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Delineating recurrent fish spawning habitats in the North Sea

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Abstract:

The functional value of spawning habitats makes them critically important for the completion of fish life cycles and spawning grounds are now considered to be "essential habitats". Inter-annual fluctuations in spawning ground distributions of dab (*Limanda Limanda*), plaice (*Pleuronectes platessa*), cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) were investigated in the southern North Sea and eastern English Channel, from 2006 to 2009. The preferential spawning habitats of these species were modelled using generalised linear models, with egg distribution being used as proxy of spawners' location. Egg spatial and temporal distributions were explored based on six environmental variables: sea surface temperature and salinity, chlorophyll *a* concentration, depth, bedstress and seabed sediment types. In most cases, egg density was found to be strongly related to these environmental variables. Egg densities were positively correlated with shallow to intermediate depths having low temperature and relatively high salinity. Habitat models were used to map annual, i.e. 2006 to 2009, winter spatial distributions of eggs, for each species separately. Then, annual maps were combined to explore the spatial variability of each species' spawning grounds, and define recurrent, occasional, rare and unfavourable spawning areas. The recurrent spawning grounds of all four species were located in the south-eastern part of the study area, mainly along the Dutch and German coasts. This study contributes knowledge necessary to the spatial management of fisheries resources in the area, and may also be used to identify marine areas with particular habitat features that need to be preserved.

Highlights

► The spawning ground distributions of dab, plaice, cod and whiting are explored from 2006 to 2009 in the North Sea ► Spawning habitat models are developed by relating egg density to six environmental descriptors ► Predicted annual habitat maps highlight suitable spawning areas and their spatial variability ► Recurrent spawning grounds are delineated for each species ► Most suitable and temporally stable spawning areas are defined for use in marine spatial planning

Keywords : egg distribution ; spawning grounds ; North Sea ; temporal variability ; habitat modelling ; GLM

1. Introduction

Fish spawning takes place in spatially limited areas (or grounds) with attributes that favour reproductive success through higher egg survival (Bellier et al., 2007 and Planque et al., 2004). Areas offering favourable environmental conditions often correspond to frontal zones (Munk et al., 2002 and Munk et al., 2009), which are transitional areas between water masses, such as upwellings, areas affected by tides, river plumes or estuaries (Bakun, 1996 and Munk and Nielsen, 2005). Monitoring fish spawning grounds has been identified as one of the key steps for an ecosystem-based approach to marine management (Anon, 2002). Spawning can indeed be affected by, and reflect, adult stock depletion, habitat disturbance, climate change and other processes (Begg and Marteinsdottir, 2002 and Rijnsdorp et al., 2009). Moreover, knowledge of the location and extent of fish spawning areas is also required for environmental risk assessment in the case of industrial developments, such as offshore energy and aggregate extraction for sand and gravel (Stelzenmüller et al., 2010). Therefore, knowledge and preservation of spawning grounds are essential for interpreting fish stock fluctuations, improving the management of stocks and hence maintaining appropriate population levels.

The eastern English Channel and North Sea sustain one of the richest commercial fisheries in the world, in terms of both diversity and abundance. These areas are also ecologically important, due to a number of fish spawning and nursery areas (ICES, 2009; Martin *et al.*, 2009). Many fish species display a year to year consistency in their spawning location, thereby reflecting a certain fidelity to particular grounds (Daan, 1981; Fox *et al.*, 2000; Fox *et al.*, 2008), and suggesting the existence of preferential spawning habitats. The frontal zones to which egg distributions are often linked may, however, vary from year to year (Munk *et al.*, 1999). Repeated *in situ* observations are an effective approach to study the spatio-temporal variability of fish spawning habitats (Bellier *et al.*, 2007), and can be carried out at high spatial resolution using the Continuous Underway Fish Egg Sampler (CUFES; Checkley *et al.* 1997). This way, grounds that are repeatedly used for laying eggs can be identified and delineated. The CUFES is relatively easy to operate and provides reliable estimates of egg abundance (Lo *et al.*, 2001) and distribution (e.g. sardine, *Sardina pilchardus* and whitehead's round herring, *Etrumeus whiteheadi*; van der Lingen *et al.*, 1998). It has successfully been used to map egg distribution and spawning grounds of pelagic fish species (Petitgas *et al.*, 2006; Lelièvre *et al.*, 2012a).

Habitat may be defined as geographical locations where biotic and abiotic conditions allow presence, or favour abundance, of a given fish species at a given life stage (Benaka, 1999). A number of statistical modelling techniques are available to predict species habitats (Guisan *et al.*, 2006; Planque *et al.*, 2011). For instance, Generalised Linear Models (GLM; McGullach and Nelder, 1989) belong to the family of linear regressions, and can be used to model the mean of response data that are not necessarily normally distributed. This approach consists in generating a model that summarises the relationship between a species' presence, or abundance, and a set of explanatory environmental variables. The model can then be used to predict the species' average distribution, using that of the environmental variables in the model (Martin *et al.*, 2012).

The present study aimed to explore spawning grounds’ spatio-temporal dynamics in the eastern English Channel and southern North Sea. Here, the focus is on four fish species, all of commercial importance: dab (*Limanda limanda*), plaice (*Pleuronectes platessa*), cod (*Gadus morhua*) and whiting (*Merlangius merlangus)*. These species spawn between January and June, with peaks in January for plaice (Simpson, 1959), February for cod, and March for whiting and dab (Munk and Nielsen, 2005). GLMs, coupled with a Geographic Information System (GIS), were used to map annual spawning habitats of each species, based on environmental variables. Then, the temporal variability of these habitats was assessed to define recurrent spawning areas, considered as the core of the spawning ground, i.e. where spawning takes place every year. Finally, areas deemed to be of upmost conservation value were delineated, based on the recurrent spawning habitats of dab, plaice, cod and whiting together.

2. MATERIALS AND METHODS

2.1 Sampling surveys

The International Bottom Trawl Survey (IBTS) takes place annually in the North Sea and part of the eastern English Channel (Fig. 1) to estimate stock abundance and recruitment level of the main exploited fish species (ICES, 2004). Taking advantage of the survey's path, data on fish eggs and environmental variables were collected from 2006 to 2009 (January, February), on-board *RV* Thalassa (Table 1).

2.2 Biological data

The four species investigated in this study spawn pelagic eggs that may drift with currents (Bunn *et al.*, 2000). Under calm conditions, eggs are expected to accumulate close to the surface, showing a clear peak in abundance in the upper layer (up to 20 m depth) (Conway *et al.*, 1997; Adlandsvik *et al.*, 2001, Pépin *et al.*, 2005). Using CTD profiles and vertical egg tows, Lelièvre *et al.*, 2012a have shown that in the southern North Sea, strong currents and winter wind conditions generally result in a well-mixed water column, so CUFES samples are usually representative of egg density over the entire water column. Although the CUFES alone cannot be used for a precise estimation of total egg density, it was shown to accurately depict the spatial distribution of eggs under the conditions of the present study.

Sub-surface samples were collected using the CUFES, which continuously pumped water 5 m below the surface, through a 5 cm diameter inlet protruding slightly from the hull and pumping water perpendicularly to the current. To enhance the catching efficiency, a metallic scoop was bolted on the side of the ship and was directed into the current. Samples were filtered over a mesh size of 500 μm, and collected every 30 minutes. For each sample, the volume of filtered water was determined using both sampling duration and the pump's recorded flow rate. Samples were fixed in a 0.9% buffered formalin seawater solution (Mastail and Battaglia, 1978; Lelièvre *et al.*, 2010a). Fish eggs were identified to species level, under a stereomicroscope (Leica MZ6), based on their size, the presence of oil globules and their degree of pigmentation (Russell, 1976; Munk and Nielsen, 2005). Species misdentification based on egg morphology is possible, but misidentification rates measured by molecular analyses were found to be small (7% for dab and 2% and 29% for cod and whiting respectively; Lelièvre *et al.*, 2010a, Lelièvre *et al.*, 2012b). Eggs were sorted into developmental stages and only stage 1 eggs (showing no embryo) were used for the present study as they were considered to accurately depict the location of the spawning grounds. Indeed, as this first developmental stage only lasts for two days or a little longer depending on temperature (Russell, 1976, Thompson and Riley, 1981, Ryland and Nichols, 1975) and as the retention time is high in the southern North Sea despite locally high tidal- and wind-induced currents (Maier-Reimer, 1977), such eggs were not expected to have significantly drifted away from their point of emission. Egg abundance (x) was then expressed as densities for a standard volume of 20 m^3 (close to that filtered during the 30 min sampling time), and log transformed ($\mathrm{Log}_{10}(x+1)$) (Legendre and Legendre, 2012).

2.3 Environmental data

Six environmental variables were tested as predictors in habitat modelling (Fig. 3): sea surface temperature (°C) and salinity (PSU), chlorophyll *a* concentration ($\mu g.l^{-1}$), depth (m), seabed sediments type and bedstress ($N.m^{-2}$). Surface temperature, salinity and chlorophyll *a* were continuously measured using a sub-surface (3-5 m) thermosalinometer and a fluorometer, respectively. Depth (m) was recorded using the vessel's sonar system. Seabed sediment types were extracted from Larsonneur *et al.* (1982) and Schlüter and Jerosch (2009), and reclassified into five broad categories: mud, fine sand, coarse sand, gravel and pebbles. Bedstress, a measure of friction on the seabed as a result of tidal currents, was estimated using a 2D hydrodynamic model, originally developed at the Proudman Oceanographic Laboratory (Aldridge and Davies, 1993). Although sediment type and bed stress may seem to bear no direct ecological relationship to pelagic fish eggs (presence and/or abundance), they are believed to be relevant proxies to the spatial distribution of demersal spawners. The latter certainly conditions the observed distribution of stage 1 eggs. Explanatory variables were tested for collinearity, based on correlation coefficients and variance inflation factor (Zuur *et al.*, 2007).

2.4 Habitat modelling

2.4.1 Model development

Spatially correlated data are not independent, which results in inflated rates of type I error, misspecification of the number of degrees of freedom and inaccurate, often over-fitted, models (Dormann, 2007). Data generated by continuous sampling tend to be highly auto-correlated, which disproportionately inflates the explanatory power of these variables, at the expense of potentially more important variables (Segurado *et al*, 2006). Although a number of methods can be used to incorporate a term of contagion encompassing the effect of spatial autocorellation in the analyses (Dorman *et al.*, 2007), these methods may overcompensate for avoiding the inflation effect (Kissling and Carl, 2008). An alternative procedure to avoid this pseudoreplication phenomenon is to subsample the original data by adopting a systematic scheme that constrains observations to be interspaced enough from each other (Segurado *et al*., 2006). This approach was preferred here as the large size of the available dataset easily permitted it. Based on a series of correlograms, it was found that a separation distance of 0.6 decimal degrees (dd) of latitude between observations was sufficient to remove autocorrelation. Three different sampling grids (A, B, and C) were hence created, each with a mesh size of 0.6 dd (Table 1), and used for model development (Fig. 2). Dataset D, shown in Fig. 2 and kept for model validation, gathered all observations not used for datasets A, B and C.

GLMs are flexible in that they can be applied to data that are not necessarily normally distributed. Bedstress, chlorophyll *a* concentration and depth were nevertheless log-transformed, and so was salinity (using $\exp(x)/10^{15}$), so as to improve the linearity of their relationship with egg density. Seabed sediments types (a categorical variable) were tested in the modelling procedure as factors, whilst the five other variables (of continuous nature) were tested as first and second order polynomial forms, as data exploration plots suggested that the shape of species-environment relationships would often be better described as curvilinear.

Histograms of egg densities highlighted a discontinuity between the zero values and positive density data. A two step modelling procedure was hence adopted, whereby the presence of eggs was modelled separately from their density level (Stefánsson, 1996; Barry and Welsh, 2002; Lauria *et al.* 2011). Presence-absence data were modelled using a binomial model with a logit link. Non null (log-transformed) densities were modelled using a Gaussian model with identity link function (McCullagh and Nelder, 1989), to predict the mean density on a log scale.

Datasets A, B and C were used, each in turn, to select the models' explanatory variables and estimate the models' parameters. Starting from an initial full model containing all the variables as main effects, predictors were removed by backward elimination, first by minimising the Akaike's Information Criterion (AIC; Akaike, 1974; Sakamoto *et al.*, 1986), and then the Bayesian Information Critetion (BIC; Schwarz, 1978). The same procedure was repeated starting from an initial full model containing all variables expressed in their second order polynomial forms. This procedure resulted, for each species, in 36 (i.e. 18 binary and 18 Gaussian) different model parameterisations,including the initial full models (see Supplementary Material).

2.4.2 Model selection

To quantitatively assess the models' predictive power, their 18 predictions were compared with observed values in dataset D, using a range of diagnostic measures. In the case of binomial models, the Receiver Operating Characteristic (ROC) curve (Guisan and Zimmermann, 2000) showing the trade off between prediction sensitivity and specificity was computed, and the Area Under that Curve (AUC) was calculated. For Gaussian models, the Mean Absolute Error (MAE) was calculated. For both model types, the coefficient of determination (R^2) was also computed (Legendre and Legendre, 2012) and models were ranked according to these three measures. The 'final' binomial model would be the one with highest R^2 and AUC values, while the 'final' Gaussian model would be the one with highest R^2 value and lowest MAE value.

2.4.3 Model evaluation

Each final model was further evaluated with complementary measures. Model fit was assessed using the adjusted coefficient of determination (Adj-R^2; Legendre and Legendre, 2012). In the case of Gaussian models, Spearman's rank correlation tests investigated whether there was a positive and significant correlation between observed and predicted values, whilst Wilcoxon signed-rank tests compared the mean and variance of observed and predicted densities (Wilcoxon, 1945) to assess whether there was a significant difference between observed and predicted values' distribution ranges. Finally, Moran's I correlogram was used to test the significance level of spatial autocorrelation in the models' residuals, with separation distance class equal to 0.8° (to insure full connectivity) and over 10 lags (to cover the entire study area) (Diniz-Filho *et al.*, 2003; Bocard *et al.*, 2011). Holm's correction of *p*-value was applied (Bocard *et al.*, 2011).

2.4.4 Combining binary and Gaussian predictions (delta model)

For each species, the final binary model (predicting presence probability) was combined to the final Gaussian model (predicting density level on a log scale) by multiplying their prediction values into a final, so-called, delta habitat model illustrating the species' egg density conditioned to its presence (Barry and Welsh, 2002). Predicted probabilities of presence were first transformed into presence-absence data based on a threshold probability indicative of species presence. This threshold was determined by comparing the confusion matrices between observed and predicted values in the full dataset (i.e. datasets A+B+C+D). Specificity was calculated as the ratio of correctly predicted absences to the total number of absences, and sensitivity as the ratio of correctly predicted presences to their total number. Two optimising criteria were considered: (1) minimising the difference between sensitivity and specificity (MDS) and (2) maximising the sum of sensitivity and specificity (MSS) (Jimenez and Lobo, 2007). When the thresholds determined by these two methods were not equal, the lowest threshold was used to lower the omission error rate.

For each species, the delta model's behaviour was assessed over the entire available dataset (A+B+C+D) by comparing predicted and observed egg densities using Adj-R^2, Spearman's rank correlation and Wilcoxon signed-rank tests. In order to provide confidence intervals for these measurements, 1,000 bootstrapped datasets were also generated.

Delta models implicitly account for interactions between explanatory variables, and may be difficult to assess. So as to facilitate ecological interpretation of the delta models, their behaviours along each relevant environmental gradient were plotted. Predicted values were shown as boxplots against observed values, so as to graphically examine the effect of the combination of binomial and Gaussian models on the shape of the relationship to each explanatory variable. Overall prediction errors were computed for each final delta model as the absolute standardised residuals from a linear regression between predicted and observed egg densities.

The packages car (Fox and Weisberg, 2011), MASS (Venables and Ripley, 2002), boot (Canty and Ripley, 2012; Davison and Hinkley, 1997), verification (Research Application Program, 2012), PresenceAbsence (Freeman and Moisen, 2008), spdep (Bivand *et al.*, 2012) were used in R (R Development Core Team, 2009), to carry out the analyses described above.

2.4.5 Annual habitat maps derived from the delta models

Maps of the six environmental variables were either readily available (i.e. sediment, depth), or produced by kriging interpolation (i.e. bedstress, and *in situ* surface temperature, salinity and chlorophyll *a* concentration for each year between 2006 and 2009). Figure 3 shows these maps, although average values are shown for surface temperature, salinity and chlorophyll *a* concentration. For each species and each year between 2006 and 2009, the delta model was mapped within a Geographic Information System (ESRI ArcGIS 9.1) by applying the regression coefficients of the binomial and Gaussian models to the maps of the corresponding set of environmental variables. The presence-absence threshold was applied to the ‘presence probability’ map (corresponding to the binary model), which was then multiplied to the ‘egg density’ map (corresponding to the Gaussian model), thereby resulting in one ‘habitat map’ per species and per year (i.e. 16 in total; Stefánsson, 1996; Barry and Welsh, 2002; Le Pape *et al.*, 2003). Maps of the prediction errors were produced by interpolation in order to illustrate their spatial patterns.

2.5 Fluctuation in spawning location

The annual habitat maps (created in section 2.4.5) were used to explore inter-annual variability in spawning location for each species between 2006 and 2009. In each annual habitat map, egg density predictions were rescaled to range between 0 and 1. Then, for each species separately, the four rescaled maps were averaged (referred to as "average map"), and a standard deviation estimated (referred to as "variability map"), within a GIS. Finally, the average and variability maps were combined in order to identify four categories of spawning areas (referred to as “habitat type”; Bellier *et al.*, 2007): (1) recurrent spawning areas, where spawning is observed every year (high mean and low standard deviation); (2) occasional, where the spawning occurrence varies greatly from year to year (high mean and standard deviation); (3) rare (low mean and high standard deviation); and (4) unfavourable (low mean and standard deviation) spawning areas, where spawning is almost never observed. The median values of both the average and variability maps were used as splitting thresholds between high and low values.

2.6 Delineating multi-species spawning areas

In order to identify zones of the study area that could be of conservation and management interests, a multi-specific habitat map was created, combining the habitat patterns of the four species considered. This was done by summing the four "average maps", one for each species (see section 2.5), resulting in the combined potential spawning ground of all four species.

In parallel, the recurrent spawning areas of each species were set to 1, and the other habitat categories (i.e. occasional, rare or unsuitable) to zero: the four resulting binary maps were summed to highlight the core spawning grounds effectively used every year by all four species.

3. RESULTS

3.1 Habitat modelling

Relationships between the six environmental variables were explored (Table 2) and were found not to be collinear (variance inflation factor < 2.5). They were therefore all tested in model development. Only models calibrated with datasets B or C were retained, and final models could contain either all tested environmental variables expressed in their polynomial forms (initial model formulation), or a lesser number of variables, selected by backward selection, using either AIC or BIC (Tables 3, 4 and 5).

Final binomial models had Adj-R² ranging from 0.03 to 0.33, depending on the evaluation dataset used, and all AUC values were >0.7 (Table 4). In most instances, little (<0.3) or no significant autocorrelation was detected in the models' residuals. Presence-absence cut-off values, determined using MSS criteria, ranged from 0.26 to 0.56, depending on the species. Final Gaussian models had Adj-R² ranging from 0.63 to 0.94 (Table 5). Spearman's rank correlations between observed and predicted values were positive and significant in all cases, and no significant difference between them was detected using the Wilcoxon signed-rank test. In most instances, little (<0.15) or no significant autocorrelation was found in the models' residuals.

3.1.1 Delta models

Delta model evaluations are shown in Table 6. For each species, the model's Adj-R² was found to be relatively high (> 0.80). Consistent with this, Spearman's rank correlation coefficients between observed and predicted values ranged between 0.31 and 0.49; these coefficients were found to be higher for dab and plaice than for cod and whiting. The Wilcoxon signed-rank test was significant for all species, indicating that there was a difference between observed and predicted means and variances of density. This revealed that the resulting delta models were unable to fully reproduce the observed range of egg density levels. The mean absolute standardised residuals varied between 0.3 and 0.8.

Fig. 4 illustrates each species' response to each of the environmental variables. Low to intermediate depth, bedstress and temperature constituted optimal environmental conditions, while intermediate to high levels of salinity were found to be suitable for all species investigated. Intermediate to high chlorophyll *a* concentration seemed unsuitable to most species, but dab. Egg density levels were higher on sand or mud for cod and dab, while plaice and whiting seemed to be more tolerant to coarser sediments.

3.1.2 Annual habitat maps

The annual habitat maps (Fig. 5) reflected these differences: the predicted distributions of dab and cod eggs were mainly located off the Belgian, Dutch, German and Danish coasts, and on the Dogger Bank. Plaice spawning habitats were predicted offshore in the central part of the study area, whilst those of whiting were more inshore, near the French coast, and along the Belgian and Dutch coasts. The distribution patterns of the models' errors were very patchy and appeared almost random in areas of high density levels, compared to areas of absence where model error was more evenly distributed.

3.2 Fluctuation in spawning location

Average distributions of dab, cod and plaice egg densities (Fig. 6) were found to cover a large part of the study area, located mainly near the Dutch, German and Danish coasts and excluding the northwestern part along and off the British coast. The average distribution of whiting was limited to the southern Bight and off the Norfolk coast. In general, higher temporal variability was located in the eastern part of the southern Bight, on the Dogger Bank and along the coasts of the German Bight.

Maps of recurrent, occasional, rare and unfavourable spawning areas resulting from the combination of the average and variability maps are also presented in Fig. 6. For dab, plaice and cod, recurrent spawning areas were mainly located in the south-eastern part of the North Sea, off the Dutch, Danish and German coasts. The north-western part of the study area, near the Scottish coast seemed to be an unfavourable spawning habitat for these species. Whiting exhibited spatially-restricted recurrent spawning areas offshore of the three estuaries, and occasional spawning areas near them. The southern Bight was rarely used for spawning, whilst the central North Sea seemed unfavourable for spawning at that time of the year.

3.3 Multi-specific spawning areas

The multispecific spawning habitat map (Fig. 7, left) highlighted that suitable winter spawning habitat covered a large area in the south-eastern part of the North Sea, including the entire German Bight and a smaller area to the south of the Dover Strait. These correspond to areas having shallow depth, and intermediate salinity and temperature. Moreover, the spawning recurrence frequency map, combined for all species (Fig. 7, right), highlighted as core spawning areas over the 2006 to 2009 period the Dogger Bank, an offshore area located southeast of it, the whole of the German bight, and a small area located south of the Dover strait.

4. DISCUSSION

The present study used GLMs to investigate and map winter spawning habitats of cod, whiting, plaice and dab, based on stage 1 egg density data and a set of environmental variables. For the first time in this area, GIS calculation combined these habitat models with annual environmental maps so as to explore annual fluctuations in habitat use, through the mapping of recurrent, occasional, rare and unfavourable spawning areas. Finally, a multi-specific integration of these results was performed to designate the most important areas for winter spawning in the southern part of the North Sea.

4.1 Strengths and weaknesses of the modelling approach

The modelling methodology developed for the present study was inspired by multi-model approaches (Burnham and Anderson, 2002; Loots *et al.*, 2010a; Planque *et al.*, 2011): a single final model was selected based on its predictive power, which was evaluated using an independent dataset. For the eight final models (two by species), only datasets B and C were retained for model calibration. Although slightly larger, dataset A did not seem to contain enough information to adequately parameterise the models. This result revealed that the approach taken, of developing models using three different calibration datasets, was more precautionary and avoided overlooking important parts of information when sub-setting the full dataset (Legendre and Legendre, 2012). In many instances, the full model was retained, showing that removing variables would negatively impact the predictive power of the models. Besides, BIC-based model selection was often found to yield better results than model selection based on AIC; BIC model selection is often preferred to AIC, when the aim is to select more parsimonious models (Wagenmakers and Farrell, 2004).

Binomial models' performances, measured using AUC, often resulted in relatively good results (AUC>0.7), regardless of the dataset used (development or independent). Adj-R² of binomial models remained lower than expected, suggesting limited explanatory power, especially for whiting. This was further highlighted by the very low presence-absence cut-off value retained for this species, for which eggs were in fact observed at low levels over most of the study area. It is possible that low density levels, below the detection threshold of the CUFES, may have caused "methodological" false absence (Lobo *et al.*, 2010) and negatively impacted the model's reliability. In contrast, Gaussian models performed well for all four species. Once the models were combined into delta models, the measured performances remained very satisfactory (based on Adj-R² and Spearman's rank correlations), although the delta models were found to predict significantly lower values than those actually observed. By construction, delta models combining presence-absence and central tendency levels of density can never reproduce the highest densities observed (Loots *et al.*, 2010 and 2011).

Nevertheless, these results highlighted that the patterns of fish egg distribution was very influenced by environmental conditions. Although these models presented high Adj-R², environment alone is not believed to be the sole driver of spawning ground choice. Local egg density may also be influenced by other factors relative to characteristics intrinsic to the population (Planque *et al.*, 2011), such as spawners' density or demographic structure (Loots *et al.* 2010a; Loots *et al.*, 2011). Moreover, spawning is known to interact with biotic controls, such as predation, competition, food availability, parasites and disease. Future studies on modelling the spawning grounds using egg distribution should account for other factors, such as demographic or biotic controls.

The methodological approach taken here was designed to limit the effect of autocorrelation by building models on spatially independent subsets of the data, and select these models based on their predictive power using an independent dataset. The low, and often non-significant, levels of spatial autocorrelation left in the models' residuals confirmed the correctness of the approach. The absence of clear pattern in the model standardised residual maps was further evidence of this. In the case of dab egg distribution, however, significant autocorrelation could still be detected, which indicated that spatial dependence could occur at larger scale than the sampling grid resolution (0.6 dd). Using a coarser resolution would have resulted in even smaller calibration datasets and an important loss of information. For this species, the use of detrending technics (Legendre and Legendre, 2012), or a model with a contagion component (Dormann *et al.*, 2007), may be solutions. However, such methods may also overcompensate for spatial autocorrelation (Segurado *et al.*, 2006; Khun, 2007; Kissling and Carl, 2008), and fail to disentangle the induced spatial dependence from the autogenic autocorrelation.

4.2 Delineating spawning habitats using environmental variables

Eggs of the four species considered in this study are pelagic and drift passively; it is hence not straightforward to define their habitat (Fuiman, 2002). Abiotic factors such as sediment types or currents are, however, expected to affect habitat use by demersal spawners. Temperature is an important variable since it affects the rate of development and the mortality of eggs, while salinity influences the buoyancy of eggs (Gibson, 2005). Finally, chlorophyll *a* concentration is a proxy for primary production. The present study revealed a clear link between environmental conditions and the spatio-temporal distribution of spawning grounds. The binomial and Gaussian models separately highlighted which variables conditioned egg presence and density levels, confirming that different ecological mechanisms were at play behind observed presence-absence and density levels, thereby justifying the two steps modelling approach. All the tested environmental variables were retained in the final delta models. This indicated that these variables were good proxies of the factors at play in the determination of these species' spawning habitats.

During the study period, chlorophyll *a* concentration was relatively low, with a four-year mean of 0.51 µg.l^{-1}, with highest concentrations mainly found along the Belgium and Dutch coasts, and over the Dogger Bank. Egg distributions appeared to be negatively linked to chlorophyll *a* concentration. However, only very high chlorophyll *a* levels have detrimental effect on egg density and only very coastal areas may truly present lower habitat suitability. In the Gulf of Tunis, where chlorophyll *a* concentrations are much lower than those observed in the southern North Sea, it was not directly correlated with the spatial distribution of fish eggs (Zarrad *et al.*, 2003).

For all four species, low to intermediate depths were found to favour both egg presence and densities. Spawning grounds are often found at shallow depths in the southern North Sea (Gibson, 2005) and depth is known to be a major element influencing fish egg distribution in other areas (e.g. Zarrad *et al.*, 2003). For instance, dab spawns in coastal waters, on the Dogger Bank and in the central North Sea, at depths between 20 and 40 m (van der Land, 1991; Rijnsdorp *et al.*, 1992). Similarly, high concentrations of plaice eggs are typically found in shallow areas, shallower than 50 m (Harding *et al.*, 1978).

The annual habitat maps resulting from the specific environmental configuration of the study area highlighted that higher salinities often favoured high egg densities. The separate effects of salinity on egg presence or density could, however, be quite variable amongst species. This revealed that the effect of salinity in the delta model may have been masked by other, more constraining, variables, such as depth. Although little is known about the salinity influence on spawning habitat, Laurence and Rogers (1976) found that cod eggs could develop within a salinity range of 28-36 PSU, and Riley and Parnell, (1984) reported that cod spawned in waters of salinity ranging between 34 and 35 PSU. Mean salinity in the study area was 34.9 PSU, decreasing to 30.2 PSU along the Belgium, Dutch and Danish coasts, due to fresh water flowing into the North Sea from numerous river estuaries (Meuse, Rhine, Escaut, Elbe and sometimes the Thames River). Therefore, these relatively low salinity areas may not always be suitable for cod, and possibly the three other spawning species.

Temperature was found to be negatively correlated to egg density in almost all the models developed here, regardless of the species, although this environmental variable may increase the presence probability of plaice and dab eggs. Temperature is known to influence the time and duration of the spawning season (Gibson, 2005), along with incubation time and egg survival (van der Land, 1991; Bunn *et al.*, 2000). During the surveys, warmest temperatures were measured close to the Scottish coast (9°C), whilst colder waters (4°C) occurred along the German and Danish coasts. This temperature range was not truly limiting for the studied species: plaice eggs have a survival range between 2 and 8°C (Harding *et al.* 1978), whiting eggs survive well at temperatures between 6°C and 9°C (Loots, 2010a) and cod eggs between 2 and 10°C (Laurence and Rogers, 1976, Righton *et al*., 2010). The shape of the relationships modelled in the present study reflected these survival ranges, with plaice, cod and dab spawning habitat being more restricted to the coolest waters (<7°C), although plaice could also tolerate relatively warmer temperatures, and whiting having a broader temperature preference.

Overall, these results confirmed that spawning areas were mainly distributed near frontal areas, which are located between low salinity coastal waters and shelf waters, in agreement with Munk *et al.* (2002 and 2009). Indeed, the hyaline front located in the eastern part of the North Sea, in the shallow Region Of Freshwater Influence (ROFI), mainly in the Dogger Bank and German Bight areas, represents areas of low salinity, resulting from freshwater inputs from rivers and the shelf sea regime of small salinity gradients. These areas are known to be extremely productive habitats that support relatively dense aggregations of early stage fish.

In the study area, bedstress was most intense in the southern part in the Dover Strait and adjacent areas. Most species appeared to prefer low to intermediate bedstress levels, though whiting was clearly more tolerant to higher bedstress levels. Plaice and dab spawning adults have already been shown to prefer areas with weak to intermediate bedstress (Loots *et al.*, 2010a, Martin *et al.*, 2010). Weak bedstress associated to fine sediment types may be representative of less disturbed areas in term of currents, which may favour spawning. In the present study cod, dab and plaice eggs were found over mud and sand, while whiting eggs could be found on a wide variety of coarse sediment types. Gibson (2005) showed that flatfish populations occur in areas where there are large areas of shallow sandy or muddy-sand sediments, which are common in the North Sea. Although many species do not feed during spawning (Rijnsdorp, 1989; Fuiman and Werner, 2002), seascape provided by substrates and associated benthic fauna might still remain fundamental for spawning location selection by bentho-demersal species. This may explain why seabed sediment type was significant in almost all models.

4.3 Fluctuation in spawning grounds location

Although only based on four years of survey data (from 2006 to 2009), the present study attempted to delineate boundaries between recurrent and occasional spawning sites. In a preliminary study of the CUFES' efficiency, species egg composition and density found in CUFES were compared to vertical egg tow samples over the same area and at the same period (Lelièvre *et al.*, 2012a). Some species egg such as flounder were better represented in CUFES possibly resulting from positive egg buoyancy or a near surface spawning behaviour. On the other hand, in low wind speeds, shallow water and weak bedstress conditions, the water column mixing may become insufficient for CUFES to accurately depict egg density over the whole water column. Change in egg catchability in the sub-surface layer may alter CUFES efficiency and, as a result, wind speed variability between the different years of study may generate change in the observed egg distribution. However, this former study also showed that differences in sampling efficiency between the two studied gears were not large enough to unduly influence distribution maps and we do not believe this effect to be significant in our present results. Hence, the methodology presented here provides a practical approach for measuring the temporal variability associated with fish egg distributions. The methodology used in Bellier *et al.* (2007) was modified to account for the fact that high variability levels may reflect both large abundance values and high inter-annual variability. Here, the rescaling of each annual map between 0 and 1 enabled to disentangle both sources of variability, and to eliminate annual change in absolute density levels, so as to focus only on the spatial variability; this resulted in an improved delineation of recurrent areas.

Dab eggs were widely distributed throughout the study area, mainly offshore (Gibson, 2005), over the Dogger Bank, which represented a recurrent spawning area and corresponded to large adults distribution patches (Martin *et al.*, 2010). However, aggregations of dab eggs could also be found near the Dutch, German and Danish coasts. These patterns were partly confirmed by previous studies that showed that dab spawning occurs throughout the south-eastern part of the North Sea, with offshore egg concentrations in the German Bight and on the Dogger Bank (Bohl, 1957; van der Land, 1991; Rijnsdorp *et al*, 1992). Although Harding and Nichols (1987) also found some egg concentrations north-east of Flamborough Head, this was not the case in the present study, maybe due to the difference in study period (end of January to end of May for Harding and Nichols' study).

Plaice spawning grounds were mainly distributed offshore from the Dutch, German and Danish coasts (Gibson, 2005). Harding *et al.* (1978) reported that plaice spawning occurs over most of the offshore and deeper parts of the southern North Sea, which corresponded in the present study to a recurrent spawning area. However and in contrast to Hessen and Rijnsdorp

(1989) and Fox *et al.* (2005b), lower egg density was also found in the eastern English Channel and in the southern Bight. The eastern English Channel was categorised as a rare spawning area, with low egg density and high inter-annual variability in January-February. This may be due to a northward extension of plaice spawning ground, or to the timing of the survey which may not coincide with its spawning season in the English Channel.

In the present study, cod eggs were mainly distributed near the Dutch, German and Danish coasts. This distribution was similar to historical patterns where eggs were the most abundant around the southern and eastern edge of the Dogger Bank and in the German Bight (Brander, 1994; Fox *et al.*, 2005; ICES, 2005b; Fox *et al.*, 2008; ICES, 2010). Although spawning aggregations may be found offshore all over the North Sea, a survey in spring 2004, showed that the most important concentration was found in a restricted area to the northwest of the Dogger Bank (Fox *et al.*, 2005b), and that egg density in the southern North Sea was much lower than in the past (Daan *et al.*, 1978). In the present study, cod spawning grounds seemed to be recurrent in the southern North Sea, and occasional in the eastern English Channel, as for whiting.

High concentrations of whiting eggs were mainly located in the eastern English Channel, in the southern Bight and south of the Dogger Bank. These areas were categorised as occasional spawning grounds, due to high inter-annual variability. These results are in agreement with historical spawning areas described by Coull *et al.* (1998), Gibb *et al.* (2004) and ICES (2010).

Results presented here highlighted a strong fidelity of adults for their spawning grounds. This has already been reported for plaice (ICES 2005a and b; ICES 2007), based on historical data (e.g. Simpson, 1959). Moreover, tagging experiments have demonstrated strong spawning site fidelity behaviour by plaice in the North Sea (de Veen, 1978, Hunter *et al.*, 2003), around Iceland (Solmundsson *et al.*, 2005), and in Scottish waters (Wright *et al.*, 2006). Studies of spawning distributions of abundant North Sea fish (e.g. for cod: Brander, 1994; Daan, 1981; Raitt, 1967, e.g. for plaice: Simpson, 1959) generally suggest a persistent use of spawning areas over time (Heath *et al.*, 1994; Hunter *et al.*, 2003; Gibb *et al.*, 2004), and this even though past population sizes may have been much larger than they currently are (Daan, 1978; Brander, 1994; Fox *et al.*, 2008). Fox *et al.* (2000) suggested that spawning locations of cod and plaice have probably not changed much over the last 30 years. Cod, whiting and plaice spawning stock biomass were at their historical low in 2006 and showed the first signs of recovery in the following years (ICES, 2013). The present study therefore explores their spawning grounds' distribution in a period of particularly intense contraction of spawners' abundance. In contrast, dab landings were above average over all the study period (ICES, 2013). Moreover, Loots *et al.* (2010a and b) and Loots *et al.* (2011) showed that spawning adults of plaice and whiting had a strong geographical attachment for their spawning grounds, which suggests a homing mechanism (Papi, 1992). Spawning site fidelity may result from an adaptative strategy to place progeny within suitable environment and allow recruitment success (Peck *et al*., 2009, Hunter *et al*., 2003). The presence of predictable transport trajectories (such as tidal streams or dominant wind direction), allowing passive transport to nursery grounds, is believed to be the main driving factor explaining geographically stable spawning site selection (Cushing, 1990, Wennhage and Pihl, 2001).

The occasional spawning areas highlighted in the present study may play an important role in population renewal. For instance, these areas may actually display higher egg densities before and/or after the surveys occurred, i.e. January-February. At that time of year, not all studied species happen to be in the same spawning condition. The studied period corresponded to the peak of spawning for both plaice (Harding *et al.*, 1978), which spawn from December to April (Munk and Nielsen, 2005) and cod (Heessen and Rijnsdorp, 1989), which has peak of spawning from the last week of January to mid-February (in the study area). However, and although their eggs were very abundant, dab and whiting's spawning seasons were just starting at the time of the surveys. Dab is believed to spawn from February to April (Htun-Han, 1978), and from February to June with a peak in April for whiting (Gibb *et al.*, 2004). Similarly, common sole spawning period is understood to only begin in March (Munk and Nielsen, 2005); as some sole eggs were identified during the survey, it may be that some individuals are able to start spawning well in advance of the bulk of their population.

For dab, plaice and cod, occasional areas were southward coastal extension of recurrent areas. These areas, corresponding to the main river plumes, may be too cold, too desalted or too rich in nutrient to always serve as suitable spawning grounds for them. Moreover, in these areas spawning may be influenced by water quality (both eutrophication and pollution) and exposure to pollutants may generate chemical changes in the eggs, causing deformities or reduced viability (Gibson, 2005). In the case of whiting, occasional areas formed the bulk of its spawning grounds and covered the entire southern Bight, clearly indicating that the survey data did not capture the peak of spawning and the core spawning grounds of this species.

4.4 Conservation of spawning areas

By 2020, at least 10 per cent of coastal and marine areas should be conserved through systems of protected areas, according to Aichi Biodiversity Target 11 (Conference of the Parties to the Convention on Biological Diversity, 2010). The establishment of Marine Protected Areas (MPAs) is one way to achieve this objective, along with being an important tool for fisheries management (Côté and Finney, 2006). Several studies have shown that MPAs can achieve conservation and fisheries management objectives by increasing biodiversity, restoring population structure and the dynamics of stocks and by facilitating the establishment of stable and productive ecosystems (Araújo and Williams, 2000; Fisher and Frank, 2002; Gell and Roberts, 2003; Roberts *et al.* 2005; Kremen *et al.*, 2008; Kraus *et al.* 2009). When spawning aggregations are the main target of commercial fisheries, some MPAs may be designed to specifically protect the corresponding areas. They are generally positioned on spawning or larval settlement areas, which requires information on fish egg aggregation and transport processes of larvae (Christensen *et al.* 2009). Thus, knowledge on spawning ground locations can directly contribute to the sustainable management of fisheries' resources, and managers may decide to prohibit the use of a given area to protect spawning and hence help maintaining a productive fishery. Other technical measures include limiting trawl mesh size to protect adults and ensure that they have the opportunity to reproduce at least once (Fuiman and Werner, 2002). Spawning and nursery grounds may also be closed to other human activities that can alter the physical or chemical properties of the habitat, and hence their suitability. One of the reasons for monitoring and delineating spawning areas over time is because they are flexible in time (which was confirmed in this study) but this is seldom taken into account in management. The use of recurrence maps, defining which areas are repeatedly used over time may inform managers on the location of the most stable spawning grounds.

The multispecific winter spawning habitat map highlighted areas that were the most suitable for the four species considered: these included the Dover Strait, a large area extending from the Dutch, German and Danish coasts to the Dogger Bank and the Flamborough Head, which are also main nursery areas (Harding and Nichols, 1987). These areas are very partially protected by existing Natura 2000 areas, as in the German Bight, and planned marine parks (e.g. that of the "three estuaries" in the eastern English Channel). This map is well adapted to a precautionary principle approach, as it reflects all potentially suitable areas to the four studied species spawning although it might be difficult to implement the protection of such large areas. On the other hand, the spawning recurrence frequency map highlighted a different area of smaller spatial extent, and located offshore in the southeastern North Sea. This map showed recurrent spawning areas, exhibiting a stronger temporal stability in both their characteristics and use by the four species, which may be easier in practical terms to protect, especially as they are located away from intensive coastal human activities. However, intensive fishing effort takes place in this area and protection of the spawning grounds against fisheries may be difficult to put into place (Coull *et al*., 1998, Jennings *et al*., 1999, Greenstreet *et al*., 2007).

5. Conclusion

Ichthyoplankton surveys are a powerful tool to better understand spawning areas (Fox *et al.*, 2005a), and the present study has provided high-resolution maps of spawning habitats, and new insights on their utilisation by spawners. Environment-driven recurrent spawning grounds were well defined and coherent with other studies, and large occasional spawning areas were also highlighted. If a policy ensuring sustainable use of marine resources is to be implemented in the southern North Sea, the knowledge on the location and functionality of spawning habitats is a critical step for selecting a combination of sites with good spatial and ecological coherence.

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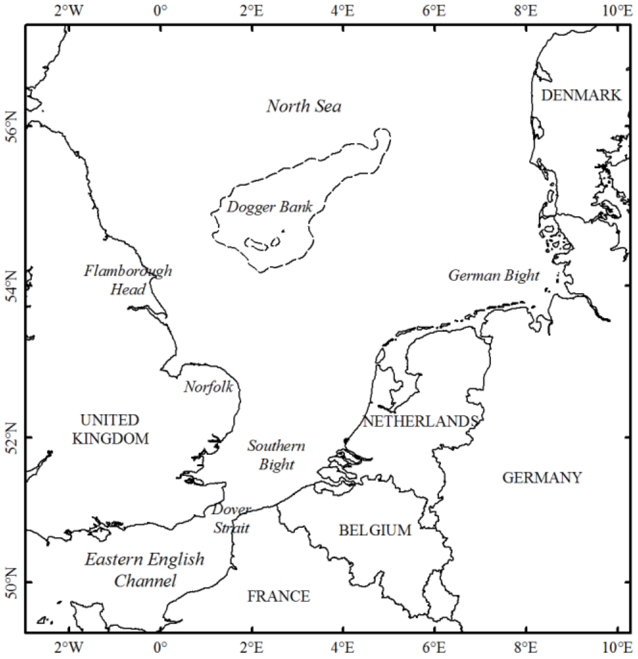

Figure 1: Study area, showing locations mentioned in the text.

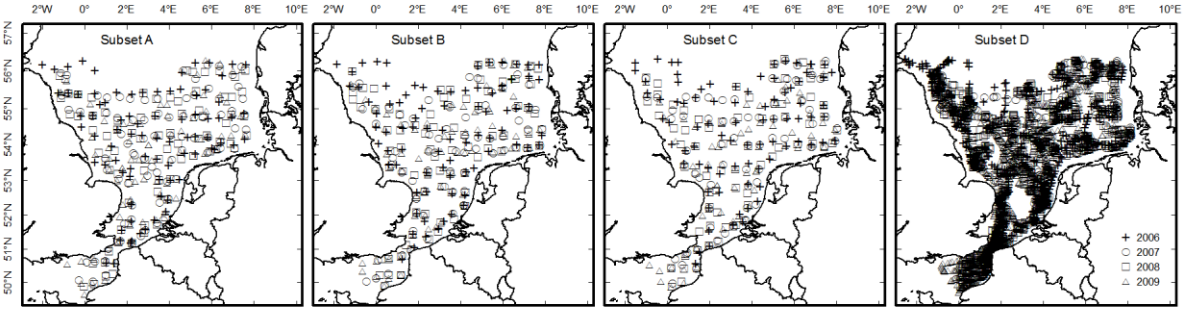

Figure 2: Sampling locations by CUFES (Continuous Underway Fish Eggs Sampler) during the French IBTS (International Bottom Trawl Survey), from 2006 to 2009. The three subsets A-B-C used for model calibration and the remaining dataset D used for model evaluation and selection are shown separately.

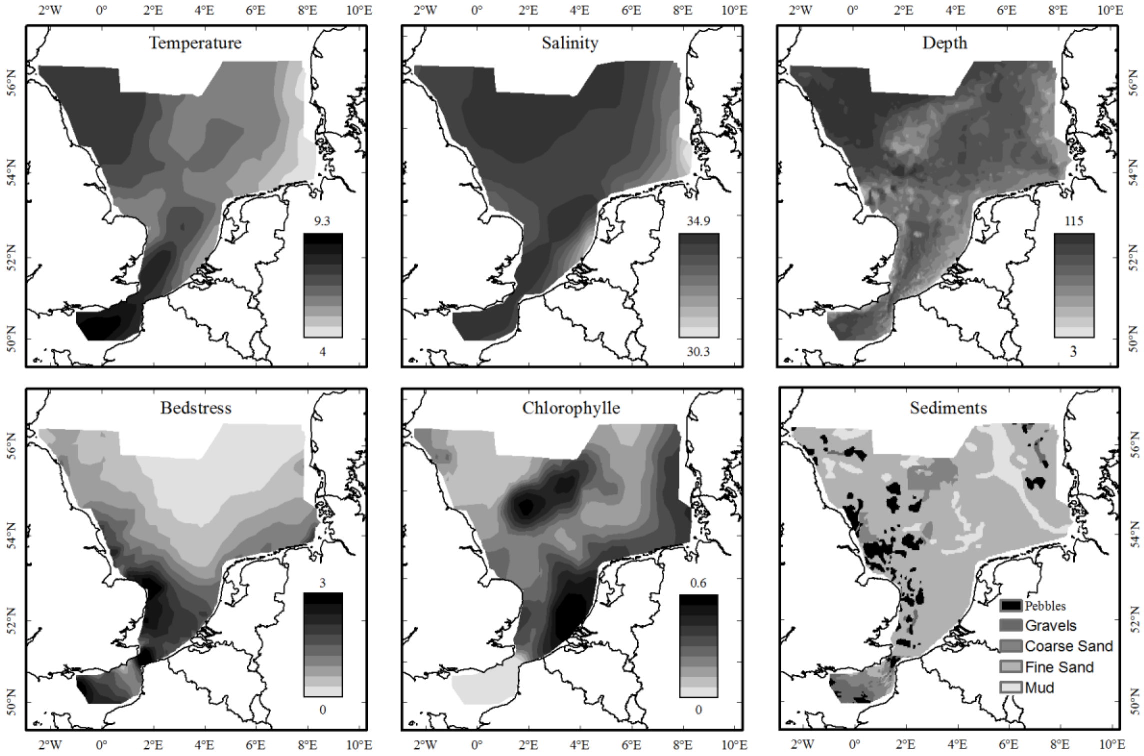

Figure 3: Maps of the five environmental variables (clockwise, starting from top-left): surface temperature (°C), surface salinity (PSU), depth (m), bed stress (N.m-^{2}), surface chlorophylle *a* concentration (µg.l^{-1}), and seabed sediment types, used as predictors in the habitat modelling procedure. For temperature, salinity and chlorophyll *a*, maps show averages for the 2006-2009 winter period of the French IBTS.

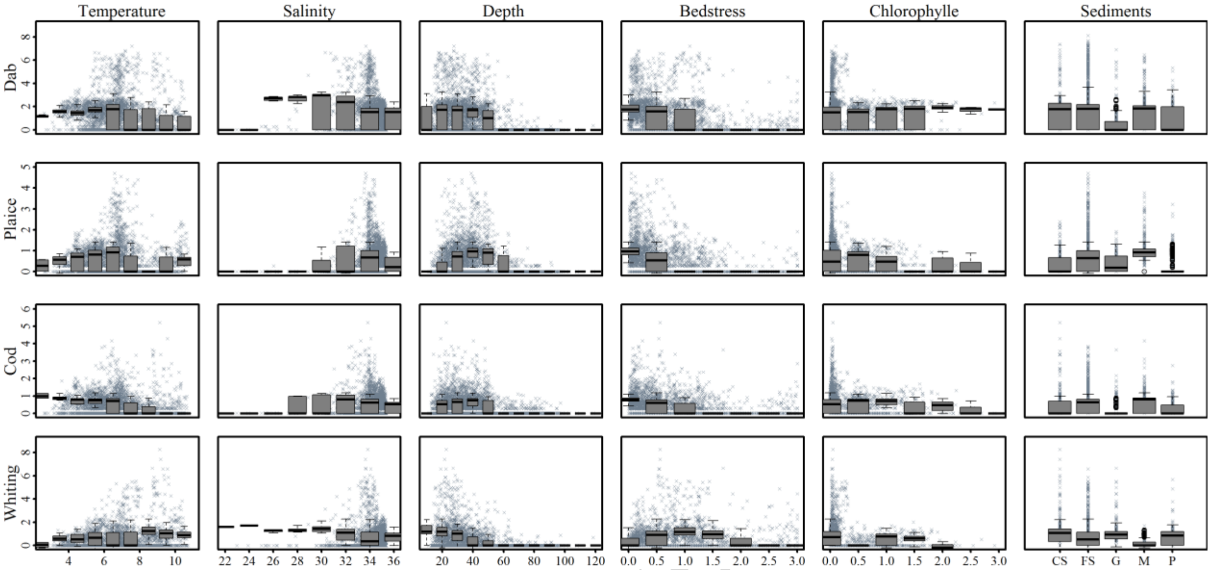

Figure 4: Plots showing predicted (boxplots) and observed (dots) egg densities, against each environmental variable (maps shown in Fig. 3). Predicted (delta model) and observed values are transformed using $\log_{10}(x+1)$, with x = number of eggs per 20 m^3. The lower, median and upper hinges of the boxplots show the 1st, 2nd and 3rd quartiles of the predicted values, respectively. The boxplots' whiskers extend to the most extreme data point that is no more than 1.5 times the interquartile range.

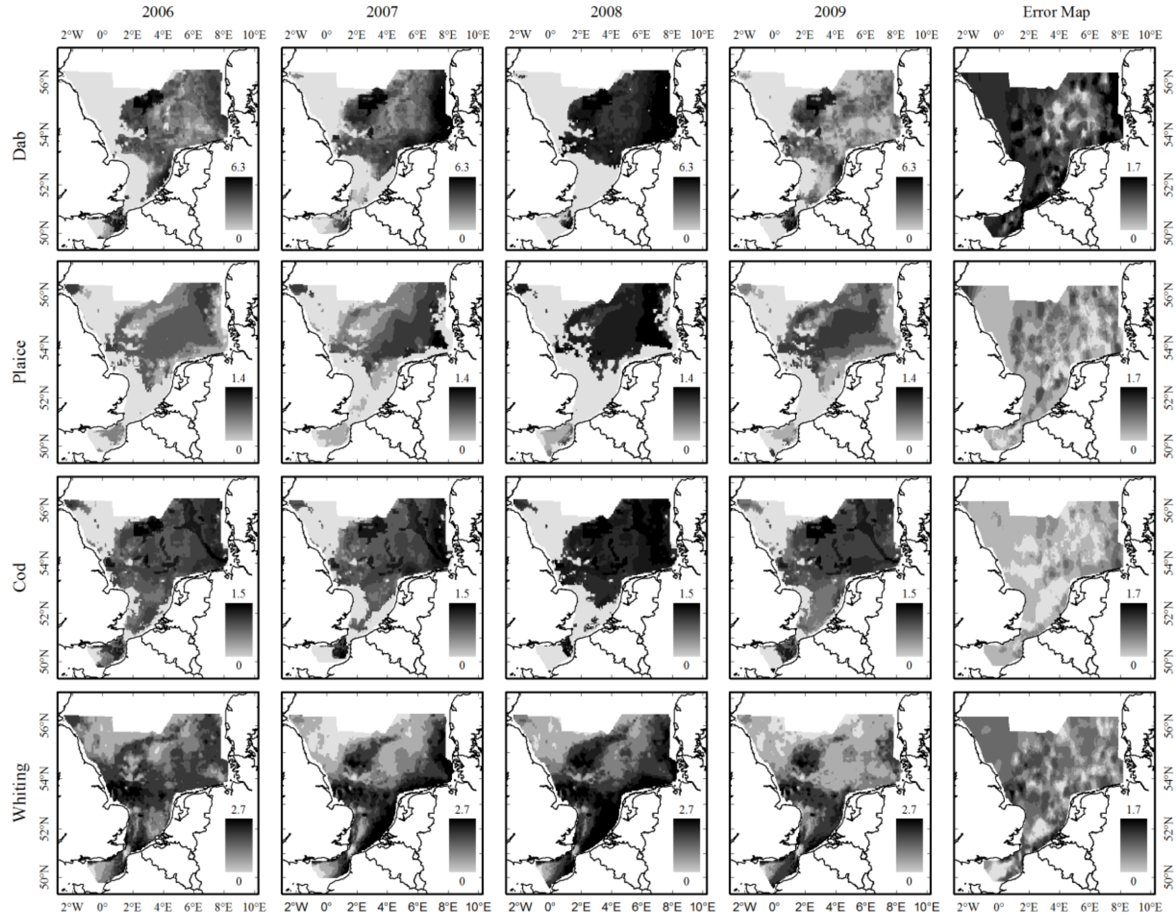

Figure 5: Winter spawning habitats of dab, plaice, cod and whiting, showing predicted egg densities (delta model) for each year between 2006 and 2009), and associated prediction errors. Egg densities are expressed as $\log_{10}(x+1)$, with x = number of eggs per 20 m^3.

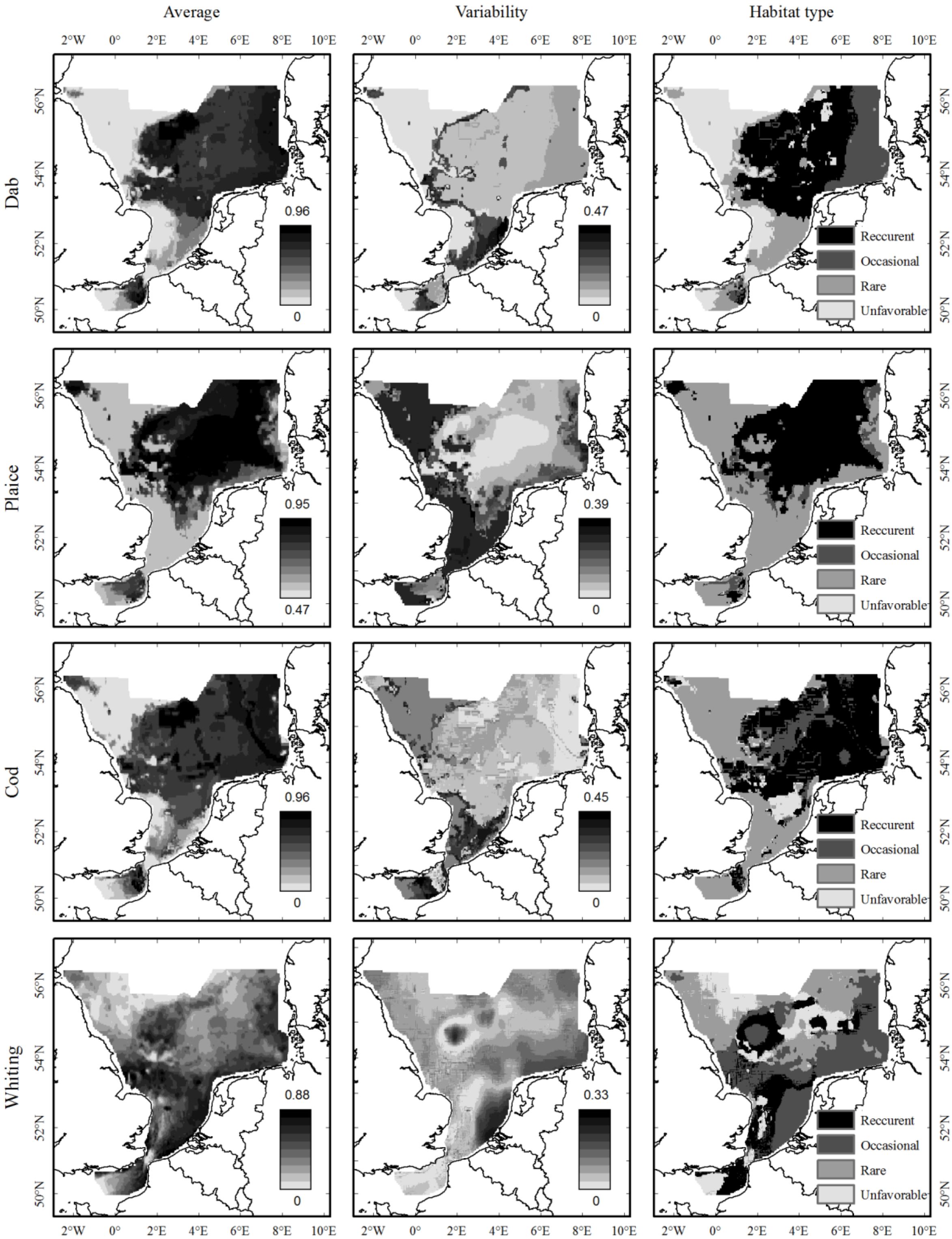

Figure 6: Maps of average, variability and type (recurrent, occasional, rare and unfavourable) of spawning habitat for dab, plaice, cod and whiting, for the period 2006 to 2009 (see main text for details).

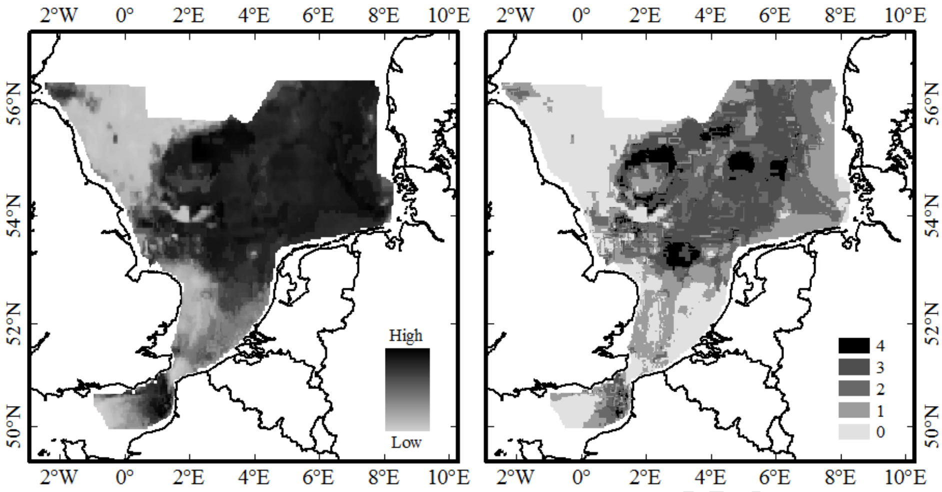

Figure 7: Mutispecific analysis (dab, plaice, cod and whiting). (left) Predicted spawning winter habitat highlighting areas that are the most suitable for the higher number of species. (right) Spawning recurrence frequency showing the number of species regularly using the area.

Table 1: Start and end dates of the French IBTS (International Bottom Trawl Survey) surveys, and number of samples collected using CUFES (Continuous Underway Fish Egg Sampler). For model development, samples were split into four separate datasets (see text for details).

Year	Start	End	Dataset A	Dataset B	Dataset C	Dataset D
2006	28 Jan	21 Feb	84	83	84	629
2007	29 Jan	22 Feb	85	77	72	637
2008	27 Jan	21 Feb	84	82	71	812
2009	14 Jan	13 Feb	82	75	78	788

Table 2: Coefficients of Spearman's rank correlation for the four continuous environmental variables, and between them and fish eggs densities (plaice, dab, cod and whiting). Temp = sea surface temperature (°C), Sal = sea surface salinity (PSU), Depth (m), Stress = bed shear stress (N.m^{-2}), Chloro = chlorophyll *a* concentration (µg.l^{-1}). Significance levels of *p*-values are shown as ***: $p < 0.001$, **: $p < 0.01$, NS: $p > 0.05$.

	Temp	Sal	Depth	Stress	Chloro	Plaice	Dab	Cod	Whiting
Temp						-0.20***	-0.28***	-0.24***	0.08***
Sal	0.30***					0.01 NS	-0.12***	0.00 NS	0.01 NS
Depth	0.37***	0.34***				0.06***	-0.24***	-0.10***	-0.22***
Stress	0.27***	-0.01NS	-0.28***			-0.33***	-0.26***	-0.24***	0.17 NS
Chloro	-0.51***	0.08***	-0.28***	0.03 NS		-0.08***	0.07***	0.05**	-0.02***

Table 3: For each species, final binomial occurrence (GLM b) and Gaussian (GLM p) models. Environmental variables are coded as follows: Temp = sea surface temperature (°C), Sal = sea surface salinity (PSU), Depth (m), Stress = bed shear stress (N.m^{-2}), Chloro = sea surface chlorophyll *a* concentration *a* (µg.l^{-1}), and seabed sediment types: fine sand (FS), gravel (G), mud (M) and pebbles (P). Variables suffixed 2 indicate second order polynomial form.

		Intercept	Temp	Temp2	Sal	Sal2	Depth	Depth2	Stress	Stress2	Chloro	Chloro2	FS	G	M	P
Plaice	GLM b	-50.02	-3.15	0.21	1.04	-0.26	76.99	-24.22	-2.44	-8.86	-1.22	2.88	0.82	1.68	0.89	0.6
	GLM p	-12.55	0.69	-0.05	-0.38		14.41	-4.49								
Dab	GLM b	-26.08	-2.43	0.14	1.08		51.9	-18.1		-11.95	-13.5	29.35				
	GLM p	-1.47	1.44	-0.1	-1.94	0.69	0.9	-0.81	-0.59	-0.93	1.34	-3.41	-0.11	-0.68	0.01	-0.05
Cod	GLM b	-28.53		-0.02	0.83		40.27	-13.57		-7.7						
	GLM p	-5.04	0.04	0	-0.45	0.1	8.13	-2.71	-0.65	0.5	0.57	-1.43	-0.05	-0.25	0.05	-0.18
Whiting	GLM b	-6.33	-0.97	0.07	0.96	-0.06	14.34	-6.07	6.94	-16.98	-11.03	25.38	0.13	2.43	0.3	0.6
	GLM p	-1.03	0.84	-0.05	-0.24			-0.69	3.09	-6.61	5.75	-17.71				

Table 4: Evaluation results for each species' binary model, showing the chosen calibration dataset (B or C), and selection criterion. Internal (using dataset A, B or C) and external (using dataset D) evaluation results are given (Adj-R^2, AUC). Model residuals were tested for spatial autocorrelation using Morans' I (only the first lag's result is shown). Significance levels (*p*-values) are shown as ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$. The presence-absence cut-off values (used for model prediction) are given, along with the optimisation criteria retained (MSS: maximised sum of sensitivity and specificity).

	Model construction		Internal evaluation			External evaluation		Presence-absence cut-off value (estimated on full dataset)	
Species	Calibration dataset	Selection criteria	Adj-R^2	AUC	Morans' I	Adj-R^2	AUC	Selected threshold	Optimisation criteria
Plaice	C	Initial	0.26	0.82 ***	0.09 NS	0.23	0.80 ***	0.4	MSS
Dab	B	BIC	0.33	0.83 ***	0.28 ***	0.22	0.79 ***	0.56	MSS
Cod	C	BIC	0.2	0.77 ***	0.05 NS	0.13	0.72 ***	0.51	MSS
Whiting	C	Initial	0.12	0.74 ***	0.07 NS	0.04	0.7 ***	0.26	MSS

Table 5: Evaluation results for each species's Gaussian model, showing the chosen calibration dataset (B or C), and selection criterion. Internal (using dataset A, B or C) and external (using dataset D) evaluation results are given (Adj-R², Spearman's rank correlation test, Wilcoxon signed-rank test). Model residuals were tested for spatial autocorrelation using Morans' I (only the first lag's result is shown). Significance levels (*p*-values) are shown as ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, NS: $p \geq 0.05$.

	Model construction		Internal evaluation				External evaluation		
Species	Calibration dataset	Selection criteria	Adj-R²	Spearman	Wilcoxon *p*-value	Morans' I	Adj-R²	Spearman	Wilcoxon *p*-value
Plaice	B	BIC	0.63	0.4 ***	NS	0.15 NS	0.81	0.3 ***	NS
Dab	C	Initial	0.85	0.3 ***	NS	0.15 *	0.84	0.4 ***	NS
Cod	B	Initial	0.79	0.2 ***	NS	0.02 NS	0.86	0.3 ***	NS
Whiting	B	AIC	0.91	0.4 ***	NS	0.08 NS	0.94	0.4 ***	NS

Table 6: Evaluation results for each species's delta model, showing Adj-R², Spearman's rank correlation and Wilcoxon signed-rank test results, along with Confidence Intervals (CI) obtained by bootstrapping. Significance levels (*p*-values) are shown as ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, NS: $p \geq 0.05$. Mean and range of absolute standardised residuals were computed for each model.

		Spearman's correlation		Wilcoxon	Absolute standardised residuals
Species	Adj-R² (CI)	rho (CI)	p-value	p-value	Mean (Min-Max)
Plaice	0.84 (0.82 - 0.88)	0.49 (0.46 - 0.51)	***	***	0.4 (0 - 1.79)
Dab	0.84 (0.83 - 0.85)	0.38 (0.35 - 0.42)	***	***	0.82 (0 - 2.57)
Cod	0.85 (0.81 - 1)	0.34 (0.31 - 0.37)	***	***	0.35 (0 - 1.44)
Whiting	0.96 (0.95-0.99)	0.31 (0.29 - 0.34)	***	***	0.51 (0 - 2.13)

Figure 1: Study area, showing locations mentioned in the text.

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HIGHLIGHTS

- The spawning ground distributions of dab, plaice, cod and whiting are explored from 2006 to 2009 in the North Sea
- Spawning habitat models are developed by relating egg density to six environmental descriptors
- Predicted annual habitat maps highlight suitable spawning areas and their spatial variability
- Recurrent spawning grounds are delineated for each species
- Most suitable and temporally stable spawning areas are defined for use in marine spatial planning