrari et al., 2010). Geostatistical aggregation curves were constructed representing the proportion of total biomass P (% of the total abundance of HSS) observed on each surface unit as a function of the proportion of space Z_t (% of the total number of hauls). A further explanation of the calculation of the geostatistical aggregation curves can be found in Petitgas (1998). Ssp was calculated according to Tamdrari et al. (2010):

$$Ssp = 2 \times \left[\sum_{i=1}^{n} \left(\frac{P(T)_{i+1} + P(T)_i}{2} \times \frac{T_{i+1} - T_i}{2} \right) - \sum_{i=1}^{n} \left(\frac{P(T)_{i+1} + P(T)_i}{2n} \times \frac{T_{i+1} - T_i}{2} \right) \right] \quad (2)$$

where n is the maximum number of hauls and P(T) is the maximum proportion of biomass accumulated in the proportion of hauls T. The Ssp index was calculated for each year and region separately. Finally, the significance of variations in the Ssp index between years was tested for each region using bootstrapping. In accordance with Petitgas (1998), the original dataset of each region (for all the years together) was randomly resampled 1000 times with replacement. The P(T) curves were then recalculated for the new dataset and the mean Ssp and 95% confidence intervals were computed using boot and boot.ci from the "boot" package in R (Canty and Ripley, 2014) and equation (2). If the annual Ssp value for a particular year was outside this confidence interval, the null hypothesis (no significant variation of Ssp among years) was rejected.

2.3. Environmental layers

The environmental data layers for the NS; depth, distance to coast, springtide, sediment type, temperature near bottom and salinity near bottom were those used in González-Irusta and Wright (2015). Distance to coast was included as previous studies in the North West Atlantic have indicated a preference for offshore spawning grounds (Scott, 1982; Waiwood and Buzeta, 1989). The 5 sediment classes were derived from EMODNET (2012) and comprised; mud—sandy mud (e.g. <1% coarser than 2 mm, and at least 20.1% <63 μm), sand—muddy sand, coarse sand, mixed sediment (including diamicton) and rock. Since rocky areas are not sampled in the IBTS, they were not included in the models. Using the same methodology and data sources, similar layers were constructed for the SWC and for 2015 since this year and this region were not included in González-Irusta and Wright (2015) (Supplementary Fig. S1 in the online version at DOI: 10.1016/j.fishres.2016.05.028). In addition, maximum temperature was calculated using monthly near bottom temperature data from the "European North west Shelf- Ocean Physics REANALYSIS from METOFFICE (1985–2012)" model, downloaded from www.myocean.eu. In each raster cell, the maximum monthly temperature value predicted by the model during the period January 2008–December 2012 was calculated and recorded in the final layer. Maximum temperature was included as a possible explanatory variable as Hiddink et al. (2005) reported that mature sized haddock did not occur in temperatures >13 °C in autumn and tag-recapture studies suggest that haddock have a limited home range (Jones, 1959).

2.4. Data analysis

The abundance of HSS across the NS and SWC was modelled separately using General Additive Models (GAMs) and the implementation gam in the package "mgcv" (Wood, 2011). Both regions were modelled separately since they were sampled with slightly different methodologies and had different survey times. Since the data were zero inflated in both regions, the abundance distribution was modelled using a two steps approach (Barry and Welsh, 2002). Two step models have been recommended for modelling the abundance distribution in zero inflated data (Zuur et al., 2009) and have been successfully applied in similar studies (Lelievre et al., 2014; Grüss et al., 2014). First the probability of presence of HSS (hauls with at least one HSS) was modelled using a binomial GAM. Then, the abundance of HSS (calculated for 30 min of trawling rounded to the nearest integer and removing the zeros) was modelled using a negative binomial GAM. We used a negative binomial instead of a log transformation of the count data following the recommendation of O'Hara and Kotze (2010) for count data with a large dispersion such as seen in the abundance of HSS data. Finally, both models were combined (delta GAM, see below). Logit and log were used as link functions in both regions for the binomial and negative binomial models respectively. Before starting the analysis, the correlation between the explanatory variables was checked for colinearity using Spearman rank correlations and Variance Inflation Factors (VIFs) for each region separately (Zuur et al., 2009).

In the NS, the maximum temperature and depth were correlated (rho = 0.72, p-value < 0.001). Thus, depth was removed from the binomial GAM in this region. In the SWC we removed the annual maximum temperature rather than depth since, contrary to that observed in the NS, there was no apparent southern limit to haddock spawning distribution. Moreover, in this region it was necessary to remove salinity since that was correlated with depth (rho = 0.83, p-value < 0.001) as well. After these changes, the VIFs were lower than 3 in both regions so all the other variables were included in the models. To avoid overfitting all the smoothers were constrained to 4 knots. This limitation reduced the potential complexity of the smoothers by limiting the maximum degrees of freedom of the smoothers to 3. The full binomial model for the NS (equation (3)) and the SWC (equation (4)) were:

$$P_p = \beta_1 + s(\mathrm{springtide}) + s(\mathrm{calendarday}) + f(\mathrm{year})$$

$$+\mathrm{f}(\mathrm{sedimenttype}) + \mathrm{s}(\mathrm{temperature}) + \mathrm{s}(\mathrm{salinity}) + \mathrm{s}(\mathrm{distancetocoast}) + \mathrm{s}(\mathrm{annualmaximumtemperature}) + \varepsilon_1 \quad (3)$$

$$\mathrm{P_p} = \beta_2 + \mathrm{s}(\mathrm{springtide}) + \mathrm{s}(\mathrm{calendarday}) + \mathrm{f}(\mathrm{year}) + \mathrm{f}(\mathrm{sedimenttype}) + \mathrm{s}(\mathrm{temperature}) + \mathrm{s}(\mathrm{distancetocoast}) + \mathrm{s}(\mathrm{depth}) + \varepsilon_1 \quad (4)$$

where $\mathrm{P_p}$ is the probability of presence of HSS, β is the intercept, s is an isotropic smoothing function (thin plate regression splines, one for each variable and model), f indicates the variables which were included as factors in the formula and ε is the error term. The full negative binomial model for the NS (equation (5)) and the SWC (equation (6)) were:

$$\mathrm{P_a} = \beta_3 + \mathrm{s}(\mathrm{springtide}) + \mathrm{s}(\mathrm{calendarday}) + \mathrm{f}(\mathrm{year}) + \mathrm{f}(\mathrm{sedimenttype}) + \mathrm{s}(\mathrm{temperature}) + \mathrm{s}(\mathrm{salinity}) + \mathrm{s}(\mathrm{distancetocoast}) + \mathrm{s}(\mathrm{depth}) + \varepsilon_3 \quad (5)$$

$$\mathrm{P_a} = \beta_4 + \mathrm{s}(\mathrm{springtide}) + \mathrm{s}(\mathrm{calendarday}) + \mathrm{f}(\mathrm{year}) + \mathrm{f}(\mathrm{sedimenttype}) + \mathrm{s}(\mathrm{temperature}) + \mathrm{s}(\mathrm{distancetocoast}) + \mathrm{s}(\mathrm{depth}) + \varepsilon_4 \quad (6)$$

where $\mathrm{P_a}$ is the predicted abundance of HSS. Selection of explanatory variables for each model was carried out using a backwards/forwards stepwise selection process based on the Akaike's Information Criteria (AIC). 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 and model separately using the variogram implementation in the gstat package (Pebesma, 2004). The semi-variance of the residuals did not show any trend with distance in any year for any model and therefore the spatial autocorrelation in the residuals was considered nil.

2.5. Combining and evaluating the models

The statistical models were then applied to the GIS layers to generate annual maps of $\mathrm{P_p}$ and $\mathrm{P_a}$ for each region. For the time-related variables (calendar day and year) the maps were computed using the mean calendar day of each survey (7 February in the NS-IBTS and 3 March in the SWC-IBTS) and the corresponding year coefficient. The $\mathrm{P_p}$ maps were then multiplied with the $\mathrm{P_a}$ maps to produce the final delta models. The accuracy of the models was tested using cross-validation. The data for each region were randomly divided into a training subsample (with 67% of the total points) and a test subsample (with the other 33%). The ability of the training subsample to predict the probability of presence was tested using the area under the curve (AUC) of the receiver operating characteristic (ROC, Fielding and Bell, 1997) and the kappa statistic (Cohen, 1960). The AUC varies between 0 and 1. Values higher than 0.9 are considered excellent whereas values between 0.9 and 0.7 indicate good prediction. Values lower than 0.7 indicate poor prediction (Hosmer and Lemeshow, 2000). The kappa statistic ranges from −1 to 1, with values higher than 0.75 indicating excellent prediction and values between 0.4 and 0.75 indicating good prediction (Landis and Koch, 1977). A more complete description of these statistics can be found in Fielding and Bell (1997). The correlation of the observed and predicted abundance values was tested using the spearman coefficient for both abundance and delta models.

The process was repeated 10 times for each region, based on different random selections of training and test subsamples. The statistics were calculated using the implementation evaluate in the R package 'dismo' and 'Kappa' in 'SDMTools'. The AUC values and kappa values were compared using a Welch's *t*-test with the threshold for good performance (0.7 and 0.4, respectively). The delta maps of each year and region were rescaled to values from 0 to 1 (Supplementary Fig. S3 in the online version at DOI: 10.1016/j.fishres.2016.05.028) and the mean and standard deviation in each raster cell for all the years combined calculated (Lelievre et al., 2014).

To evaluate the models performance in accounting for changes in abundance, the year effect coefficient for the North Sea region was correlated with Spawning Stock Biomass (SSB; ICES, 2015). As the assessment SSB ignores mature age 2 haddock unlike our study, the age 2 SSB for each year was obtained from:

$$SSB\ age2 = N_2 \times W_2 \times M_2$$

where N_2 and W_2 were numbers and mean weight at age 2 from the assessment (ICES, 2015) and M_2 was the proportion mature at age 2 derived from IBTS SMALK data. This biomass of mature age 2 haddock was then added to the SSB given in the assessment report before comparing with year coefficients. As the coefficients are relative to the first year analysed (2009), we computed the differences between each year and 2009. These differences in the year coefficient were then compared with the SSB using a Pearson's correlation.

3. Results

The density curves showed important differences between regions but not among years (Fig. 2). There were denser aggregations of spawning haddock in the NS than in the SWC. In the NS, practically 100% of the total biomass was aggregated in only 25% of the hauls or less, compared with 60% of hauls in the SWC. The mean value for the Ssp in the NS calculated using bootstrapping was 0.98 (95% CI:0.93–1) whereas in the SWC, the mean value of the Ssp was 0.91(95% CI: 0.86–0.98). In both regions the Ssp for all the years was inside the correspondent confidence interval, and therefore, the null hypothesis of no significant variation of Ssp among years was accepted. The analysis of both aggregation curves and Ssp values indicates that the spatial dynamics of haddock during the studied years correspond to Dynamic D2; "consistent spatial pattern".

In the NS region all the variables of the binomial full model were kept in the final model, whereas in the SWC region only sediment type, depth, springtide and distance to coast were retained (Table 1). Therefore, from the 6 variables tested in the full model for both regions, only springtide, sediment type and distance to coast were included in both. Maximum temperature was the most important explanatory variable in the NS binomial model, with a delta deviance 5 times greater than the second most important variable, springtide (Table 1). There was little difference in the deviance explained between springtide and other significant explanatory variables. The timing of the surveys appeared appropriate to study of spawning as calendar day only showed a small positive impact on the probability of presence during the first survey weeks of the NS-IBTS (from calendar day 15–30, Fig. 3a), after which there was practically no effect. Depth was only included in the full model for the SWC. In this region a peak in the probability of presence in areas around 100 m depth was observed (Fig. 3b). There was an optimum springtide value in the NS, with a small but positive trend for values ranging from 0 to 0.5 $\mathrm{ms^{-1}}$ and a clear negative trend for higher

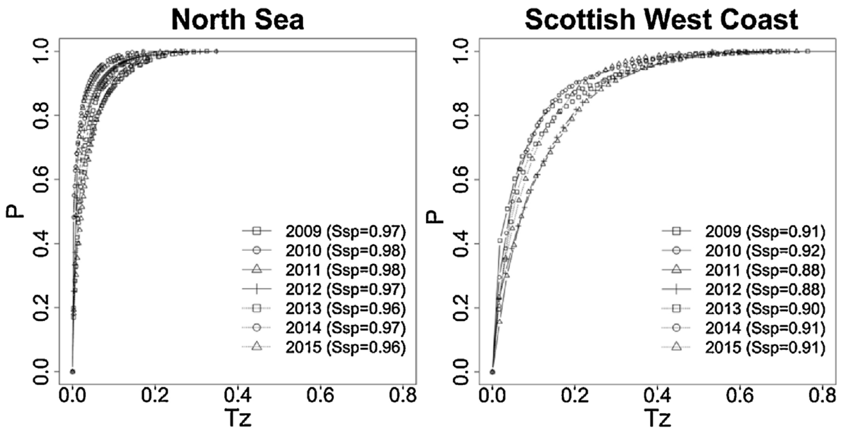

Fig. 2. Geostatistical aggregation curves and Ssp values for each year and surveyed region. The curves show the proportion of total biomass (P) per surface unit (T_z). Units for Tz and P are percent.

Table 1
Relative importance (Δ deviance), degrees of freedom (d.f.) or estimated degrees of freedom (e.d.f.) and statistical significance of the explanatory variables for the two binomial models (NS and SWC) and the two negative binomial models (NS and SWC).

	NS Model				SWC Model			
Binomial model	Δ deviance	d.f./e.d.f.	Chi-square	P-value	Δ deviance	d.f./e.d.f.	Chi-square	P-value
Sediment type	8.62	3	13.65	<0.001	8.87	3	12.63	0.005
Year	47.60	6	57.10	0.003	–	–	–	–
Temperature near bottom	28.43	2.98	58.43	<0.001	–	–	–	–
Salinity near bottom	16.24	2.03	6.39	0.046	–	–	–	–
Springtide	57.99	2.77	79.95	<0.001	26.34	2.15	17.91	<0.001
Calendar Day	20.35	2.64	21.02	0.001	–	–	–	–
Distance to coast	6.59	1.01	6.9	0.009	10.24	1.70	2.07	0.01
Max. Annual Temperature	318.85	2.59	31.96	<0.001	–	–	–	–
Depth	–	–	–	–	17.72	2.82	2.97	<0.001
Negative binomial model	Δ deviance	df/edf	Chi-square	P-value	Δ deviance	Df/edf	F	P-value
Sediment type	6.83	3	33.95	<0.001	3.19	3	20.33	<0.001
Year	9.65	6	34.48	<0.001	8.85	6	37.54	<0.001
Salinity near bottom	6.40	2.77	40.23	<0.001	–	–	–	–
Calendar Day	4.81	2.54	19.81	<0.001	4.64	2.83	26.14	<0.001
Temperature near bottom	3.76	2.73	15.63	0.0013	0.76	1.81	11.66	0.004
Distance to coast	7.03	2.83	39.36	<0.001	5.27	2.68	31.47	<0.001
Depth	–	–	–	–	3.45	2.38	11.94	0.006

values, although due to increasing uncertainty it was not possible to determine a trend for values $>0.9\,\text{ms}^{-1}$ (Fig. 3c). In the SWC the springtide had a negative effect for values $>0.5\,\text{ms}^{-1}$ (Fig. 3d). Distance to coast had a positive effect on the probability of presence in the SWC, whereas in the NS the effect was negative (Fig. 3f and e respectively). Sand and coarse sand were the sediments with the highest coefficients in the NS and the SWC (Fig. 3g and h respectively). In the NS, maximum temperature had a very strong and negative effect on the probability of presence for values higher than 14 °C, similar to the effect observed in this region for salinity values lower than 34.7 psu (Fig. 3i and j respectively). Near bottom temperature had a positive effect on the probability of presence for values ranging from 4 to 7.5 °C (Fig. 3k). Finally, the effect of year on the probability of presence for the NS was significant, with 2010 having a significantly lower coefficient than 2009 and that for 2012 being significantly higher (Fig. 3l).

The negative binomial model was similar for both regions. All the variables included in the initial model were selected in the SWC (salinity was not in the initial model in this region) whereas in the NS only depth was not included. The effect of the explanatory variables on the P_a is shown in Figs. 4 and 5. Springtide and distance to coast had a different effect on P_a in the SWC than in the NS (Figs. 4a–b and c–d, respectively). In the SWC, the springtide effect was linear and negative whereas in the NS the effect was positive from 0 to 0.4 and negative for higher values. Distance to coast had a positive effect for areas closer than 70 km in the SWC whereas in the NS this effect was slightly negative. The effect of this variable at distances further than 85 km from the shore was negative in both regions. The effect on P_a was positive for calendar days 20–40 and then negative after this value, with no effect for values between days 60–75 (Figs. 4e and f). The effect of calendar day during the time both regions were sampled (days 45–65) was negative in both models. Temperature had a positive trend between 5–7 °C and a negative trend for warmer temperatures in the NS (Fig. 4h). There was a negative trend for the SWC (Fig. 4g) but, as the temperature was >7 °C during the surveys of this region, this appears consistent with the NS response. Depth was only included in the SWC model and showed a negative effect on P_a for areas deeper than 100 m (Fig. 4i). Salinity was only included in the NS model with a peak in the effect on P_a for values around 35.1 psu (Fig. 4j). The sediment type showed a very similar effect on P_a in both regions except for mixed sediments. After excluding mixed sediments, mud had the lowest coefficient values in both regions (Fig. 5a and b). In the same way, the temporal evolution was also similar, with the lowest coefficient occurring in 2010, followed by an increase until reaching maximum values in 2012 after which it decreased. Differences in year coefficient from 2009 were significantly ($t = 3.23$, $df = 4$, $p\text{-value} = 0.032$) and positively related with SSB with a Pearson's correlation coefficient of 0.85.

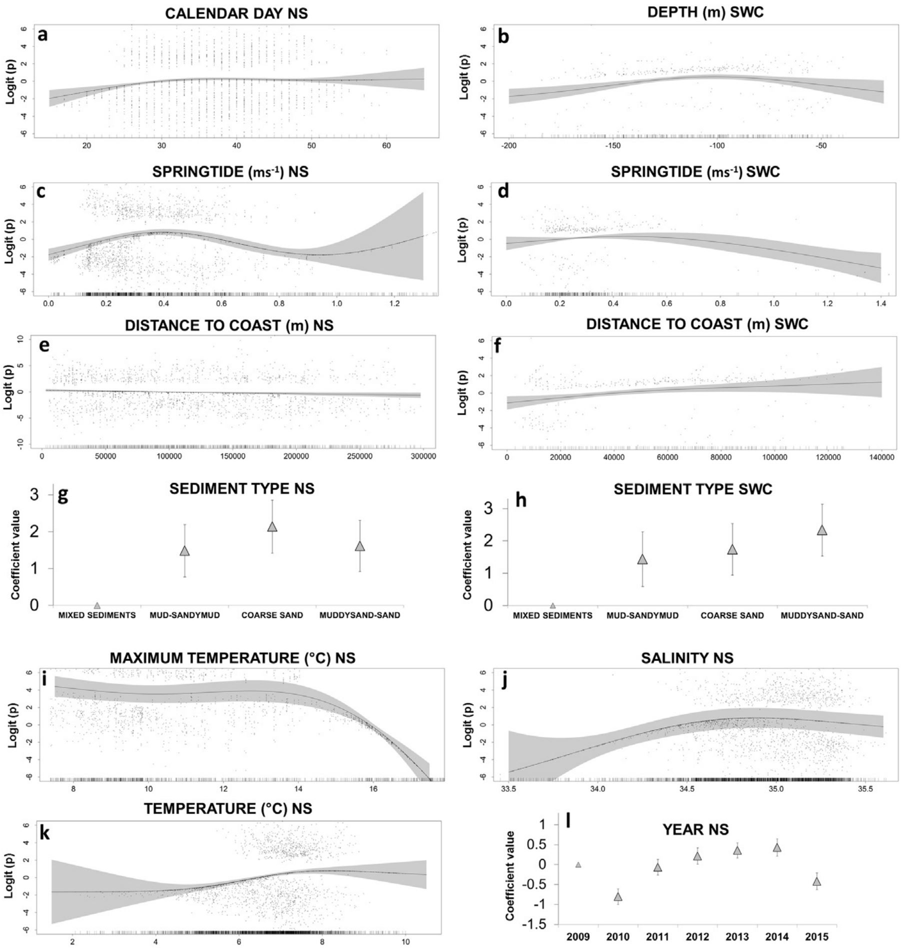

Fig. 3. Effect on the predicted probability of presence of haddock in spawning stage (P_p) of the continuous explanatory variables (3a–f and 3i–k) and value of the coefficients for the different levels in the variables included as factors (3g, 3h and 3l). The shaded area represents the nominal confidence intervals (95%). The points are the residuals. The error bars in the coefficient values represent the standard deviation. The range of values showed in Fig. 3j was focused in the centre of the distribution and it did not show the entire range of values in order to improve the interpretability.

Table 2
Values of the mean metrics used to evaluate the binomial models, the negative binomial models and the delta models.

		AUC	KAPPA	SPEARMAN	N	Explained deviance
NORTH SEA REGION	Binomial model	0.85± 0.08	0.48 ± 0.02	–	2331	38.4%
	Negative binomial model	–	–	0.38 ± 0.04	668	27.9%
	NS Delta Model	–	–	0.57 ± 0.01	–	–
SCOTTISH WEST COAST REGION	Binomial model	0.8 ± 0.03	0.5 ± 0.05	–	393	19.8%
	Negative binomial model	–	–	0.52 ±0.06	285	36.5%
	NS Delta Model	–	–	0.57 ±0.06	–	–

The binomial model from the NS explained a higher percentage of deviance (38.4%) than the model for the SWC (19.8%), although both models showed significantly higher scores than the AUC and Kappa thresholds for good performance for (Table 2). In contrast, the negative binomial model for the NS explained a lower percentage (27.9%) than the same model for the SWC (36.5%). The spearman coefficients had values of 0.37 ± 0.04 and 0.52 ± 0.06 for the negative binomial model in the NS and the SWC respectively but were higher in the delta models (0.57 ± 0.01 and 0.57 ± 0.06 in the NS and SWC respectively, Table 2).

Fig. 6 shows the delta maps of the predicted distribution of HSS in the NS and SWC by year. The maps of predicted P_p and P_a used to obtain the delta maps are shown in the Supplementary Fig. S2 in the online version at DOI: 10.1016/j.fishres.2016.05.028. In the NS there were two main spawning areas lying to the west and east of the Fladen grounds, with lower abundance in the latter. There was a clear and well defined southern limit to spawning haddock in some years (e.g. 2012, 2014, 2015) corresponding to 15–16 °C contours of the maximum temperature layer (Supplementary Fig. S1 in the online version at DOI: 10.1016/j.fishres.2016.05.028). Moreover, some of the deeper areas close to the Norwegian trench and some of the more coastal waters were also predicted to be unsuitable. On the SWC there was no latitudinal limit for haddock spawning, although there were three areas of predicted high abundance of HSS in the offshore, west and north of the Outer Hebrides and Ireland, whilst inshore waters such as the Minch, the Little Minch and the northern part of the Sea of the Hebrides were mostly unsuitable for haddock spawning. The distribution of mean rescaled values, after ranging the delta abundance, indicate the spawning grounds that tended to be important throughout the seven year modelled period (Fig. 7a). The temporal variability of the spawning distribution, based on the standard deviation, was higher in the SWC

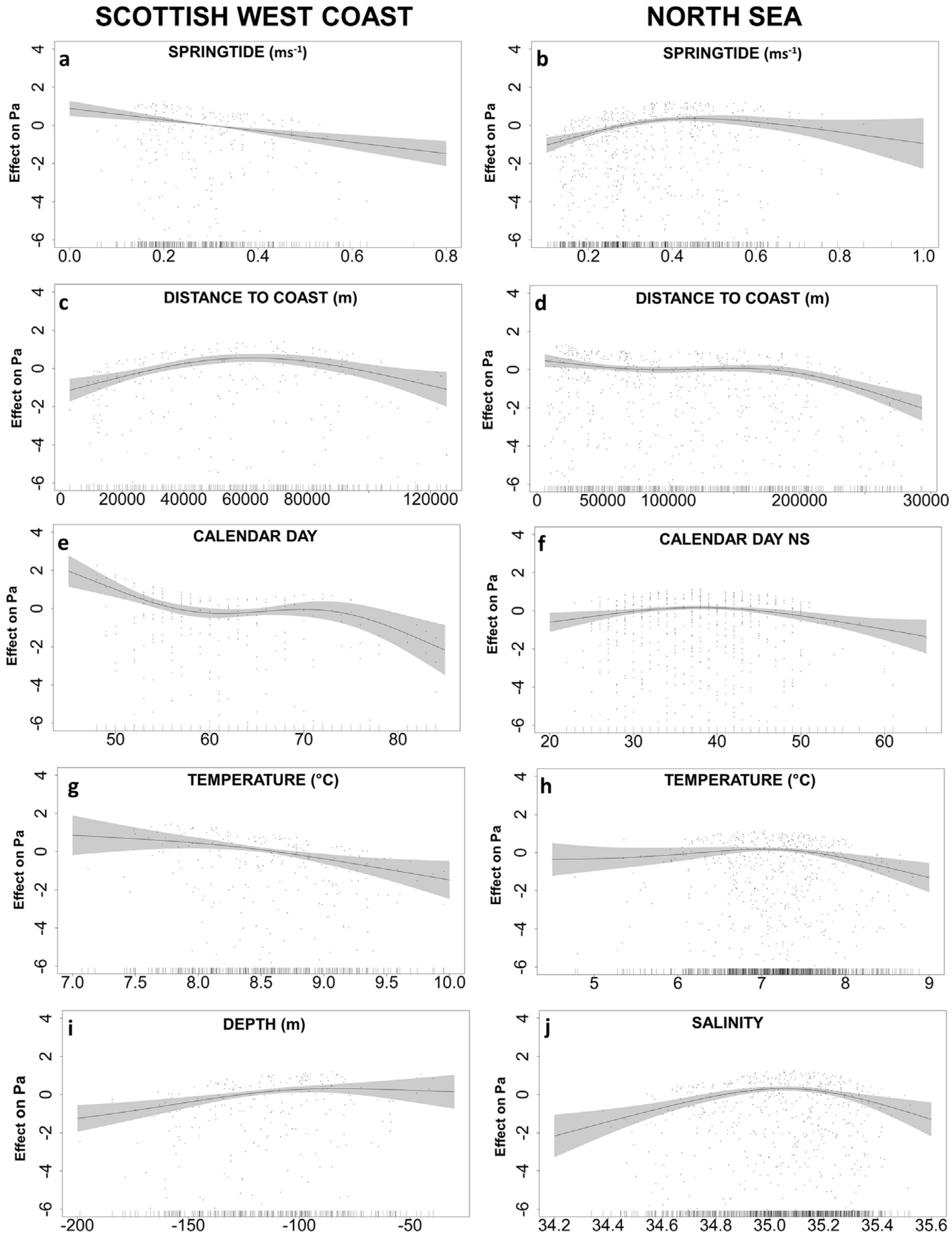

Fig. 4. Effect on the predicted abundance of haddock in spawning stage (P_a) of the continuous explanatory variables. The shaded area represents the nominal confidence intervals (95%). The points are the residuals. Region and parameters are stated in the header of the plots.

than in the NS (Fig. 7b). In the SWC this variation was associated with inter-annual variation in predicted abundance at the three main spawning grounds, although all three were occupied in all years (Supplementary Fig. S3 in the online version at DOI: 10.1016/j.fishres.2016.05.028). In contrast, areas with high standard deviation in the NS corresponded to areas that were only occasionally used most of which were located south of the Fladen grounds and especially off the north east English coast.

4. Discussion

Prediction of the physical habitat preference of spawning haddock was not confounded by changes in annual abundance as local density changed in proportion to abundance, consistent with the D2 spatial dynamics model (Petitgas, 1998). This spatial dynamic model, also called consistent spatial pattern means that the changes in local abundance are proportional to changes in total abundance (included in the model in the variable year) and therefore during the studied period there were not density effects that modified the habitat suitability defined by the physical factors. The correlation between the year effect in the NS abundance model and SSB derived from assessments (ICES, 2015) demonstrates that annual changes in abundance were accurately reflected by the model. During the study period (2009–2015), the range in SSB was low and towards the mean of the range for all years assessed. Consequently, this limited variation in abundance may explain why no density dependent effect was detected. The difference in density curves between the NS and SWC can be explained by spawning haddock avoiding the southern NS, which leads to a much higher proportion of zero hauls than in the SWC. The D2 model of spatial dynamics has been found to explain density changes for a range of gadoids (Houghton, 1987), including Atlantic cod in the NS during quarter 1 (Lewy and Kristensen, 2009) and the northern Gulf of St. Lawrence (Tamdrari et al., 2010) and young hake (*Merluccius merluccius*) in the Bay of

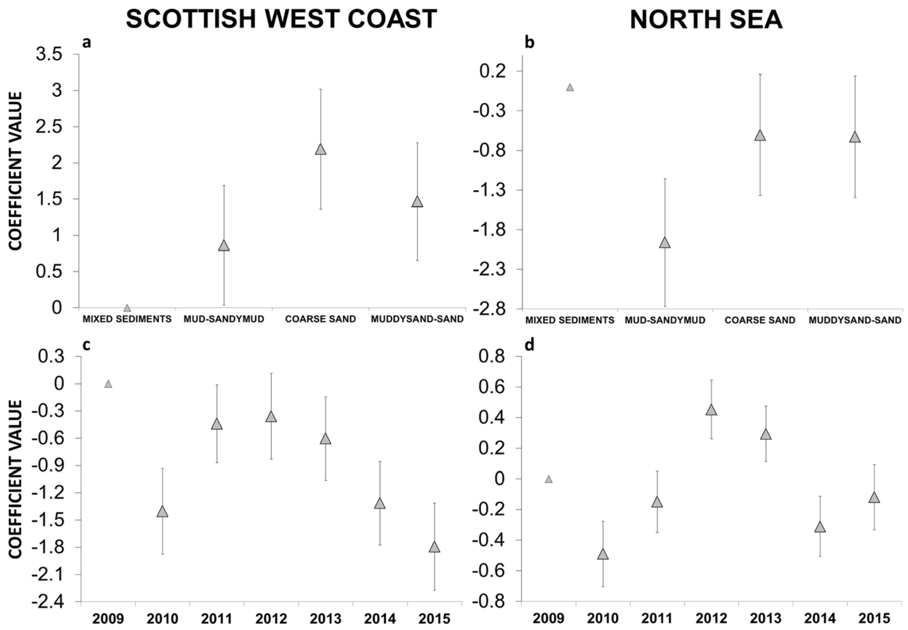

Fig. 5. Coefficientvalues for the different levels of the explanatory variables included as factors in the model. The error bars show the standard deviation for each coefficient.

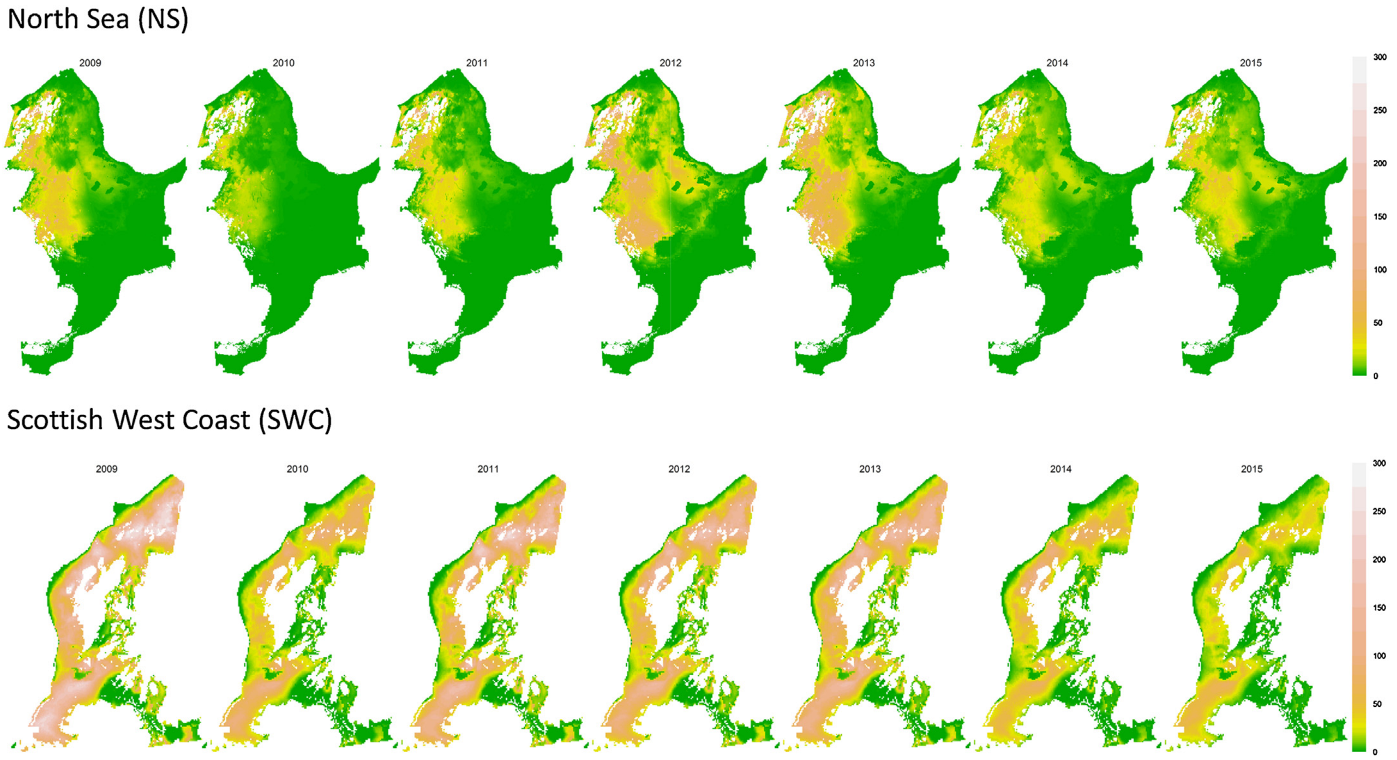

Fig. 6. Annual maps showing the distribution of the predicted abundance of Haddock in Spawning Stage (HSS) for the 7 February in the NS (upper row) and the 3 March in the SWC (lower row). Note the different map scales for regions.

Biscay (Petitgas, 1998). However, Marshall and Frank (1995) did find evidence for density dependent habitat selection in juvenile haddock from the south-western Scotian Shelf, suggesting that the nature of spatial dynamics may change with life-stage. Here it is important to remember that we only consider spawning individuals where competition is most likely to be related to space rather than for a food resource. Waiwood and Buzeta (1989) reported that haddock distribution contracted as sexual maturation progresses in the south west Scotian Shelf, which is probably linked to the males courting behaviour (Hawkins and Amorim, 2000). Consequently, any intra-specific competition is most likely to be limited to males competing for space in spawning arenas.

The two-stage GAM approach used in this work supports earlier evidence about the relevance of this method to model zero inflated data (Lelievre et al., 2014; Grüss et al., 2014). The models for the NS and the SWC showed a sound performance, with high values in all the evaluation statistics used for each model (binomial, negative binomial and delta). The binomial models showed

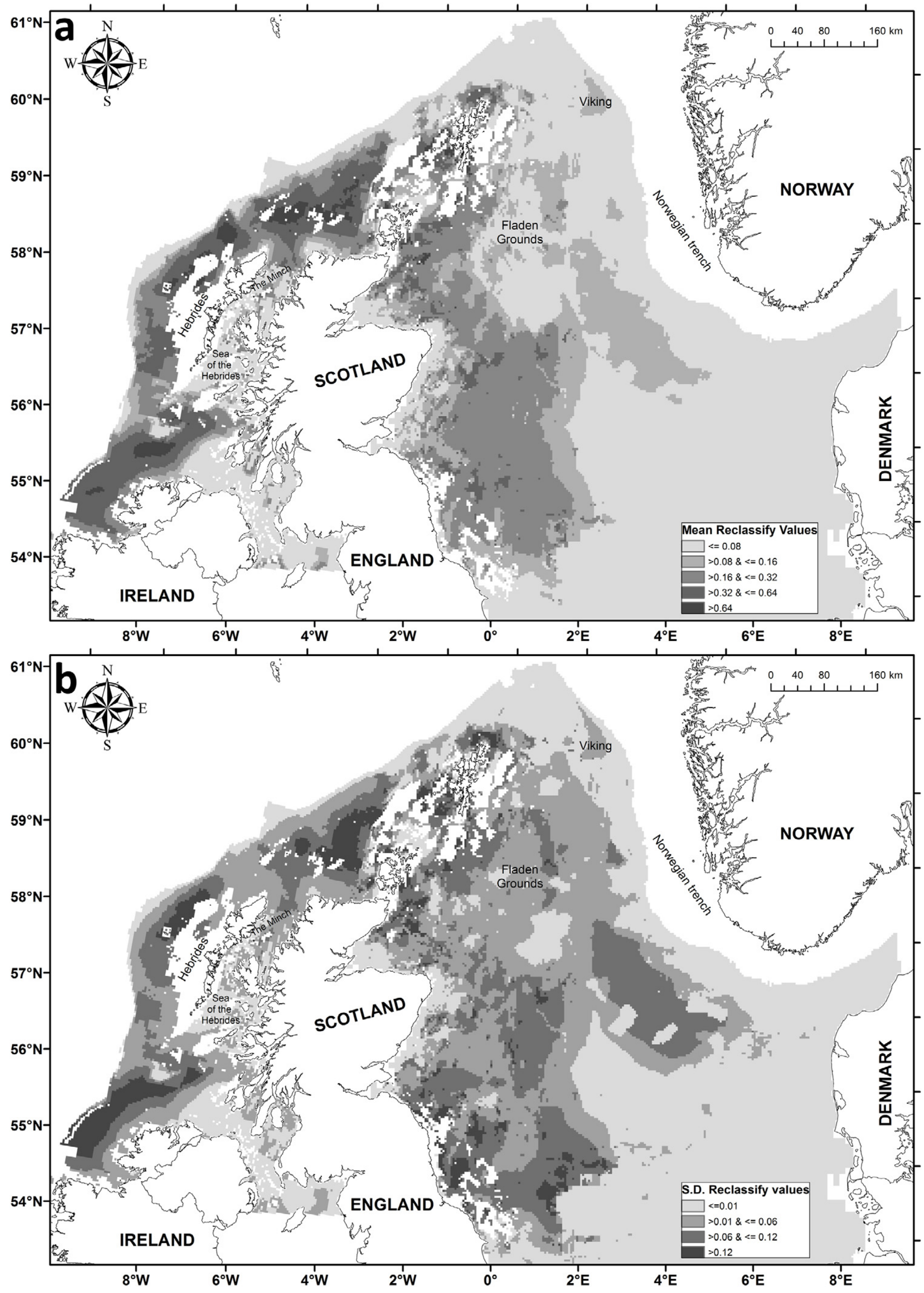

Fig. 7. Distribution of the spawning grounds of haddock in the NS and the SWC. The upper map (a) shows the mean value for the whole studied period after ranging the delta maps to values from 0 and 1. The lower map (b) shows the standard deviation.

AUC and Kappa values significantly higher than the threshold for a good performance. Furthermore, the abundance models and the delta models showed Spearman coefficient values higher than previous works (Lelievre et al., 2014; Grüss et al., 2014; González-Irusta and Wright, 2015) even when a cross-validation was used. The explained deviance for each model was also in the range of values observed in previous works.

The timing of the surveys proved to be appropriate for examining spawning occurrence as the calendar day effect on the probability of presence was limited to only the early part of the NS survey. However, the effect of calendar day on predicted abundance indicates that spawning intensity varied over the study period. The highest predicted abundance around day 40 (9 February) in both survey regions, suggested that this was the peak spawning date. Past evidence indicates that spawning begins around February and continues through to May with peaks usually in March (Saville, 1959; Wright and Gibb, 2005; Morgan et al., 2013). Consequently, spawning may have been early in the surveyed years. However, the two surveys do not cover the entire spawning period so there may have been a second and more major peak in spawning intensity later in the season. The protracted spawning period of haddock partly arises from individual spawning duration as these determinate group-synchronous spawners produce many batches of eggs at intervals of several days over the spawning period (Hislop et al., 1978). In addition, there are demographic differences in spawning time with most first time spawning age-2 females spawning later than older age-classes (Wright and Gibb, 2005; Morgan et al., 2013). With the exception of 2011, haddock >3years old dominated the spawning stock biomass (see ICES, 2015) which may explain the early peak in spawning intensity suggested by this study.

An optimum temperature for spawning of around 7 °C was indicated from the density—temperature relationships for NS and SWC regions. Similar to the analysis of mature haddock by Hedger et al. (2004), there was a positive temperature relationship in the NS up to 7 °C. However, the negative trend for the warmer SWC region indicates that haddock has a narrow temperature preference. This suggests there is an optimum temperature for spawning in the northern shelf haddock stock. Spawning south west Scotian Shelf haddock were also found to occur over a narrower temperature range than other maturity stages collected at the same time (Waiwood and Buzeta, 1989) further suggesting haddock may have a preferred spawning temperature. Temperature or the rate of temperature change can interact with photoperiod in the regulation of reproductive cycles with some species requiring a chilling phase to achieve gametogenesis and spawning (Wang et al., 2010). Temperature may also act as a cue for fish to migrate to spawning grounds (Sims et al., 2004). Ultimately, temperature preferences may reflect selection for a spawning time that promotes optimum conditions for the larvae, including the match between hatching and prey conditions (Wright and Trippel, 2009). The preferred temperature found in this study corresponds to the mean of the optimum range (4–10 °C) described by Laurence and Rogers (1976) for haddock embryos reared in laboratory conditions and the optimum temperature for haddock larval growth in the Gulf of Maine (Campana and Hurley, 1989) and Georges Bank (Buckley et al., 2004). Spawn timing is clearly important in haddock as Platt et al. (2003) found a fivefold increase in survival rate in haddock from the eastern Nova Scotian shelf coinciding with just a 2–3-week difference in the spring bloom and Wright and Gibb (2005) found a strong selection for offspring hatched in the early to mid-season in the NS.

The higher salinity spawning haddock preferred in the NS survey corresponds to areas of Atlantic inflow (Turrell, 1992) and similarly the high density of spawning haddock on the western edge of the European shelf is consistent with a preference for Atlantic rather than coastal waters. This preference for offshore areas is also consistent with the effect of the variable "distance to coast" on predicted abundance, especially in the SWC where salinity was not included in the full model. Other studies of egg and adult distribution have also found a preference for salinities >35 psu (Saville, 1959; Heath et al., 1994) and offshore waters (Scott, 1982; Waiwood and Buzeta, 1989). Laurence and Rogers (1976) found that haddock embryos had an optimum range from 30 to 36 psu and a lower tolerance to low salinities compared with other gadoid species such as cod, which could explain the avoidance of coastal waters found in this study.

The probability of spawner presence was not affected by the type of bottom sediment which agrees with previous works which have reported haddock spawning over various substrates including rocks, gravel, smooth sand and mud (Klein-MacPhee, 2002). However, the density of spawning haddock was significantly affected by sediment type. Spawning haddock density was low in mud rich areas, preferring sand and coarse sands. This preference agreed with the observed increase in haddock density with springtides up to 0.5 ms^{-1} in the NS, as grain size is largely related to spring tide with flows 0.25–0.5 ms^{-1} favouring sand patches whilst <0.25 ms^{-1} favours mud (Stride, 1982). Although the relationship with springtide was negative in the SWC, it is important to highlight that there were practically no values lower than 0.18 ms^{-1} in this region and the coefficient for mud was the lowest in this region as well. Waiwood and Buzeta (1989) similarly found that South west Scotian Shelf haddock spawned on sand/gravel grounds. A possible reason for this sediment preference is that male haddock court females using acoustic and visual displays (Hawkins and Amorim, 2000; Casaretto et al., 2015) and so fine sediments that are readily re-suspended may interfere with courtship. The avoidance of fine sediments could explain why spawning haddock aggregations were not found over the mud rich Fladen grounds in the central northern NS in either this or previous studies (Thompson, 1928; Saville, 1959).

The lack of persistent spawning grounds in the Fladen grounds and further south led to a split in the main spawning areas of the NS between the northeast and the north west. This geographical split may be relevant to population structure as Jones (1959) found very little exchange of tagged haddock between the two areas and the differences in transferrin allozyme frequency reported by Jamieson and Birley (1989) correspond to this divide. Only haddock from the west spawning area have undergone substantial changes in maturity schedules (Wright et al., 2011) and these changes cannot be explained by environmental exposure as differences in maturity–size relationships are maintained when juveniles from the two regions were reared under a common environment (Wright and Tobin, 2013). Possibly then the geographical distribution of spawning habitat might have a role as an isolating mechanism.

The absence of spawning in the southern NS in all years studied is consistent with the rarity of any life-stage of haddock in the southern North Sea (Hislop et al., 2015) although the environmental limits explaining this are not clear. Hedger et al. (2004) proposed that it was the shallow (<50 m) depth of the southern NS that was a constraint on mature haddock distribution but this alone would not explain the absence of spawning haddock in some deeper areas of the southern Bight and English Channel. Spawning haddock were found in some northern NS areas <40 m as has also been found in the Scotian Shelf (Waiwood and Buzeta, 1989) and some Norwegian fjords (Casaretto et al., 2014). The coincidence between the maximum temperature boundary of 15–16 °C and the southern extent of spawning provides a possible alternative explanation. As temperatures >13 °C appear unsuitable for haddock (Hiddink et al., 2005) and haddock appear to have a limited home range relative to subareas of the North Sea (Jones, 1959), mature fish may be less likely to migrate to spawn in waters which they avoided during autumn.

The predicted distribution of spawning haddock from this study generally conformed to historic reports but there was a southward shift in the main focus of NS spawning. In the early 1900′s Thomson (1924) reported that the greatest concentration of spawning fish was observed in the northern part of the NS on the plateau between the Orkney-Shetlands Isles and Norway and areas north and west of Cape Wrath and Butt of Lewis. Saville's (1959) egg surveys indicated a similar concentration to that reported by Thomson (1924) and Thompson (1928). Surveys between 1969 and 1975 found that spawning was concentrated in the area northwest of Orkney and Shetland, although the north east NS was not surveyed (Tormosova, 1980). The concentrations of haddock eggs found by Heath et al. (1994) in 1992 overlapped with those reported by Saville (1959), although it was noted their distributions were concentrated further north and west. In the present study however, the major concentration was off the east coast of Scotland despite this being a minor area in past studies. Whether this reflects decadal or inter-annual changes is unclear as Saville's (1959) study of egg distributions did suggest that the focus of the spawning concentrations could change from one year to the next, although little inter-annual variability was found in this study. Warm Atlantic inflows to the north and west of the study area relative to the cooler more optimal temperatures off the east coast of Scotland may explain the recent southward shift in spawning distribution. The variation in predicted spawning abundance off the north east English coast does appear consistent with the rare reported usage of these areas. The limited spawning activity in most coastal areas is apparent from most studies since the plankton surveys of Damas (1909). Similarly the preference for depths >100 m but within the 200 m depth is consistent with historic surveys (Schmidt, 1909; Thompson, 1928; Saville, 1959; Heath et al., 1994).

The persistence of some spawning areas of haddock indicated by this and past studies highlights the need for managers to consider the potential impact of marine developments on haddock. By identifying the physical characteristics and recent persistence of spawning aggregations the present study provides a guide for future marine developments. We do acknowledge that the geographical scale of our environmental layers and fish sampling are an important constraint on the resolution of distinguishing individual spawning grounds. Work into identifying such areas from haddock spawning calls indicate that some can be relatively small compared to the scale that we consider (Casaretto et al., 2014) and so for any future development further fine scale sampling would be required to determine the precise locations of spawning. Nevertheless, the charts currently used to consider haddock spawning are based on the historic incidence of spawning staged haddock (e.g. Coull et al., 1998) and fail to identify many of the major spawning areas that we find are currently in use. Persistence of spawning grounds could also help inform managers as to whether regular seasonal closures were appropriate for haddock conservation. Haddock fisheries often target spawning aggregations (Halliday, 1988), and there is some evidence that closed areas can benefit haddock conservation and allow profitable fisheries through spillover (Murawski et al., 2000). Whilst the importance of protecting spawning aggregations is still debatable, the aggregative behaviour can cause localized increases in catchability which can lead to higher fishing mortality (Halliday, 1988) and fishing may disturb the spawning behaviour of haddock and delay the completion of spawning (Casaretto et al., 2014). Given these potential impacts of fishing on spawning haddock, future research should consider whether fishing pressure in the northern shelf stock did become more concentrated on the persistent spawning grounds we identified. Targeted fishing on spawning aggregations may highlight a need to consider seasonal closed areas for this species.

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