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Spawning grounds of whiting (*Merlangius merlangus*)

J.M. González-Irusta*, P.J. Wright

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

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ABSTRACT

Targeted fishing and marine developments can alter the suitability of essential habitat such as spawning areas. Past studies of North Sea whiting (*Merlangius merlangus*) distribution have led to differing views about the comparative importance of extrinsic and intrinsic constraints on adult distribution in the North Sea. In this study the importance of environmental influences on spawning distribution was examined using GAMs in a two steps approach, after demonstrating from geospatial analyses that there were no confounding density dependent effects on distribution during the period of low stock size investigated. The binomial model (probability of presence) showed a lower predictive power than the negative binomial model (abundance) although the final model (delta model) showed similar performance to previous studies. Whiting showed high plasticity in spawning ground selection with extensive areas of the North Sea appearing suitable across the study period. Nevertheless, a divide between two centres of persistent spawning aggregation was found consistent with the boundary previously suggested from parasite, genetic, otolith chemistry and demographic trends. In addition to aggregations suggested by past egg surveys, another spawning area off the north east Scottish coast was identified. The study identified springtide as a key physical determinant of whiting spawning distribution, which may be linked to the need for larvae to be advected offshore. Contrary to past studies, peak abundance was found around 125 m bottom depth, although there may have been differences in physical preferences related to the region of the North Sea studied. The persistence of some spawning aggregations of whiting indicates the need for marine spatial planning to consider the potential impact of marine developments in these areas.

1. Introduction

There is a growing appreciation of the need to monitor and protect spawning aggregations due to the potential threats from anthropogenic impacts, such as targeted fishing (Van Overzee and Rijnsdorp, 2014) and marine developments that can alter the suitability of habitat (Stelzenmuller et al., 2010). This has led to a considerable effort to model the distribution and persistence of spawning areas for commercial fish species. Distribution Models (DMs) that statistically model the physical habitat characteristics of a species (Guisan and Zimmermann, 2000) have been widely used to identify the environmental influences on spawning distribution (Loots et al., 2011; Lelievre et al., 2014; González-Irusta and Wright, 2016a,b; Asjes et al., 2016). However, it is also important to recognise that population characteristics such as philopatry, demographic structure, and spatial density dependent processes can also influence distribution (MacCall, 1990; Colloca et al., 2009; Loots et al., 2011). Hence distribution can be seen as the product of both these extrinsic and intrinsic constraints on local density (Planque et al., 2011).

The whiting, *Merlangius merlangus,* is a piscivorous gadoid found across the North East Atlantic from southeast Iceland and Norway south to the Mediterranean (Hislop et al., 2015). It is a major piscivore in the North Sea (Greenstreet and Hall, 1996) and the subject of an important mixed demersal fishery (ICES, 2016). In the North Sea (NS), most whiting mature by age 2 and individuals spawn repeatedly (Hislop, 1975). The extended spawning period from January until June arises from this repeat spawning and a later onset of spawning with latitude (Hislop, 1984). Tag-recapture studies suggest a general northerly movement of whiting in the summer and a return movement for those spawning in the southern NS and eastern Channel (Williams and Prime, 1966), while in the northern NS they tend to be more resident or move south in the summer (Tobin et al., 2010). Tag-recapture data from individuals released and caught in successive spawning seasons does not suggest that whiting repeatedly return to the same spawning ground (Tobin et al., 2010).

Although treated as a single stock in the NS and eastern Channel there has long been evidence for two sub-populations distributed to the north and south of the Dogger Bank, which extends from around 54°N off the English coast to 57°N as the NS enters the Skagerrak. Kabata (1967) found differences in the incidence of parasite species in whiting

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

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north of 56°N and south of 54°N indicative of little movement between regions. Similarly, releases of tagged whiting in the north west and southern NS found little exchange north or south of 56°N (Williams and Prime, 1966; Hislop and MacKenzie, 1976; Tobin et al., 2010). Studies using microsatellite DNA have also suggested genetic divergence between the northern and southern NS (Rico et al., 1997; Charrier et al., 2007), although there is uncertainty in these results since levels of diversity were very low and some microsatellites used deviated significantly from Hardy Weinberg equilibria. Nevertheless, de Castro et al. (2013) found differences in SSB and recruitment trends between the north and south regions, consistent with the existence of population structuring.

Studies of NS whiting distribution have led to different views about the comparative importance of extrinsic and intrinsic constraints on adult distribution in the NS. Using commercial landing per unit effort data and bottom trawl survey data, Zheng et al. (2001, 2002) found that catch rate was related to temperature during the spawning period and so proposed that the annual distribution would be expected to shift in relation to Atlantic inflow. In contrast, in an analysis of spawning fish caught in bottom trawl surveys, Loots et al. (2011) concluded that whiting has a high spatial fidelity, with temperature and salinity only affecting the geographical extent. Ichthyoplankton surveys of the central and southern NS between 2006 and 2009 only partially supported the view of recurrent spawning areas (Lelievre et al., 2014). Further, none of the studies explicitly considered biomass-dependent spatial dynamics which may confound statistical relationships between species density and environmental conditions as individuals may occupy less optimal habitats as abundance increases (Petitgas, 1998). The purpose of this study was to determine the importance of environmental influences on spawning distribution with due regard for possible density dependent effects on distribution. DMs would be expected to reflect physical habitat suitability when the local density remains a constant proportion of the population abundance, i.e. the D2 consistent spatial pattern model described by Petitgas (1998). Consequently, geostatistical aggregation curves and the spaces selectivity index (Matheron, 1981; Petitgas, 1998) were used to establish the appropriate dynamic model for spawning whiting. Geostatistical aggregation curves were used to define the scale of spawning aggregations according to the method of Colloca et al. (2009). Persistence of these aggregations were used to assess previous evidence for two major areas of spawning (Loots et al., 2011) consistent with putative sub-population boundaries.

2. Material and methods

2.1. Biological data

The abundance of Whiting in Spawning Stage (WSS) was downloaded from ICES DATRAS (DAtabase of TRAwl Surveys; http://ices.dk/marine-data/data-portals/Pages/DATRAS.aspx) from the North Sea International Bottom Trawl Survey (NS-IBTS). This survey takes place during the 1st quarter (from the second fortnight of January to the start of March) and covers the early part of the spawning period of whiting (Hislop, 1984). The NS-IBTS involves eight different countries and two hauls separated by at least 10 Nm are taken by different countries for almost all ICES statistical rectangles (ICES, 2012). The sampling effort and abundance by haul of WSS is 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) which overestimated the abundance of WSS and CTD coverage in 2008 was incomplete in the southern NS. Age and maturity analysis from all ICES demersal areas was carried out according to ICES protocols (ICES, 2012) and the percentage of each maturity stage for each length class in each haul was estimated. The abundance of WSS by haul (H_a) was calculated according to:

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

The values of the environmental variables included in the analysis were obtained using the haul location estimated as the mean point between the shoot and haul position, to extract the value at this point from the environmental layers. Since we were modelling the spawning grounds of whiting within the suitable habitat of this species and not their total distribution only hauls with at least one whiting caught (regardless of maturity stage) were included in the analysis.

2.2. Density dependence and environmental layers

Geostatistical aggregation curves (Matheron, 1981; Petitgas, 1998) and the space selectivity index (Ssp) were used to establish the type of spatial dynamics of whiting during the study period. The geostatistical aggregation curve Q(T) relates the abundance of WSS, Q(z), to the area, T(z), measured in this work as the number of hauls occupied by densities greater than the threshold z. In other words, T(z) denotes the proportion of hauls (used in this work as a proxy for area) where WSS density is greater than z. So, for instance for a z of 3, T(z) will be the proportion of hauls with densities of WSS higher than 3. Q(z) measures the maximum fish abundance that is in any proportion T(z) of the total area. The maximum fish abundance in only one haul will be the maximum density present in hauls, the maximum number of fish in two hauls will be the sum of the maximum and second higher densities and so on. The curve Q(T) relates Q(z) to T(z) and gives the maximum abundance that can be in any proportion T of the total area (number of hauls in this work). 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 total abundance accumulated in the proportion of hauls T. P(T) is the equivalent to Q(T) but using proportion of the total abundance P(z) instead of number of fish Q(z). The statistical significance of variations in the Ssp index between years was tested using bootstrapping. In accordance with Petitgas (1998), the original dataset of each area (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 (Canty and Ripley, 2015) and Eq. (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. The environmental data layers; bathymetry, distance to coast, springtide (tidal currents), sediment type, temperature near bottom and salinity near bottom were those used in Gonz & lez-Irusta and Wright (2016a). Rocky areas are not accessible to trawling gears and therefore this seabed type was not included in the models. Current velocities are subject to both tidal and non-tidal processes. As in Gonz & lez-Irusta and Wright (2016a), tidal currents were represented in the springtide layer. Furthermore, to include the possible influence of residual circulation (i.e. non-tidal, long-term average), current velocities were obtained from a reanalysis model for the European North West Shelf region for the period 1985 & 2012 (provided by the UK Met Office via the Copernicus Marine Environment Monitoring Service http://marine.copernicus.eu/). The U (water flow velocity in direction east-west) and V (water flow velocity in direction North-South) velocity components were combined according to:

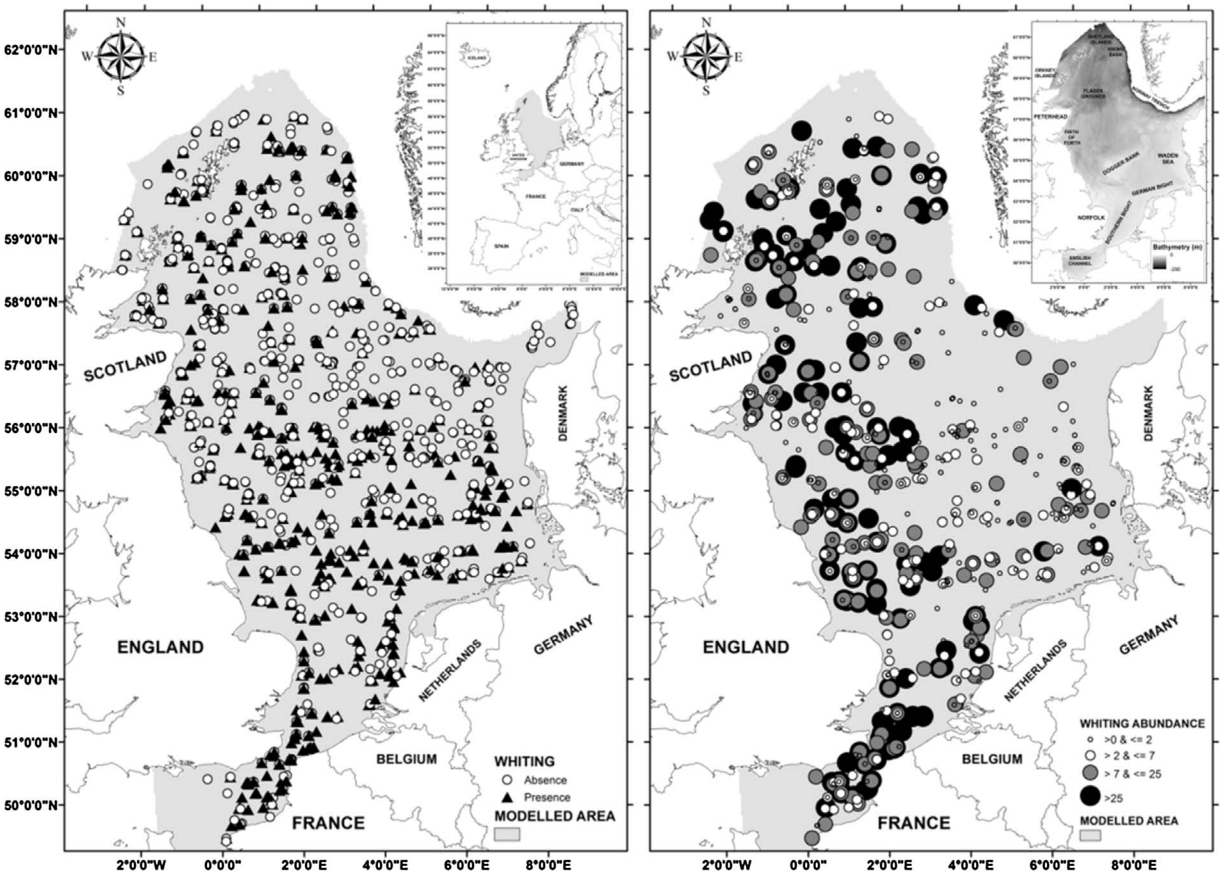

Fig. 1. Whiting presence absence distribution (left map) and Whiting in Spawning Stage (WSS) abundance distribution (right map) based on ICES 1st quarter IBTS. The two small maps show the location of the study area (left) and the main geographical features cited in the text (right).

$$\textit{Water Flow Velocity (WFV)} = \sqrt{u\ velocity^2 + v\ velocity^2} \tag{2}$$

This WFV environmental layer represents the density and wind-driven currents with a variability of more than one day. The layers for 2015 and for WFV which are not in González-Irusta and Wright (2016a) are shown in Supplementary Fig. 1. Finally, in order to consider potential spatial effects produced by unmeasured drivers that could result in otherwise unexplained patterns, the location of each trawl (longitude and latitude) was also included in the model year by year.

2.3. Data analysis

General Additive Models (GAMs) were used to model the abundance of WSS in the NS with the implementation gam in the package “mgcv” (Wood, 2011). Since the data were zero inflated, the abundance distribution was modelled using a two steps approach (Barry and Welsh, 2002). In recent years this approach has been successfully applied to model fish distribution in several studies (Loots et al., 2011; Lelievre et al., 2014; Grüss et al., 2014; González-Irusta and Wright, 2016b, Asjes et al., 2016). First the probability of presence of WSS (hauls with at least one WSS) was modelled using a binomial GAM with a logit link function. Then, the abundance of WSS (calculated for 30 min of trawling rounded to the nearest integer and removing the zeros) was modelled using a negative binomial GAM with a log link function. To avoid overfitting all the smoothers were constrained to 4 knots in both binomial and negative binomial GAMs. Finally, both models were combined (delta GAM, see below). Prior to the analysis, the correlation between the explanatory variables was tested using Spearman rank correlations and Variance Inflation Factors (VIFs) (Zuur et al., 2009). The VIFs were lower than 3 and the Spearman rank coefficients lower than 0.5 in all the cases so colinearity between the explanatory variables was not a problem. To avoid overfitting all the smoothers were constrained to 4 knots (the exception was the spatial effect which was constrained to 16 knots). The full binomial model was:

$$Pp = \beta1 + s(\text{springtide}) + s(\text{calendar day}) + f(\text{year}) + f(\text{sediment type}) + s(\text{temperature}) + s(\text{salinity}) + s(\text{distance to coast}) + s(\text{depth}) + s(\text{WFV}) + s(\text{longitude, latitude, by} = f(\text{year})) + \mathcal{E}1$$

Where P_p is the probability of presence of WSS, β1 is the intercept, s is an isotropic smoothing function (thin plate regression splines), f indicates the factors and ε_1 is the error term. Furthermore than the environmental layers, calendar day and year were also included in the full models. The calendar day was included to account for differences in WSS distribution related with the whiting spawning cycle whereas the year term was included to consider the effects of spawning stock abundance on distribution. The predicted abundance of WSS (P_a) was modelled using a negative binomial model which in the full model included the same variables as the binomial model. Both models were built using a backwards/forwards stepwise selection process based on the Akaike’s Information Criteria (AIC). After selection both the final binomial and negative binomial model were applied to the GIS layers to generate annual maps of P_p and P_a for the studied area. The maps were computed using the mean calendar day (5th February), the temperature and salinity values for that year and the corresponding year coefficient and finally the P_p maps were multiplied with the P_a maps to produce the final delta models. Delta models are the final prediction, combining the probability of presence of WSS with the abundance in the areas where they are present. 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 deviance residuals was analysed for each year and modelled 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.

2.4. *Evaluating the models*

The accuracy of the models was tested using cross-validation. The data 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 checked using the test subsample and the statistics; Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC, Fielding and Bell, 1997) and kappa (Cohen, 1960). The same methodology was used to check the ability of the model to predict abundance. In this case, 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, with a different random selection of training and test subsample each time. The statistics were calculated using the implementation of 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; Landis and Koch, 1977; Hosmer and Lemeshow, 2000) and with 0.5 and 0 (random models).

2.5. *Combining the delta maps*

For combining the prediction of the seven years in one unique final map, we applied the methodology used by Colloca et al. (2009) and applied more recently by Asjes et al. (2016) to combine the prediction of aggregations of different years. Applying this methodology the delta maps were converted to binary maps using an abundance threshold for each year. The threshold was computed using geostatistical aggregation curves calculated from the abundance prediction (using the cells as surface unit) and the point where the tangent line to the curve had a 45° slope. This point was adopted as a threshold for the identification of the spawning grounds for each year since this correspond to a change in the spatial distribution of fish from a dispersed distribution pattern to an aggregated pattern. A more complete explanation of the methodology is available in Colloca et al. (2009). Once the seven maps were converted to binary maps the Index of Persistence (I_i) was computed as:

$$I_i = \frac{1}{n}\sum_{k=1}^{n} F_v \tag{3}$$

where n is the number of years considered and F_v is the value in each binary map (0 or 1). The Index of Persistence (I_i) ranges between 0 (cell i never had a value higher than the threshold) and 1 (cell i always had a value higher than the threshold) for each cell in the study area. The I_i allow us to show one unique map with the distribution of the spawning grounds of whiting in the NS.

3. Results

There were no apparent differences in the density curves among years, reaching maximum values in the accumulated proportion of total abundance in a small percentage of the total area ($Tz < 0.25$) in all cases (Fig. 2). The mean value for the Ssp in the NS calculated using bootstrapping was 0.98 with a 95% confidence interval ranging from 0.94 to 1. The Ssp values for all the years were inside this confidence interval (Fig. 2) and therefore, the null hypothesis, of no significant variation of Ssp among years, was not rejected. The analysis of both aggregation curves and Ssp values indicate that the spatial dynamics of whiting during the study period corresponds to Dynamic D2; consistent spatial pattern.

The binomial model explained 19.2% of the deviance (Table 1). From the initial 10 variables included in the full binomial model, 6 variables were kept in the final model. Sediment type, temperature near bottom, water flow velocity and distance to coast were not included in the final model. The spatial effect (the longitude and latitude of the haul) was clearly the most important variable (Δ deviance = 232.06), followed by year (34.31), depth (32.09), calendar day (21.97) and springtide (21.77). Salinity was the least important variable (10.85) and its effect on the probability of presence was not statistically significant. The spatial effect differed between years (Supplementary Fig. 2). In most years there was a latitudinal effect on the probability of presence of WSS (P_p) with a higher probability of presence in the southern NS than the northern NS. Furthermore, in 2011, 2012 and 2013 there was also a longitudinal effect, especially in the northern NS

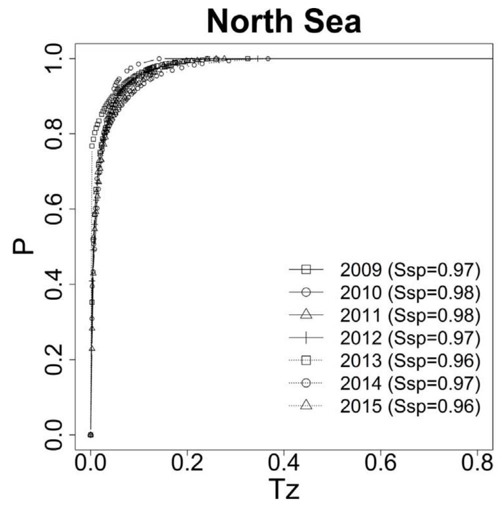

Fig. 2. Geostatistical aggregation curves and SSP values for the studied period (2009 & 2015). The curves relate the maximum proportion of the total abundance of WSS (P) present in any proportion of the total area (Tz). The Ssp values were compute according to Eq. (2).

Table 1
Relative importance (Δ deviance), degrees of freedom (df) or estimated degrees of freedom (edf) and statistical significance (P-value) of the explanatory variables for the binomial and the negative binomial models.

	Δ deviance	d.f./e.d.f.	Chi-square	P-value
	Binomial model (19.2% Deviance explained)			
Spatial effect 2009	232.06	6.0	35.52	< 0.001
Spatial effect 2010		4.3	39.08	< 0.001
Spatial effect 2011		7.6	38.74	< 0.001
Spatial effect 2012		6.5	22.29	0.006
Spatial effect 2013		8.4	14.62	0.19
Spatial effect 2014		7.3	17.04	0.06
Spatial effect 2015		13.6	51.72	< 0.001
Year	34.31	6	28.72	< 0.001
Depth	32.09	3.0	17.18	< 0.001
Calendar day	21.97	2.9	26.33	< 0.001
Springtide	21.77	2.2	10.51	0.01
Salinity	10.85	2.9	5.41	0.14
	Negative Binomial model (65.2% Deviance explained)			
Spatial effect 2009	114.3	11.6	55.36	< 0.001
Spatial effect 2010		8.5	35.77	< 0.001
Spatial effect 2011		12.9	65.75	< 0.001
Spatial effect 2012		9.3	50.98	< 0.001
Spatial effect 2013		10.7	54.43	< 0.001
Spatial effect 2014		9.0	42.82	< 0.001
Spatial effect 2015		8.2	43.54	< 0.001
Temp	19.3	2.9	27.34	< 0.001
Springtide	12.38	2.8	44.31	< 0.001
Year	11.57	6	28.39	< 0.001
Sediment Type	4.33	2	24.98	< 0.001
Depth	2.08	2.9	29.71	< 0.001
Water Flow Velocity	0.57	1	4.38	0.04

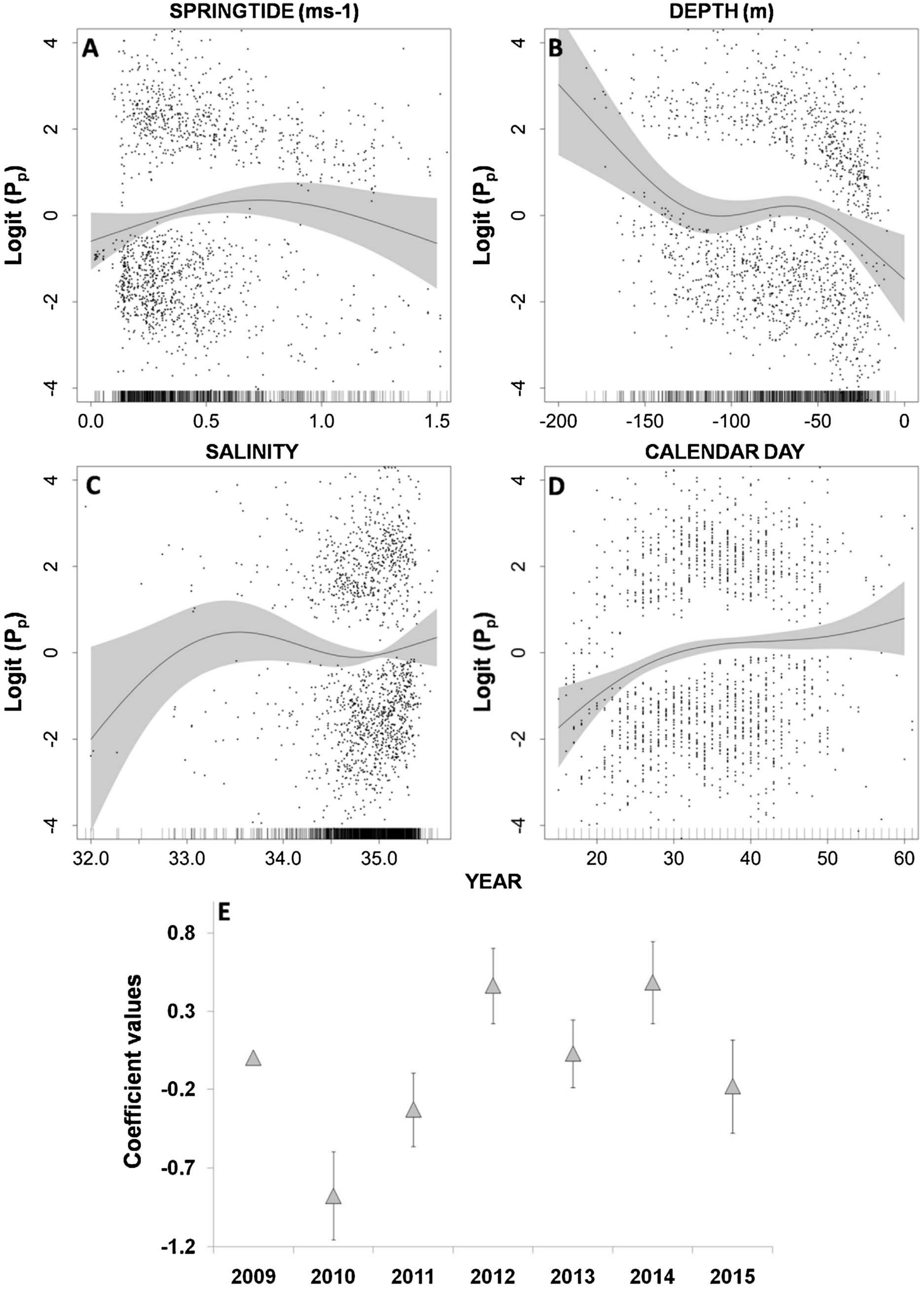

Fig. 3. Effect on the predicted probability of presence of whiting in spawning stage (Pp) of the continuous explanatory variables (3A & D) and value of the coefficients for the different levels in the variables included as factors (3E). The shaded area represents the nominal confidence intervals (95%). The points are the residuals. The error bars in the coefficient values represent the standard deviation.

where there was a higher probability of presence in Scottish waters than in Norwegian waters. The probability of presence of WSS (P_p) showed a positive relationship with springtide from values ranged from 0.1 ms^{-1} to 0.8 ms^{-1} and a negative relationship for areas exposed to stronger springtide currents (Fig. 3). Calendar day had a positive effect on $P_{p,}$ especially in the first 15 days and in the last 10. Salinity had a negative effect on Pp for values ranging from 34.5 to 35.5 and for values lower than 33 and no clear effect for the rest of values. The depth effect on P_p was positive for values ranging between 0 and 60 m depth and between 100 & 200 m depth and slightly negative from 60 to 100 m depth. Finally, the inter-annual variation of the coefficient values did not show any clear temporal trend, the coefficients for 2010 and 2014 being the lowest and highest, respectively.

The final negative binomial explained 65.2% of the deviance (Table 1). In this case the variables; spatial effect, temperature near bottom, springtide, year effect, sediment type, depth and WFV were kept in the model and all of them had a significant effect on the predicted abundance of WSS (P_a). As observed in the binomial model, the spatial effect was the most important variable (Δ deviance = 114.3), followed by temperature (19.3), springtide (12.38) and year (11.57). Sediment type, depth and WFV had lower values of Δ deviance (4.333, 2.08 and 0.57 respectively). The spatial effect showed a common trend among years (Supplementary Fig. 3) with a positive gradient from the north-east to the south-west on the predicted abundance of WSS (P_a). Near bottom temperature showed a peak in P_a at around 7.5 °C (Fig. 4). The effect of springtide on P_a was positive for values ranged from 0.1 ms^{-1} to 0.9 ms^{-1} and negative for higher values. Water Flow Velocity (WFV) had a linear and positive effect on P_a and depth showed a peak for values around 125 m, with a negative effect on P_a for deeper areas. Coarse sand had the highest coefficient value in sediment type and muddy sand-sand the lowest, with a similar value to mud-sandy mud. The year coefficient showed a positive trend with a higher coefficient at the end of the study period than in the initial years. The coefficient for 2010 was the lowest and the coefficient for 2015 the highest (Fig. 4).

The AUC, kappa and the Spearman coefficient for the binomial, negative binomial and delta models are given in Table 2. The values of AUC and Kappa were lower than the threshold for a good performance (0.7 and 0.4 respectively) but significantly higher than 0.5 and 0 (t values = 26.18 and 23.28 respectively, P-value < 0.001). The Spearman coefficient was 0.44 ± 0.05 and 0.37 ± 0.04 for the abundance and delta models, respectively.

The probability of presence maps (Fig. 5A) showed high temporal variability, especially in the northern NS. The Firth of Forth, the Fladen Grounds and the waters around Orkney and Shetland showed some years with high P_p values and others with low values. There was a high probability of presence for all the years in the southern NS, English channel and Southern Bight, whereas the German bight, Dogger bank and the Waden sea showed higher inter-annual variability. The abundance maps (Fig. 5B) showed a more discrete distribution in relation to the maps of presence (Fig. 5A) although also showed high inter-annual variability. The areas with highest P_a values changed during the study period being located in the English Channel, off Norfolk, the Southern Bight or the waters around Orkney and Shetland Isles, depending on year. Finally, in the delta model maps (Fig. 5C, obtained by multiplying the maps of Fig. 5A with the maps of Fig. 5B), the main aggregations of WSS were located in the southern NS (English Channel, Southern Bight and off Norfolk) and in some specific areas of the north-west NS (Rattray Head and waters between Orkney and Shetland islands). Moreover, in some years the whiting spawning grounds expanded to include the German Bight in 2009 and 2015, the central NS in 2010 and 2011, west of the Norwegian Trench in 2013 and Viking bank in 2015.

Temporal variation is summarised in Fig. 6 which shows the distribution of the Index of Persistence, an index which ranges between 0 and 1 and indicates the number of years selected as suitable for spawning using the threshold previously described (see Supplementary Fig. 4). Except the eastern part of the central NS, the Firth of Forth, the Moray Firth and the north-east of Shetland, all the study area was selected as suitable for spawning at least once during the study period. The persistent whiting spawning grounds were mainly located in the western NS, from the south to the north, although with three main areas; two of them in the north-west (off Peterhead and between Orkney and Shetland Isles) and the other in the southern NS (in the English Channel and the Southern Bight), the latter being consistently classified as suitable for spawning (I_i = 1).

4. Discussion

Despite high inter-annual variation in the aggregation and extent of the NS classified as suitable for spawning, it was possible to distinguish two main spawning areas, one in the south and west NS and the other in the northern NS. The divide between these two areas was largely consistent with the boundary previously suggested from parasite (Kabata, 1967), genetic (Charrier et al., 2007) and demographic trends (de Castro et al., 2013). Based on historic tag-recapture studies and otolith microchemistry, the boundary between these two aggregations is likely to reflect the extent of adult and juvenile movements (Williams and Prime, 1966; Hislop and MacKenzie, 1976; Tobin et al., 2010) and may vary dependent on environmental influences. The aggregations identified in this study broadly correspond to those identified from an analysis of previous years of the IBTS survey supporting the regional fidelity proposed by Loots et al. (2011). An ichthyoplankton survey of the central and southern NS in 2009 (Lelievre et al., 2014) found a similar southern distribution to the present study. Based on the less persistent aggregations in the present study, it appears whiting spawning distribution extends northwards, reaching the southern part of the Firth of Forth and eastwards in some years, including to the German Bight. This eastward expansion into the German Bight was also observed in four annual ichthyoplankton surveys (Lelievre et al., 2014). However, in contrast to Lelievre et al. (2014), the Dogger bank was not identified as a spawning ground in this study in any year.

Prediction of the physical habitat preference was not confounded by density dependent habitat selection as local density changed in proportion to total abundance, consistent with the D2 spatial dynamics model (Petitgas, 1998). Although Loots et al. (2011) proposed that a density-dependent effect on spawning whiting distribution was likely based on changes in the spatial extent of spawning adults in relation to population abundance they did not test to see whether these changes resulted from a density effect at a local scale or was proportional to the total abundance, as was observed in this study. However, it is possible that the different conclusions about density & dependent effects reflect the period studied as Loots et al. (2011) considered the years from 1980 to 2007, which corresponds to near peak abundance to the lowest spawning biomass, while our study covered the period 2009 & 2015, when the spawning stock was around the precautionary spawning biomass level (ICES, 2016). Consequently, the lack of a density dependent response in the present study may just reflect the persistent low stock size. This focus on depleted stocks may also explain why the D2 model of spatial dynamics has been found to explain density changes for a range of gadoids including Atlantic cod in the NS during quarter 1 (Lewy and Kristensen, 2009) and the northern Gulf of St. Lawrence (Tamdrari et al., 2010), young hake (*Merluccius merluccius*) in the Bay of Biscay (Petitgas, 1998) and North Sea haddock (González-Irusta and Wright, 2016b). As we were able to discount possible density dependent effects at a local scale in our study we were better able to define the physical characteristics of spawning habitat than previous studies.

The spatial effect was the most important variable in both models (presence-absence and abundance models) and was the main reason for the predicted inter-annual variability in distribution. Although it is not possible to determine the drivers behind this spatial effect, it could be linked to previous evidence for different trends in stock biomass between the northern and southern North Sea sub-stocks (Castro et al.,

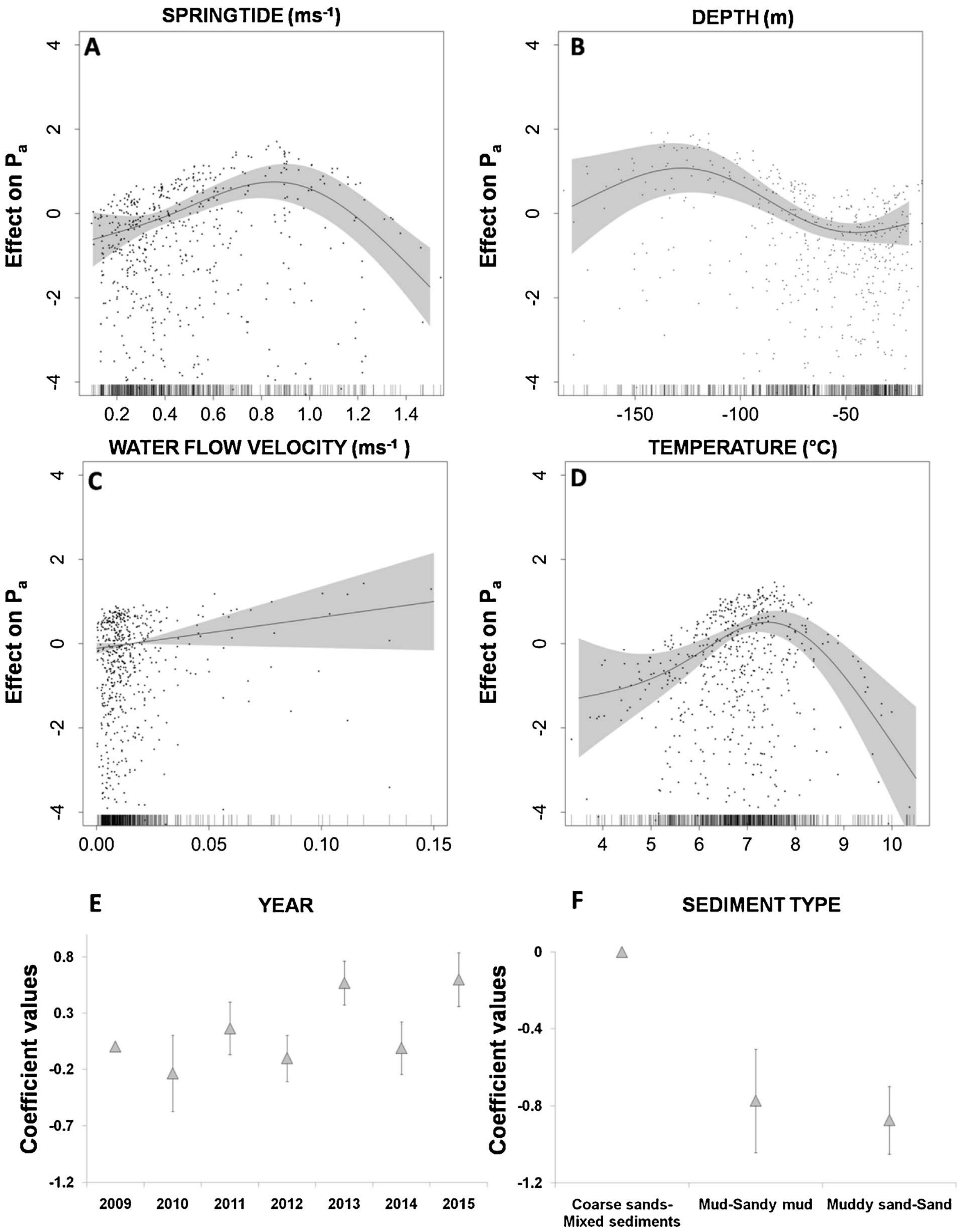

Fig. 4. Effect on the predicted abundance of whiting in spawning stage (Pa) of the continuous explanatory variables (4A & D) and value of the coefficients for the different levels in the variables included as factors (4E and F). The shaded area represents the nominal confidence intervals (95%). The points are the residuals.

2013). Other potential influences on this variable could include the proximity to prey and fishing effort as well as the scale of migrations which tend to be limited in this region (Tobin et al., 2010). Near bottom temperature was the second most important variable in terms of deviance explained in the abundance models. Whiting seems to aggregate to spawn in areas with temperatures around 7.5 °C which agrees with previous works on whiting spawning grounds based on early stage egg distribution (Höffle et al., 2017; Lelievre et al., 2010) and with other work analysing adult whiting distribution (Zheng et al., 2001, 2002). However, this was not an important limiting factor on the extent of spawning grounds as most NS grounds had a near bottom temperature range within the observed abundance peak (e.g. 5 & 8 °C). Although

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

		AUC	KAPPA	SPEARMAN
NORTH SEA AREA	Binomial model	0.66 ± 0.02	0.25 ± 0.03	&
	Negative binomial model	&	&	0.44 ± 0.05
	Delta Model	&	&	0.37 ± 0.04

whiting eggs have been found over a greater range of current velocity than some other species (Lelievre et al., 2014), the present study is the first to identify springtide as a key physical determinant of whiting spawning distribution. Springtide was included in both binomial and negative binomial models and it was the second most important environmental variable in the abundance model, showing a key role not only on the distribution of WSS but in its aggregation as well. The persistent nature of this environmental variable may help explain why Loots et al. (2011) found that their population memory term, based on the overlap in distribution from one year to the next, was very important in explaining whiting distribution. Clearly, if whiting regularly aggregate in areas of high springtide it could lead to the same strong relationship between spawner distribution in successive years that Loots et al. (2011) had ascribed to an intrinsic population factor. As the available tag-recapture experiments show individuals dispersing between successive spawning years (Tobin et al., 2010), it appears unlikely that the year to year similarity in whiting distribution arises from spawning fidelity as Loots et al. (2011) had proposed.

The other variable reflecting residual current velocities in the area (WFV) also had a significant positive effect on WSS aggregation and it was included in the abundance models. This variable probably reflects the importance of increased Atlantic inflow previously postulated by Zheng et al. (2001). Choice of hydrographic regime can be key to reproductive success with some species choosing areas that are generally retentive and productive whilst others depend on areas of advection to enable their progeny to reach suitable nursery areas (Harden-Jones, 1968). In the latter case, the presence of predictable transport trajectories (such as tidal streams or dominant wind direction) have been hypothesised to be the main driving factor explaining geographically stable spawning site selection (Cushing, 1990; Wennhage and Pihl, 2001). The main areas persistently used by spawning whiting, off east Scotland, waters between Orkney and Shetland Isles and in the south west North Sea are characterised by a predictably high tidal stream (Simpson et al., 1981; http://www.renewables-atlas.info), consistent with this hypothesis. Pelagic young of the year are predominantly found in offshore waters while recently settled whiting occur extensively throughout coastal waters (Bastrikin et al., 2014; Hislop et al., 2015) and otolith microchemistry studies indicate that spawning adult aggregations are supplied from juveniles over an extensive geographic range (Tobin et al., 2010). This scale of life-stage connectivity is therefore consistent with extensive dispersal of early life-stages and so a preference for areas of moderate to high springtide could be seen as an adaptation to facilitate offspring dispersal.

As fine sediments don't occur in areas of high springtide the observed avoidance of mud may simply reflect the hydrographic preference of whiting. Whiting are partly an income breeder (Hislop, 1975), depending on concurrent food intake for reproductive investment and so suitable foraging areas near spawning areas could be

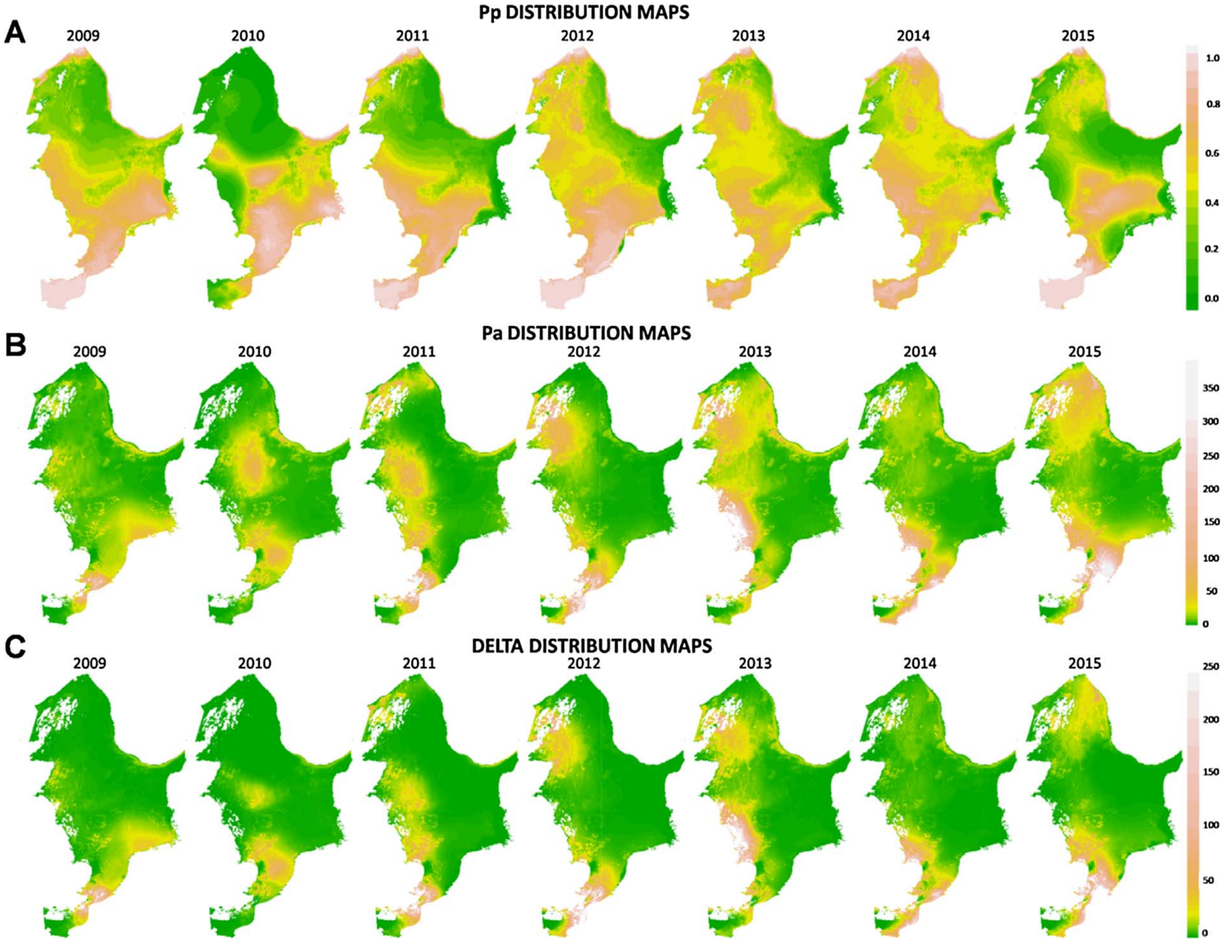

Fig. 5. Distribution maps for the seven years studied of; A) the probability of presence of WSS (P_p) B) abundance of WSS in presence areas (P_a) C) Abundance of WSS in the delta model ($P_p \times P_a$).

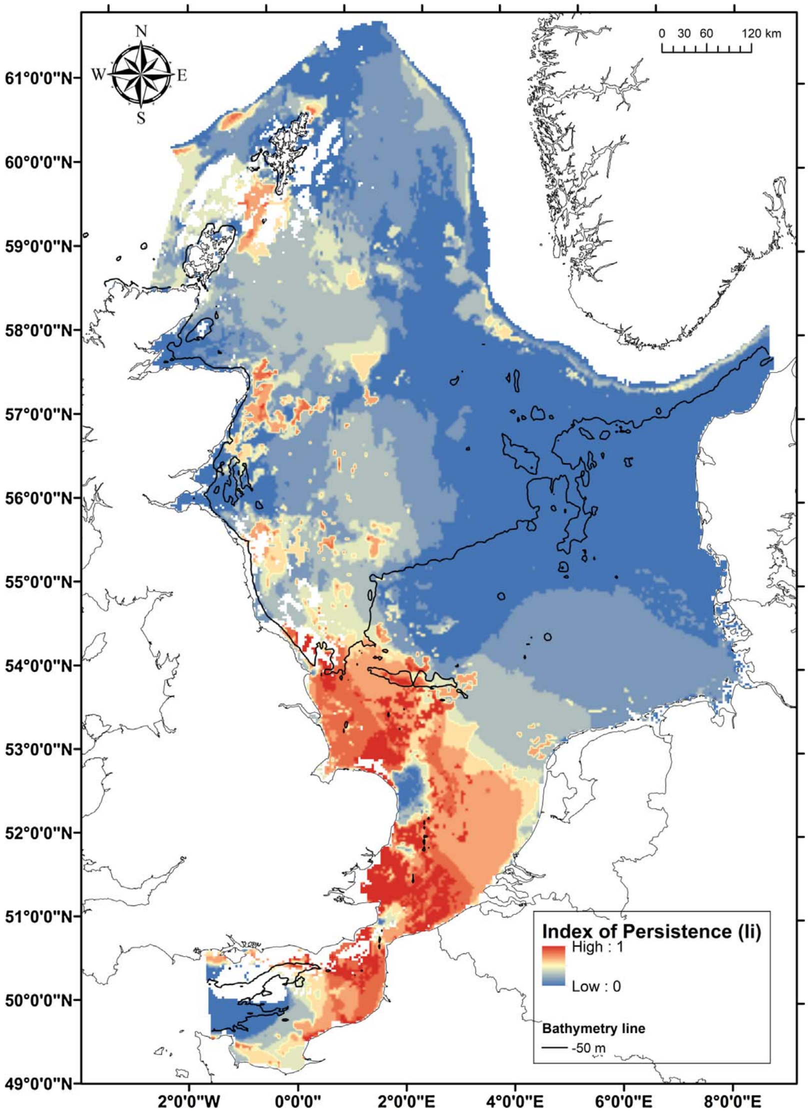

Fig. 6. Distribution of the Index of Persistence (I_i) of whiting spawning ground in the North Sea. A value of 0 means than this cell was not classified as suitable for any year during the study period whereas a value of 1 means that this cell was classified as suitable for all the years.

important. For example, coarse sand is important to sandeels (*Ammodytes marinus*; Wright et al., 2000), a key prey species upon which whiting are known to aggregate (Temming et al., 2007). Contrary to past studies (Aurich, 1941; Lelievre et al., 2014), whiting were not found to prefer spawning in shallow waters as the peak abundance was around 125 m. However, this is probably misleading due to the availability of suitable areas in the shallow southern North Sea compared to the deep northern North Sea. Past evidence from the southern and central North Sea suggests a peak in abundance in the 20 & 40 m range (Aurich, 1941; Lelievre et al., 2014). The timing of the surveys was early relative to the protracted spawning period of whiting (Hislop, 1984), as seen by the probability of presence increasing with the calendar day. Historically, whiting commenced spawning in January in the English Channel and spawning continued until June in the northern North Sea (Scott, 1913; Bal, 1940; Hislop, 1984). However, differences in the onset and spawning duration across the North Sea (Hislop, 1984) may explain why calendar day did not have a significant effect on abundance. Clearly, because of the survey timing, it is possible that any whiting that initiated spawning later may have used sites other than the areas detected in this study. Nevertheless, known latitudinal differences in spawning onset that might have affected the northern extent of spawning did not appear to be a problem as spawning whiting were found across the North Sea.

The delta model showed a similar performance to previous studies on fish density distribution (Lelievre et al., 2014; Grüss et al., 2014; González-Irusta and Wright, 2016a,b), although the performance of both models (binomial and negative binomial) showed a different performance. The binomial model showed a low explained deviance (19.2%) and a poor predictive performance (AUC and kappa values). These results were similar to previous attempts to model the distribution of whiting spawning grounds in the southern North Sea (Lelievre et al., 2014) and show the difficulty of predicting the presence of WSS. Although whiting seems to aggregate to spawn, more or less isolated individuals in a spawning stage were found in hauls all across the North Sea (Fig. 1) and therefore to model this distribution was challenging. Species such as whiting with a broad niche are less limited by the environmental constraints than species with a narrow niche at this spatial scale (Brotons et al., 2004) and usually receive lower scores in evaluation statistics (Reiss et al., 2011; Gonz & lez-Irusta et al., 2015). A more finely resolved set of environmental variables and the inclusion of other variables relevant for whiting spawning areas (such as prey distribution) may have improved the predictive power of the binomial models. In contrast, the negative binomial (abundance) model explained a higher percentage of deviance (65.2%) with a good spearman coefficient (0.44), similar to the work of Lelievre et al. (2014) and others on spawning distribution of gadoids (González-Irusta and Wright, 2016a). The delta model evaluation statistics were affected by the poor binomial model performance, as evidenced from the lower spearman coefficient value (0.37) compared to the negative binomial model (0.44). Nevertheless, the delta model still achieved similar scores based on the spearman coefficient to similar previous studies (Lelievre et al., 2014; Gonz & lez-Irusta and Wright, 2016a). The difference in presence and abundance model performance may be explained by a lack of a clear physical constraint on whiting spawning distribution across the North Sea but a clear preference for certain physical features that led to aggregation.

The persistence of some spawning areas of whiting indicated by this and past studies highlight the need for managers to consider the potential impact of marine developments on whiting. Whiting spawning areas include locations with strong tidal currents up to the lower level relevant to tidal energy devices. Although the area defined as persistent use is relatively large it does at least inform marine spatial planning of the need to consider this species in any development proposals off the east coast of Scotland and England. This is important given that the North Sea stock is still at a low state (ICES, 2016) and the dynamics of the northern and southern sub-populations can differ (de Castro et al., 2013), making regional depletion more likely. The persistence of major spawning aggregations, corresponding to previously identified population structure, also highlights that it is possible for managers to monitor spawner biomass at a population level, as a previous study has attempted to do (de Castro et al., 2013). We do acknowledge that the scale of our environmental layers and fish sampling are an important constraint on the resolution of distinguishing individual spawning grounds. Nevertheless, the information currently used to consider whiting spawning are based on the historic incidence of spawning staged whiting (e.g. Coull et al., 1998) and include spawning areas that are currently not in use.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2017.07.005.

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