

# What controls the spatial distribution of the North Sea plaice spawning population? Confronting ecological hypotheses through a model selection framework

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The spatial dynamics of spawning fish are crucial because they influence the survival rates of eggs and larvae and ultimately impact the reproductive success of populations. The factors that control these dynamics are complex and potentially many, and they interact. A model-selection-based approach was developed to confront various hypotheses of control of the spatial distribution of spawning population of North Sea plaice (*Pleuronectes platessa*). For each hypothesis or combination thereof, statistical models were constructed. These were then ranked and selected based on their ability to adjust and predict observed spatial distributions. The North Sea plaice population seems to have developed strong attachment to specific spawning sites, where geographic location and population memory are important controlling factors. Temporal changes in spatial distribution patterns appear to be influenced primarily by population size and demography. Variations in hydrographic conditions such as temperature and salinity do not appear to control interannual fluctuations in spatial distribution. This means that, for reproduction, applying conventional habitat models may falsely attribute major controlling effects to environmental conditions. It is concluded that a multiple-hypothesis approach is essential to understanding and predicting the present and future distribution of the North Sea plaice population during its spawning season.

**Keywords:** AIC, multi-model inference, North Sea plaice, spatial distribution, spawning population.

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## Introduction

Plaice (*Pleuronectes platessa*) are flatfish that are heavily exploited in the North Sea (Rijnsdorp and Millner, 1996). Its status has been evaluated by stock assessment, and information is available for the period 1957–2007 (ICES, 2008). Its spawning distribution has been studied mainly through the spatial distribution of eggs (Harding *et al.*, 1978; ICES, 2005), and little attention has been paid to the distribution of spawning adults (though see Cushing, 1990; Hunter *et al.*, 2004; Metcalfe, 2006).

Many processes play a role in the control of a population's spatial distribution. Environmental control finds its ecological basis through the ecological niche theory of Hutchinson (1957), which is delimited by a hypervolume of  $n$  dimensions, each an environmental factor that limits species survival, growth, and/or reproduction. Spawning populations have ecological preferences for particular environmental ranges and, because the environment displays positive spatial autocorrelation, i.e. is more similar in adjacent than in distant locations (Legendre, 1993; Fortin and Dale, 2005), the distribution of spawners is also autocorrelated. Fish distribution is also affected by attracting or repulsing interactions such as during the spawning period, when males and females tend to concentrate at relatively small spatial scales to

minimize gamete loss and to maximize reproductive success. Such conspecific attraction may also lead to the distribution of fish being autocorrelated in space.

Internal controls on spawning distribution are related to the status of a population, mainly its size and its demography. Differences in spatial location of the preferred spawning grounds can exist between young and old spawning fish (Rijnsdorp, 1989). One can therefore reasonably expect that the spatial distribution of spawning will fluctuate dependent on the demographic structure of the adult population. Population size can influence the spatial distribution through spatial density-dependence. This issue was formalized by Fretwell and Lucas (1970), Sutherland (1983), and MacCall (1990) using the concept of ideal free distribution. Under that concept, individuals possess a complete knowledge of their surrounding environment and are able to select their habitat in an ideal way to maximize their fitness. In density-dependent habitat selection (Rosenzweig, 1991; Marshall and Frank, 1995; Shepherd and Litvak, 2004), fish distribution contracts to refuge defined by an environmental preference at a low population size and extends to less suitable areas at high levels. This phenomenon can lead to a species abundance–area relationship (Swain and Morin, 1996; Fisher and Frank, 2004;

Blanchard *et al.*, 2005). Moreover, the spatial distribution of fish populations tends to have a degree of persistence over years, and spawning grounds tend to be recurrent for many fish stocks (Hunter *et al.*, 2003; Solmundsson *et al.*, 2005). The maintenance of a spatial population pattern across years and generations is likely driven by conservatism at a population level, determined by individual memory as well as social behaviour between individuals of the same population (Corten, 2002; Petitgas *et al.*, 2006). In summary, the spatial distribution of spawning fish may be controlled, possibly simultaneously, by a number of processes that include environmental conditions, spatial dependence, density-dependent habitat selection, demographic structure, population conservatism, and site attachment.

Investigating the role of such a variety of hypotheses on the control of spawning fish spatial distribution can be achieved using multi-inference model and information theoretic approach, as suggested by Hilborn and Mangel (1997), Burnham and Anderson (2002), Johnson and Omland (2004), Stephens *et al.* (2007), and Diniz-Filho *et al.* (2008). In such an approach, several models reflecting various hypotheses of control are compared based on a distance metric between model predictions and observations. The selection procedure can result in several models being reasonably good candidates for “best model”. Hypotheses contained in the models can thus be inferred to influence the spatio-temporal variability of the population’s distribution pattern.

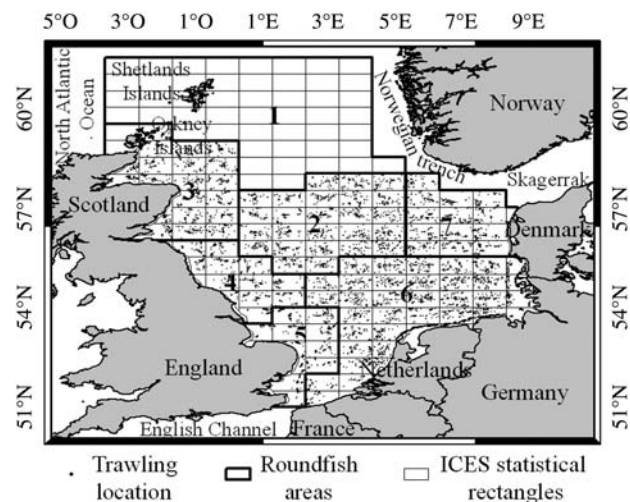
The aim of the present study is to develop such an approach based on statistical models to identify the processes, among those that have been previously cited, that control the spatial distribution of spawning North Sea plaice.

**Material and methods**

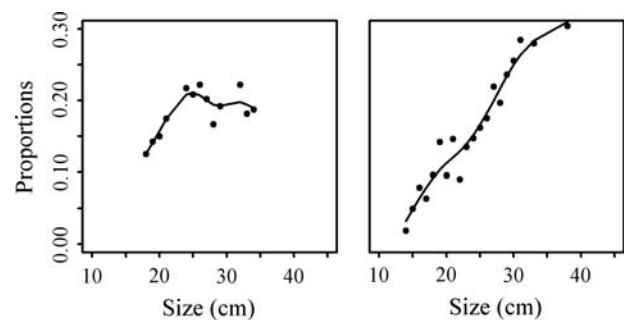
The first quarter of the International Bottom Trawl Survey (IBTS) is carried out each year in the North Sea from January to March to collect the data necessary for the stock assessment of several important demersal fish (ICES, 2007, 2008). The network of sampling stations is based on ICES statistical rectangles of 1° longitude by 0.5° latitude (Figure 1). Each rectangle is visited by two countries which carry out a standardized trawl of 30 min using a 36/47 GOV trawl. Trawl locations are selected randomly by the country among a predefined set of three or four sites inside the rectangle. This results in a minimum of two sites per rectangle being trawled each year. For each trawl, the catch is sorted by species and counted. Length measurements and sexual maturity stage are recorded, and otoliths are removed for several key species, on a proportion of fish for seven standard “roundfish” areas (ICES, 2004; Figure 1). Fish are classified into four stages of maturity, for which stage 3 is “spawning individuals” with fluent gonads (ICES, 2004). From 1980 to 2007, 11 343 bottom trawls were made, an average of 405 bottom trawls annually. The data are available through the DATRAS database (Data for TRAWL Surveys, <http://datras.ices.dk/Home/Default.aspx>), which is coordinated by ICES.

**Biological response**

Abundance data on plaice spawners in IBTS first quarter data were extracted for the years 1981–2007. Abundance was computed from the available proportion of spawning adults within a given length class (Figure 2). As sexual maturity of plaice has only been recorded since 2001, there were insufficient data to estimate the proportion of spawning adults within each size class for each



**Figure 1.** Map of the North Sea, showing the trawl stations of the first quarter (January–March) of the IBTS from 1980 to 2007 for which the abundance of spawning adult North Sea plaice is given. Countries involved in the IBTS, ICES statistical rectangles, standard roundfish areas, and main locations are also indicated.



**Figure 2.** Proportions of adult stage 3 (spawning adults) North Sea plaice per size class. Left, areas 2–4 pooled. Right, areas 5–7 pooled. No data are available for area 1. The datapoints represent the proportions observed, and the lines the adjusted proportions using a smoothing spline for missing size classes.

year and each area. Therefore, data on sexual maturity from 2001 to 2007 were pooled to calculate these proportions for the combined northwest (2, 3, and 4) and southeast (5, 6, and 7) areas. No data on the sexual maturity of plaice in area 1 were available. Data on males and females were also combined because there were too few data to calculate the proportions of spawning adults for each sex. This reduced the total number of trawl station results available to 7317 (Figure 1). For each of these station, the abundance of spawning adults was calculated from the product of the total abundance within each size class and the corresponding proportions of spawning adults in that size class.

**Hypotheses of control**

Ten possible control factors were modelled: persistence and non-persistence of the environment, three scales of spatial dependence, population size, the annual and the spatial age structure, geographic location, and population memory. Persistence of the environment is the environmental factor that is spatially structured, but it did not change during the period of study (depth,

mean annual bottom shear stress, and sediment type at each location). Non-persistence of the environment is another environmental condition that is spatially structured, and it has changed during the period of study (bottom temperature and salinity). Spatial dependence (also termed spatial autocorrelation) describes the spatial structure present in the distribution of plaice. Potentially, it may be shared with other controls such as persistence and non-persistence of the environment. Population size is the annual population estimate, in biomass and numbers. The annual age structure (referred to as annual demography) is the proportion of each cohort each year, and the spatial age structure (referred to as spatial demography) is the distribution of each cohort at each trawling station in each year. Geographic location corresponds to the absolute coordinates (latitude and longitude), and population memory is the degree of persistence of plaice distribution from one year to the next. Geographic location supposes that plaice return to the same spawning site each year, whereas population memory reflects the understanding that current spatial distribution depends on past distribution.

Five environmental variables were used in the analysis: depth (m), bottom temperature ( $^{\circ}\text{C}$ ), bottom salinity, seabed stress ( $\text{N m}^{-2}$ ), and sediment type. Depth and bottom temperature and salinity were measured at each trawling location from 1981 to 2007. Salinity was transformed using the equation  $\exp(\text{salinity})/10^{15}$  to be closer to normality. Seabed stress is a measure of the shear friction of water on the seabed caused by the tidal current. It was estimated using a two-dimensional hydrodynamic model (Aldridge and Davies, 1993) maintained by the Proudman Oceanographic Laboratory, and running on a regular grid of  $1/8^{\circ}$  of longitude by  $1/12^{\circ}$  of latitude (WGS 1984 datum). The grid of points was then interpolated using ArcMap's Spatial Analyst extension (ESRI, 2005) to create a continuous raster layer of resolution  $1 \text{ km}^2$ . The seabed stress was log-transformed to be closer to normality. Sediment type originated from the seafloor sediment of the North Sea built during the MARGIS project (Schlüter and Jerosch, 2008). Sediment classification was summarized into five classes: fine sand, coarse sand, mud, pebbles, and gravels. A value of seabed stress and sediment type was allocated to each trawl by resampling the corresponding maps at trawl locations using ArcMap's Hawth's Analysis Tools extension (Beyer, 2004). Depth, seabed stress, and sediment type were grouped to represent persistence of the environment, whereas bottom temperature and salinity were retained to represent non-persistence of the environment.

Spatial dependence in the distribution of spawning plaice was modelled using principal coordinates of neighbour matrices (PCNMs). PCNMs are specifically designed to describe the spatial structure present in the distribution of an organism over a wide range of scales (Borcard and Legendre, 2002; Dray *et al.*, 2006; Bellier *et al.*, 2007). Extraction of these PCNMs was made following Borcard and Legendre (2002). A Euclidean distance matrix was built using latitude and corrected longitude of the 7317 trawling stations. The longitude correction [ $\text{longitude} \times \cos(\{\text{latitude} \times \pi\}/180)$ ] transforms decimal degrees of longitude into decimal degrees of latitude that are of constant distance using a Mercator-type projection formula. The resulting distance matrix was then truncated by recoding all distances above a particular threshold to four times that threshold. The threshold was taken as the maximum distance between two neighbouring stations to keep all stations connected. A principal coordinate analysis was then performed on this truncated distance matrix,

leading to 7317 potential PCNMs from which only positive PCNMs (eigenvectors with positive eigenvalues) were retained.

PCNMs that described the spatial structure present in plaice distribution were then selected. Following Borcard and Legendre (2002), log-transformed abundances were detrended before selection to remove the significant spatial trend (adjusted  $r^2 = 0.196$ ,  $p < 0.001$ ) that could not be modelled using PCNMs. This was accomplished using a quadratic trend based on latitudinal and corrected longitudinal coordinates of the trawl stations. PCNMs were then confronted with these detrended log-transformed abundances following Blanchet *et al.* (2008). In the first step, a global test including all positive PCNMs was performed to model the biological response. As that test was significant, the analysis was carried on to the next step, which consists of forward selection. In forward selection, the significance of each PCNM is assessed using a test of 999 Monte Carlo permutations and according to a  $p$ -value and the adjusted  $r^2$  (explained variance) of the model calculated with all the PCNMs. PCNMs are successively tested and the selection procedure stops if either the newly added PCNM is not significant at the chosen  $p$ -value threshold or it makes the adjusted  $r^2$  of the whole model increase more than that calculated for the model with all PCNMs. To avoid building spatial models with too many variables (and so to risk biasing the weight of the different hypotheses), only highly significant PCNMs that explained most of the variability in the biological response were retained. In this context, the adjusted  $r^2$  was not restrictive enough (too high) to reduce the final number of PCNMs effectively, so a very low value ( $p < 0.001$ ) for the alpha criterion was chosen. Once this value of the alpha criterion had been chosen, the adjusted  $r^2$  did not play a significant role in reducing the number of selected PCNMs.

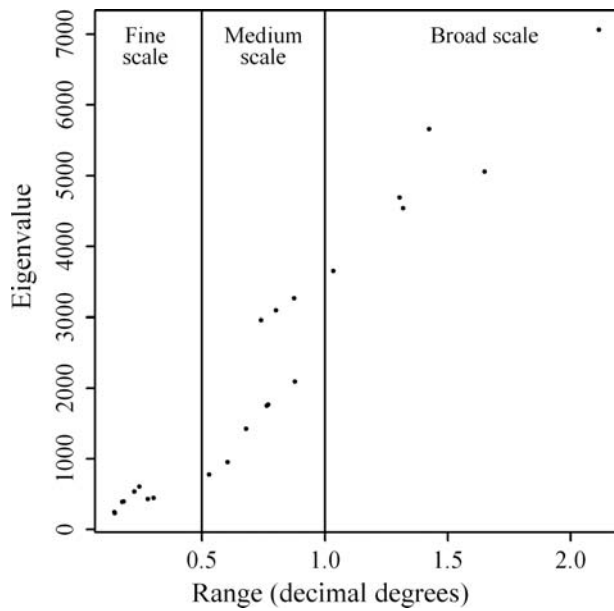
The spatial scale of these PCNMs was determined following the method outlined in Bellier *et al.* (2007). A variogram with a Gaussian model was adjusted, using least-square regression (Webster and Oliver, 2001), to determine the range of the variogram that represented the spatial scale described by each PCNM. The eigenvalue of each PCNM was plotted against their range (Figure 3) to group PCNMs describing equivalent spatial scales into three submodels: broad, medium, and fine scale (Bellier *et al.*, 2007). These submodels were used as three distinct hypotheses of control. The free software R combined with the PrCoord Tool 1.0 of CANOCO 4.5 software (ter Braak and Smilauer, 2002) was used for PCNM extraction. The "forward.sel" function of the "packfor" package (Dray *et al.*, 2009) was used for forward selection of the PCNMs. Experimental and theoretical variograms were calculated using the geoR package (Ribeiro and Diggle, 2001).

Control through demography was expressed through both spatial (at each trawl) and annual (each year) demography using the percentage of each cohort from 1 to 5 years old. These have been provided annually since 1957 (ICES, 2007) by an ICES Working Group charged with stock assessment using virtual population analysis. The proportion of each age in each size class was applied to the total number of fish caught in each trawl.

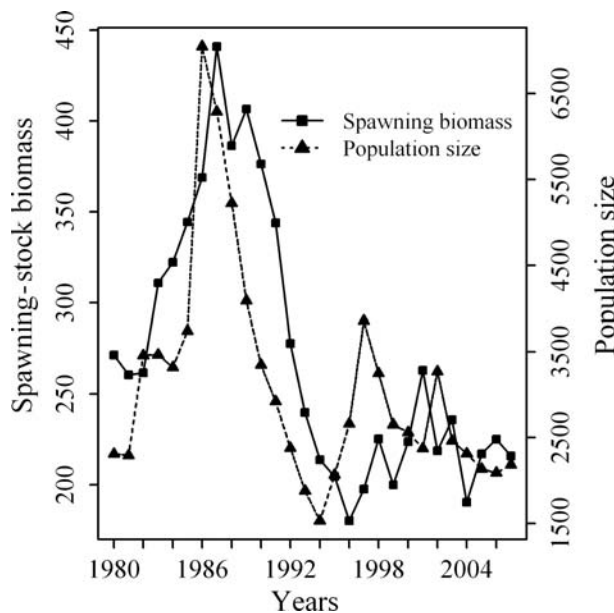
Control through population size was integrated using the spawning-stock biomass of the year as well as total population size. These indices are also provided by ICES (ICES, 2008) for each year for the period 1957–2007 (Figure 4).

Spatial persistence of population distribution over years was expressed using geographic location and population memory. The identity of the ICES statistical rectangles was used as





**Figure 3.** Plot of the values of the 23 selected PCNMs against their eigenvalue. Ranges were obtained by fitting a Gaussian model as a theoretical variogram to each spatial predictor. Three scales were determined: broad scale, eigenvectors with a range between 111 and 233 km (1–2.1 decimal degrees of latitude); medium scale, eigenvectors with a range between 55 and 111 km (0.5–1 decimal degrees of latitude); and fine scale, eigenvectors with a range between 0 and 55 km (<0.5 decimal degrees of latitude).



**Figure 4.** ICES estimation (by the IBTS Working Group) of North Sea plaice population size (thousands of fish) and spawning-stock biomass ('000 t) from 1980 to 2007.

a categorical variable to represent the geographic location. The memory of the population was expressed through the observed abundance of spawning adults in the previous year. Each trawl station was allocated the observed abundance of the previous year using the spatial joining tools of ArcMap 9.1. For trawl

positions for which there was no observation in the previous year for reasons of time constraints or poor weather, the observed abundance at the closest location was used instead. This reduced the total number of trawling stations available from 1981 to 2007 to 6313.

**Model structure**

Generalized additive models (Hastie and Tibshirani, 1990; Guisan *et al.*, 2002) were used to build the models. They allow one to relate, in a non-linear way, a biological response to several explanatory variables using smoothing functions. As is often the case with ecological data, the abundance of spawning adults displayed a zero-inflated distribution. The modelling procedure had to be split into two steps: a binomial model with a logit link and a Gaussian model with an identity link were constructed on presence/absence and non-null log-transformed abundance. For the binomial model, the various hypotheses of control were tested: geography, persistence and non-persistence of the environment, the three spatial submodels, annual demography, population size, and memory. For the Gaussian model, spatial demography was also added.

**Model adjustment and prediction**

Models were fitted (adjusted) to one part of the dataset and applied to predict another part of the dataset to investigate the effect of the dataset on the models and hypothesis selection. In strategy (a), Predict 2000s, models were fitted to data from the beginning of the study period (1981–1999) and applied to predict the spatial distribution of plaice for the later part of the study period (2000–2007). In all, 4410 and 3190 trawls were used to fit binomial and Gaussian models, respectively, and 1088 and 843 trawls, for binomial models and Gaussian models, respectively, were used for prediction. In strategy (b), Predict 1980s, models were fitted at the end of the study period (1990–2007) and applied to predict the situation at the beginning of the study period (1981–1989). In this instance, 4268 and 3229 trawls were used to fit binomial and Gaussian models, respectively, and 962 and 647 trawls were used for prediction.

The degrees of smoothing were adjusted simultaneously on the corresponding fitting period for all variables of the same hypothesis (Table 1). Finally, for each class of model (binomial or Gaussian), all combinations of the hypotheses were calculated, resulting in 2<sup>n</sup> candidate models (where *n* is the number of hypotheses). Models were implemented using R (R Development Core Team, 2008). The “gam” package (Hastie, 2006) was used to construct the binomial and Gaussian models. The “step.gam” function of the MASS library (Venables and Ripley, 2002) was used to adjust the degrees of smoothing of the explanatory variables.

**Model-selection procedures**

For each strategy, two selection procedures were adopted. Models were selected through both their ability to fit and to predict the spatial distribution of plaice and were compared based on their goodness-of-fit using the Akaike Information Criterion (AIC; Akaike, 1974) and AIC differences (Burnham and Anderson, 2002; Johnson and Omland, 2004), which are calculated according to the following formulae:

$$AIC_i = -2 \log L_i + 2p_i, \tag{1}$$

**Table 1.** The formulae for the hypotheses.

Hypotheses	Binomial models	Gaussian models
Strategy (a) "Predict 2000s"		
G	as.factor(StatisticalRectangle)	as.factor(StatisticalRectangle)
Ep	s(Depth, 4) + s(Bedstress, 4) + as.factor(Sediments)	s(Depth, 4) + s(Bedstress, 4) + as.factor(Sediments)
Enp	s(Temperature, 4) + s(Salinity, 4)	s(Temperature, 4) + s(Salinity, 4)
Bs	s(Ax1, 4) + s(Ax3, 4) + s(Ax4, 4) + s(Ax5, 4) + Ax6 + s(Ax8, 4)	Ax1 + s(Ax3, 4) + s(Ax4, 4) + s(Ax5, 4) + s(Ax6, 4) + s(Ax8, 4)
Ms	Ax9 + s(Ax10, 4) + s(Ax11, 4) + s(Ax14, 4) + s(Ax15, 4) + s(Ax16, 4) + s(Ax18, 1) + s(Ax21, 4) + s(Ax23, 4)	s(Ax9, 4) + s(Ax10, 4) + Ax11 + s(Ax14, 4) + s(Ax15, 4) + s(Ax16, 4) + s(Ax18, 4) + s(Ax21, 4) + s(Ax23, 2)
Fs	s(Ax26, 4) + s(Ax32, 4) + s(Ax41, 4) + s(Ax43, 4) + s(Ax47, 3) + s(Ax49, 4) + s(Ax84, 4) + s(Ax88, 3)	s(Ax26, 4) + s(Ax32, 4) + s(Ax41, 4) + s(Ax43, 4) + s(Ax47, 4) + s(Ax49, 4) + s(Ax84, 4) + Ax88
Ps	s(PopulationSize, 4) + SpawningStockBiomass	s(PopulationSize, 4) + s(SpawningStockBiomass, 4)
Da	s(Age1a, 2) + s(Age2a, 4) + s(Age3a, 4) + Age4a + Age5a	Age1a + s(Age2a, 4) + s(Age3a, 4) + Age4a + s(Age5a, 4)
Ds	–	s(Age1s, 4) + s(Age2s, 4) + s(Age3s, 4) + s(Age4s, 4) + s(Age5s, 4)
M	s(PreviousYearAbundance, 4)	s(PreviousYearAbundance, 4)
Strategy (b) "Predict 1980s"		
G	as.factor(StatisticalRectangle)	as.factor(StatisticalRectangle)
Ep	s(Depth, 4) + s(Bedstress, 4) + as.factor(Sediments)	s(Depth, 4) + s(Bedstress, 4) + as.factor(Sediments)
Enp	s(Temperature, 4) + s(Salinity, 3)	s(Temperature, 4) + s(Salinity, 4)
Bs	s(Ax1, 4) + Ax3 + s(Ax4, 4) + s(Ax5, 4) + s(Ax6, 4) + s(Ax8, 4)	s(Ax1, 4) + s(Ax3, 4) + s(Ax4, 4) + s(Ax5, 4) + s(Ax6, 4) + s(Ax8, 4)
Ms	Ax9 + s(Ax10, 4) + s(Ax11, 4) + s(Ax14, 4) + s(Ax15, 4) + s(Ax16, 4) + s(Ax18, 1) + s(Ax21, 4) + Ax23	s(Ax9, 3) + s(Ax10, 4) + s(Ax11, 4) + s(Ax14, 4) + s(Ax15, 4) + s(Ax16, 4) + s(Ax18, 4) + s(Ax21, 4) + Ax23
Fs	s(Ax26, 4) + s(Ax32, 4) + s(Ax41, 4) + s(Ax43, 4) + s(Ax47, 4) + s(Ax49, 4) + s(Ax84, 4) + s(Ax88, 4)	s(Ax26, 4) + s(Ax32, 4) + s(Ax41, 4) + s(Ax43, 4) + s(Ax47, 4) + s(Ax49, 3) + s(Ax84, 4) + s(Ax88, 3)
Ps	PopulationSize + s(SpawningStockBiomass, 4)	PopulationSize + s(SpawningStockBiomass, 4)
Da	Age1a + s(Age2a, 4) + s(Age3a, 3) + Age4a + Age5a	Age1a + Age2a + s(Age3a, 4) + Age4a + s(Age5a, 4)
Ds	–	s(Age1s, 4) + s(Age2s, 4) + s(Age3s, 4) + s(Age4s, 4) + s(Age5s, 4)
M	PreviousYearAbundance	s(PreviousYearAbundance, 4)

The explanatory variables for each hypothesis for the binomial and the Gaussian models were fitted on the corresponding fitting period for strategy (a), Predict 2000s, and strategy (b), Predict 1980s. An s means that a smoothing function has been used, and the corresponding degree of smoothing is indicated in parentheses. PCNMs are denoted by the term Ax. Hypotheses: G, geography; Ep, persistence of the environment; Enp, non-persistence of the environment; Bs, broad-scale submodel; Ms, medium-scale submodel; Fs, fine-scale submodel; Ps, population size; Da, annual demography; Ds, spatial demography; M, population memory.

where  $AIC_i$  is the AIC of the  $i$ th model,  $\log L_i$  the log-likelihood of the  $i$ th model, and  $p_i$  the number of parameters (explanatory variables) of the  $i$ th model. Then

$$\Delta_i = AIC_i - AIC_{\min}, \quad (2)$$

where  $\Delta_i$  is the AIC difference for the  $i$ th model, and  $AIC_{\min}$  is the lower AIC over all candidate models (i.e. the AIC of the “best” model).

In the binomial model, the log-likelihood of formulation (1) is calculated between predicted probabilities of presence (from 0 to 1) and binary observed presence/absence (0 or 1) using the following formula (McCullagh and Nelder, 1989):

$$-2 \times \log L_i = -2 \times \left( \sum_{j=1}^n Y_j \times \log \hat{Y}_{i,j} + (1 - Y_j) \times \log(1 - \hat{Y}_{i,j}) \right), \quad (3)$$

where  $Y$  is the vector of observed presence/absence and  $\hat{Y}_i$  the vector of predicted probabilities of presence of the  $i$ th model for  $j$  observations and predictions. In the Gaussian model, the log-likelihood is calculated between predicted and observed log-transformed abundances using the formula (McCullagh and Nelder, 1989)

$$-2 \times \log L_i = -2 \times \left( \sum_{j=1}^n \frac{(Y_j - \hat{Y}_{i,j})^2}{\sigma^2} - 2 \times j \times \log(\sigma) + C \right), \quad (4)$$

where  $Y$  is the vector of observed non-null abundances,  $\hat{Y}_i$  the vector of predicted abundances of the  $i$ th model,  $\sigma^2$  the residual sum of squares between predicted and observed abundances,  $j$  the number of observations, and  $C$  is a constant.

According to formulations (1) and (2), the best among all candidate models is that with the lowest AIC, and  $\Delta_i = 0$ . It is the model with the best adjustment to observed data and parsimony in the number of explanatory variables. Models were ranked in increasing order of  $\Delta_i$ . Only binomial and Gaussian models with  $\Delta_i < 10$  were selected because models with higher values of  $\Delta_i$  are unlikely to include the best model (Burnham and Anderson, 2002).

Models were also compared in terms of their ability to predict using the log-likelihood between observations and prediction according to formulations (3) and (4). The log-likelihood value being negative, the best model is that with the highest log-likelihood. Other models were compared with this best model using a likelihood ratio test (LRT; Burnham and Anderson, 2002):

$$LRT_i = -2(\log L_i - \log L_{\max}), \quad (5)$$

where  $LRT_i$  is the LRT of model  $i$ , and  $\log L_{\max}$  is the log-likelihood of the best model (hence with a value of LRT of 0). Models were ranked according to their LRT from smallest to largest. The same selection threshold of 10 as for  $\Delta_i$  was used to retain only a reduced set of selected models.

The AIC was calculated with the AIC function of the “stats” package in R (R Development Core Team, 2008), and the log-likelihood using the “dbinom” and “dnorm” functions in R.

### Model evaluation

Binomial and Gaussian models selected based on the LRT were reapplied to the corresponding prediction dataset of each strategy within the same range used to fit the Gaussian models (more restrictive, because they are based on fewer observations). The predicted probabilities of presence and predicted log-transformed abundance were then combined in a delta approach where they are multiplied (Stefánsson, 1996) to predict spatial distribution. This resulted in several predicted distributions, through combination of binomial and Gaussian models. Predicted distributions were compared graphically with observed distributions by a Taylor diagram (Taylor, 2001), through the use of three similarity indices. These were standard deviation, root-mean-squared error (RMSE), and a Spearman correlation coefficient. Plot of the standard deviation allows one to establish whether the model is able to reproduce the same variability in its prediction as those in the observations. The RMSE is computed as the root of the mean of the squared differences between each prediction and each observation. It incorporates both the variance of the model and its bias. The Spearman correlation coefficient and the RMSE allow one to quantify the correspondence between the observed and predicted patterns. Delta model predictions were compared with observations over the whole study period of 1981–2007. Also, predictions from a pure environmental delta model and a control delta model (a combination of the worst determined binomial and Gaussian models) were plotted for comparison with selected models. The Taylor diagram was computed using the “plotrix” package (Lemon *et al.*, 2008) in R.

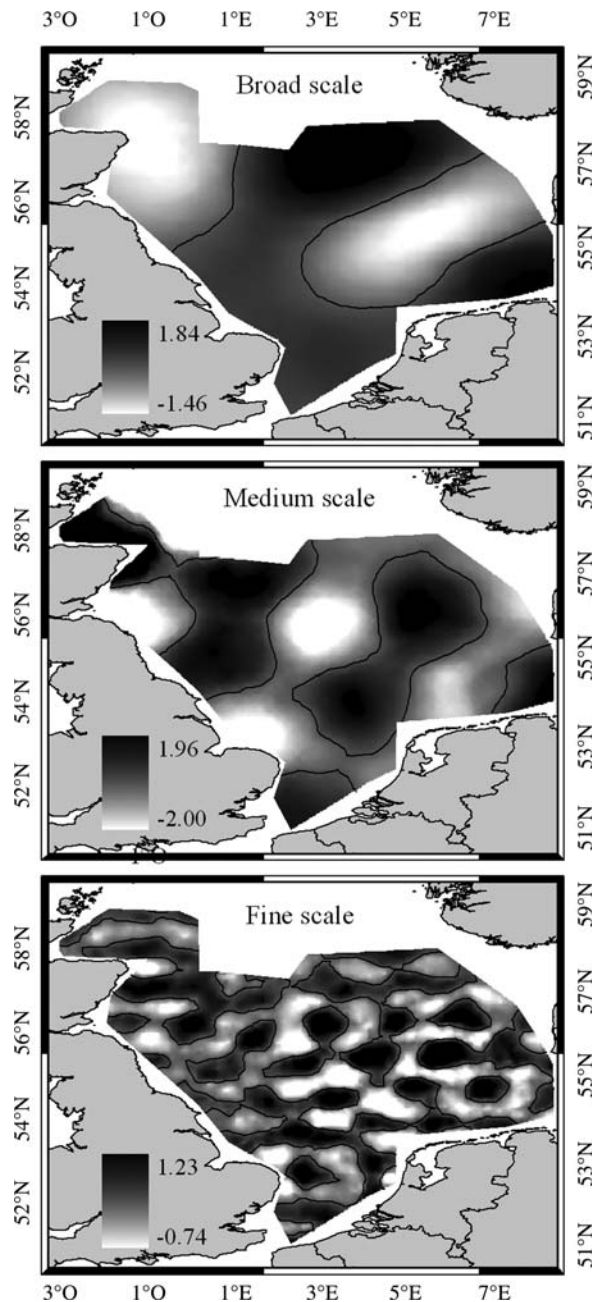
## Results

### PCNM extraction and selection

PCNMs were used to depict spatial dependence in the distribution of spawning plaice. A threshold of 1.13 (decimal degrees of latitude) was used to truncate the distance matrix between stations. In all, 2965 positive PCNMs were extracted from the principal correspondence analysis, and 23 were determined as significant by forward selection ( $p < 0.001$ ; adjusted  $r^2 = 0.26$ ). From these 23 PCNMs, three submodels representing three spatial scales were identified (Figure 5): broad scale (111–233 km), medium scale (55–111 km), and fine scale (<55 km). Six PCNMs accounted for the broad scale, nine for the medium scale, and eight for the fine scale.

### Model selection

Nine hypotheses were confronted using binomial models, and ten using Gaussian models, which resulted, respectively, in 511 and 1023 possible models. Based on the selection procedures, 41 models were selected (Table 2). The selected models depended on the selection criterion, which means that the best-fitted models to the data were not those with the best predictive power. Models selected based on their predictive power were more numerous (Table 2) and less complex in terms of the number of hypotheses and explanatory variables than those selected based on their adjustment to the data (Figure 6). The selected models were also not the same according to the strategy



**Figure 5.** PCNM spatial submodels (arbitrary units): top, broad-scale submodels; centre, medium-scale submodels; and bottom, fine-scale submodels. Black lines denote zero values. See Figure 3 for more detail on the scales of the submodels.

and type of model (Table 2); binomial models were less complex than Gaussian models (Figure 6).

The frequencies of each hypothesis within the set of selected models were estimated (Table 3). Three hypotheses dominated: population size, population memory, and spatial demography. Persistence of the environment and broad- and medium-scale submodels were also important, but less frequent. Geography, non-persistence of the environment, fine-scale submodel, and annual demography were the less frequent hypotheses and the ones that showed strong differences in the selected models according to the type of model and selection procedure (Table 3). Geography

was more frequent in models selected from prediction, and especially in Gaussian models. Non-persistence of the environment and fine-scale submodel were more frequent in Gaussian models selected from fitting and more frequent in binomial models selected from prediction. Annual demography was more frequent in selected Gaussian than in selected binomial models.

### Model evaluation

For strategy (a), Predict 2000s, combinations of the nine binomial and four Gaussian models, selected from prediction, were reapplied to the period 2000–2007 and resulted in 32 predicted distributions. For strategy (b), Predict 1980s, combinations of the unique binomial model with the 12 Gaussian models, selected from prediction, were reapplied to the period 1981–1989 and resulted in 12 predicted distributions. The Taylor diagram comparing these predicted distributions with the observed distribution is presented in Figure 7. A pure environmental model and a control model (determined as the worst among all models) are also shown. For strategy (a), Predict 2000s, the control model is the combination of the binomial model containing non-persistence of the environment and annual demography, and the Gaussian model containing annual demography. For strategy (b), Predict 1980s, it is the combination of geography, non-persistence of the environment, medium- and fine-scale submodels, and annual demography with the annual demography. Maps of the corresponding predicted distributions are presented in Figure 8.

The models selected were clearly distinct from the pure environmental and the control models. Predictions from the selected models have better correlation, higher standard deviations, and lower RMSEs with observations than the environmental and the control model, confirming that the selected models have greater predictive power. The predicted distribution patterns from the best model are more similar to the observed distribution than to the others (Figure 8). The selected models had similar correlations, standard deviations, and RMSEs, which make them hard to distinguish using the Taylor diagram. Selected models of strategy (a), “Predict 2000s”, and strategy (b), “Predict 1980s”, can be distinguished on the diagram, although they have similar values of correlation ( $r^2$  close to 0.7), RMSE ( $\sim 0.7$ ), and standard deviation (0.75–0.80).

### Discussion

#### The influence of the selection procedure

The selection procedure based on either fitting (measured using the AIC) or prediction (based on LRT) performances had an impact on model selection. Models selected based on their fitting performances were usually more complex than those selected on their prediction performances, suggesting that selection based on the AIC tends to promote more complex models that are possibly overfitted to the data. This may arise because data are autocorrelated in both space and time, with the true number of independent observations being smaller than the number of empirical ones. Such a phenomenon would artificially inflate the weight of the first term of the AIC (the model adjustment) compared with the second term (the parsimony of the model), so promoting fitting performance over model parsimony. Moreover, whereas PCNMs are constructed to account for autocorrelation (Dray *et al.*, 2006; Bellier *et al.*, 2007), it seems that their use as explanatory variables does not solve the statistical

**Table 2.** The formulae for the models selected.

Selection procedure	Model formulae	$\Delta_i$	LRT	Selection procedure	Model formulae	$\Delta_i$	LRT
Strategy (a) "Predict 2000s"				Strategy (b) "Predict 1980s"			
Fitting ( $n = 6$ )	<i>Binomial</i> ( $n = 4$ )			Fitting ( $n = 9$ )	<i>Binomial</i> ( $n = 5$ )		
	Ep + Enp + Bs + Ms + Ps + Da + M	0	40.9		Ep + Enp + Bs + Ms + Ps + M	0	61.4
	Ep + Enp + Bs + Ms + Da + M	0.7	71.6		Ep + Bs + Ms + Ps + M	2.3	79
	Ep + Bs + Ms + Ps + Da + M	3.9	39.7		Ep + Enp + Bs + Ms + Fs + Ps + M	6.6	66.3
	Ep + Bs + Ms + Da + M	8.9	103.5		Ep + Bs + Ms + Fs + Ps + M	7.8	83.2
	<i>Gaussian</i> ( $n = 2$ )				Ep + Bs + Ms + Ps + Da + M	8.9	40.5
	Ep + Enp + Bs + Ms + Ps + Da + Ds + M	0	157.3		<i>Gaussian</i> ( $n = 4$ )		
	Enp + Bs + Ms + Ps + Da + Ds + M	7.5	153.6		Ep + Enp + Bs + Ms + Fs + Ps + Da + Ds + M	0	28
Prediction ( $n = 13$ )	<i>Binomial</i> ( $n = 9$ )				Ep + Bs + Ms + Fs + Ps + Da + Ds + M	3	13.3
	Ep + Enp + Bs + Ps + M	130.3	0		Ep + Enp + Bs + Ms + Fs + Ps + Ds + M	3.8	31.4
	Ep + Enp + Bs + M	149.4	1.2		Ep + Bs + Ms + Fs + Ps + Ds + M	6.8	18.5
	Ep + Enp + Bs + Fs + Ps + M	128.3	3.6	Prediction ( $n = 13$ )	<i>Binomial</i> ( $n = 1$ )		
	Ep + Enp + Bs + Fs + M	148.2	4.6		Ep + Ms + Fs + Ps + Da + M	149.7	0
	Enp + Bs + Ms + Ps + M	74.3	8.2		<i>Gaussian</i> ( $n = 12$ )		
	Enp + Bs + Ms + M	97.5	8.6		G + Ep + Ms + Ps + Da + Ds + M	105.5	0
	Ep + Enp + Bs + Ms + Ps + M	56.3	9.1		G + Ms + Ps + Da + Ds + M	109.7	2
	Ep + Enp + Bs + Ms + M	81.2	9.5		Ep + Bs + Ms + Ps + Da + Ds + M	23.4	3.3
	Enp + Bs + Ms + Fs + Ps + M	87.1	9.6		G + Ep + Ps + Da + Ds + M	82.6	4.7
	<i>Gaussian</i> ( $n = 4$ )				G + Ep + Bs + Ms + Ps + Da + Ds + M	118.3	4.7
	Bs + Ms + Fs + Ps + Ds + M	55.2	0		G + Bs + Ms + Ps + Da + Ds + M	120.1	6.8
	Ep + Bs + Ms + Fs + Ps + Ds + M	50.6	1.5		G + Ep + Bs + Ps + Da + Ds + M	83.8	7
	Bs + Ms + Ps + Ds + M	45.5	4.9		G + Ep + Ms + Ps + Ds + M	106.8	7.3
	Ep + Bs + Ms + Ps + Ds + M	38.1	6.0		G + Ep + Ms + Ps + Da + Ds	157.9	7.8
	Bs + Ms + Ps + Da + Ds + M	45.1	8.9		G + Ps + Da + Ds + M	88.1	8.2
	Ep + Bs + Ps + Da + Ds + M	51.1	9.6		Bs + Ms + Ps + Da + Ds + M	45.1	8.9
					Ep + Bs + Ps + Da + Ds + M	51.1	9.6

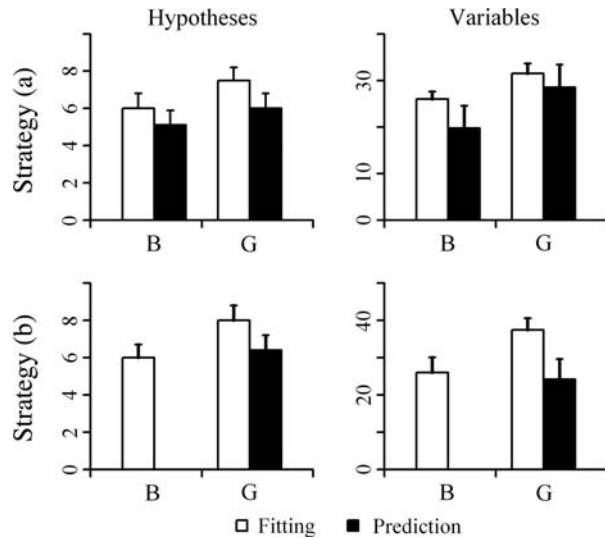
The models were selected according to their capability to fit ( $\Delta_i$ ) and predict (LRT) the observed distribution; those selected from fitting are those with a  $\Delta_i < 10$ , and those selected from prediction are those with an LRT of  $< 10$ . For selection based on fitting, the LRT is also given as an informative value as well as the  $\Delta_i$  for selection based on prediction. In both cases,  $\Delta_i$  and LRT values are  $> 10$ , which show that best-fitting models are not those that predict best. Formulae are presented for selected binomial and Gaussian models for strategy (a), Predict 2000s, and strategy (b), Predict 1980s. Hypotheses: G, geography; Ep, persistence of the environment; Enp, non-persistence of the environment; Bs, broad-scale submodel; Ms, medium-scale submodel; Fs, fine-scale submodel; Ps, population size; Da, annual demography; Ds, spatial demography; M, population memory.



problem of autocorrelation for model selection. Burnham and Anderson (2002) did not exclude the possibility that an AIC-based selection may result in an overfitted model. They advised users to avoid “models with a great many parameters”

more than is thought to be really needed. To preclude an unreasonable number of competing models (Diniz-Filho *et al.*, 2008), models were constructed as the combination of hypotheses rather than as individual explanatory variables. Moreover, all the degrees of smoothing were not considered, but were determined before the combination of the various hypotheses, also limiting the final number of competing models.

Model overfitting resulting from the AIC selection is a critical issue. It can lead to inappropriate promotion of complex hypotheses that contain many variables. Such models may display a good adjustment to the data, but low predictive power. This is illustrated by the fine-scale submodel hypothesis (containing eight variables), which was retained in AIC selection, but rejected when selecting model predictive performance. Inversely, this can lead to undervaluing hypotheses such as pure geography. When categorical factors are used, each category is counted as one parameter in the model. Here, geographical models based on 114 statistical rectangles treated as factors are strongly penalized because their AIC value is so inflated. Conversely, when a selection procedure is based on prediction, the number of variables is not taken into account in the LRT, so the geography is not penalized more than the other hypotheses. For these reasons, we argue that model selection based on prediction is more relevant to inferring the role of the various hypotheses of control on the spatial distribution of spawning plaice.



**Figure 6.** The complexity of selected binomial and Gaussian models. Complexity is represented by the mean number of hypotheses and explanatory variables in the models retained. The mean and the standard deviation of the number of hypotheses and explanatory variables are given for strategy (a), Predict 2000s, and strategy (b), Predict 1980s, for binomial and Gaussian models and for the two selection procedures. No value has been calculated for the binomial model from the prediction of strategy (b) because only one model was selected.

**The influence of datasets on model and hypothesis selection**

The results of the present study reveal that selected models are not the same, according to the period on which they are adjusted and applied. The approach has proven to be informative because it has been shown that these differences in selected models demonstrate

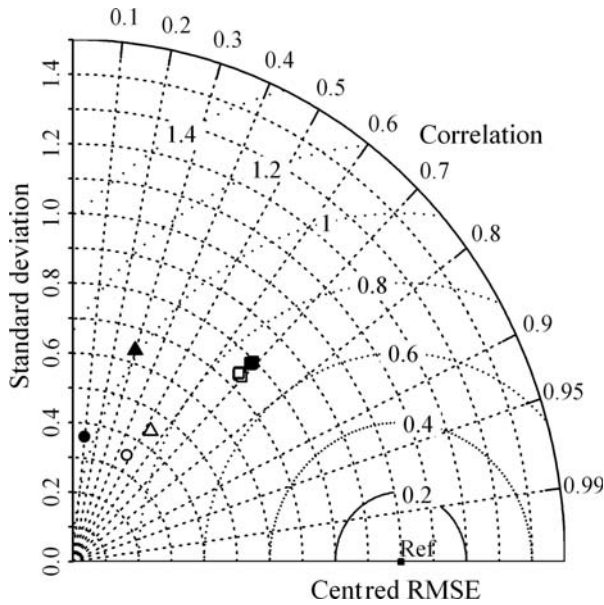
**Table 3.** Frequencies of the different hypotheses, giving the percentage of the model in which each hypothesis is present.

Hypotheses	All models	Strategy (a) "Predict 2000s"	Strategy (b) "Predict 1980s"	Binomial models	Gaussian models
Fitting-based selection					
G	0	0	0	0	0
Ep	++++	++++	++++	++++	++++
Enp	+++	+++	++	++	+++
Bs	++++	++++	++++	++++	++++
Ms	++++	++++	++++	++++	++++
Fs	++	0	+++	+	+++
Ps	++++	+++	++++	++++	++++
Da	+++	++++	++	+++	+++
Ds	++++	++++	++++	-	++++
M	++++	++++	++++	++++	++++
Prediction-based selection					
G	++	0	+++	0	+++
Ep	+++	+++	+++	+++	+++
Enp	++	+++	0	++++	0
Bs	+++	++++	++	++++	+++
Ms	+++	+++	+++	+++	++++
Fs	+	++	0	++	+
Ps	++++	+++	++++	+++	++++
Da	++	0	++++	+	+++
Ds	++++	++++	++++	-	++++
M	++++	++++	++++	++++	++++

Recoding was according to five levels: 0 (absence), + (<25%), ++ (25–50%), +++ (50–75%), +++++ (75–100%). For each selection procedure, results are indicated for the whole set of models selected as well as according to the model class (binomial or Gaussian) and strategy: (a) Predict 2000s, and (b) Predict 1980s. Hypotheses: G, geography; Ep, persistence of the environment; Enp, non-persistence of the environment; Bs, broad-scale submodel; Ms, medium-scale submodel; Fs, fine-scale submodel; Ps, population size; Da, annual demography; Ds, spatial demography; M, population memory.

that some hypotheses have different relevance according to the period considered. The non-persistence of the environment for the beginning of the period (1980s and 1990s) was more relevant to explaining the plaice distribution observed in the 2000s.

However, when models are defined from the environmental conditions of 1990s and 2000s to explain observations in the 1980s, the non-persistence of the environment is no longer relevant. Conversely, geography and annual demography were determined as more relevant hypotheses to predict the spatial the distribution in the 1980s than during the 1990s and 2000s. These aspects will be discussed below, addressing the role of each hypothesis on the spatial distribution of plaice.

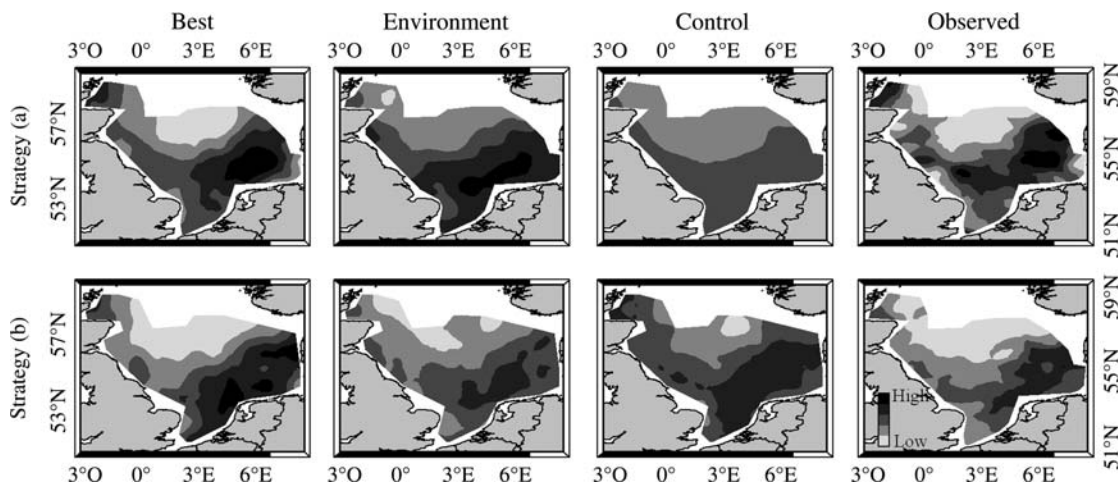


**Figure 7.** Plot of the Taylor diagram. Only the part representing a positive correlation is shown. Observations and predictions of selected (square), environmental (triangle), and control (circle) models are compared for strategy (a), Predict 2000s (filled symbols), and strategy (b), Predict 1980s (open symbols), using the standard deviation, the RMSE, and the Spearman correlation. Observations are symbolized as a point referred to as the reference point and are normalized so that the standard deviation is equal to 1, the correlation equal to 1 (the correlation between the observations and themselves), and the RMSE equal to 0 (the difference between the observations and themselves). Values of the indices for the predictions are plotted with the standard deviation on the y-axis, the correlation on the radii of the circle, and the RMSE on concentric circles around the reference point.

**Relevance of the different factors to the spatial distribution of spawning plaice**

The analysis of the hypotheses retained in selected models from prediction reflects differences in the relevance of some hypotheses according to the type of model (either binomial or Gaussian). This suggests that the presence/absence of spawning plaice at a certain location is not controlled in exactly the same way as abundance. According to the frequencies of the various hypotheses in models selected from prediction, five hypotheses can be shown to be important (present in more than 50% of selected models) in determining presence/absence of spawning plaice: persistence of the environment, broad and medium scale, and population size and memory. Geographic location and population demography (annual and spatial) appear to be additional factors in controlling the abundance.

The importance of persistence of the environment in determining the spatial distribution of both presence/absence and abundance of spawning plaice means that its spatial distribution is primarily controlled by geographic variation in depth, seabed stress, and sediment type. Whereas non-persistence of the environment was present in most of the models selected, we think that it is not a hypothesis that can explain the spatial distribution of spawning plaice. We argue that the difference in frequency of both geographic location and non-persistence of the environment according to the period considered reflects an overlapping effect between them in the 1980s on the spatial distribution of plaice. In the 1980s, the effect of geography was embedded in non-persistence of the environment, and although the non-persistence of the environment changed subsequently, the spatial distribution of plaice did not really change, revealing the importance of



**Figure 8.** Maps of the distribution of spawning adult plaice. Maps for the best selected model, the environmental model, and the control model were computed from predicted values of these models for the years 2004 [strategy (a), Predict 2000s], and 1985 [strategy (b), Predict 1980s]. The corresponding maps of the observed distribution of spawning adults for the same two years are also shown.

geography. This means that it is more likely the spatial structure of the non-persistence of the environment (highlighted by the importance of the geographic location) that is important rather than the pure environmental effect of non-persistence of the environment. Therefore, the present study does not provide proof that temporal changes in temperature and salinity could explain temporal variations in plaice spatial distribution during the spawning season. This lesser importance of non-persistence of the environment contrasts with the results of most studies based on habitat modelling (Koubbi *et al.*, 2003, 2006; Loots *et al.*, 2007; Planque *et al.*, 2007; Vaz *et al.*, 2008). In those models, the environment was generally the only hypothesis tested. As a result, one or several environmental variables were often retained in the final habitat model because they explained some variation in distribution. The results of the present study show that when control by fluctuations in the environment is confronted with other hypotheses, it may not be as important as originally thought. This means that non-persistence of the environment may not directly control the spatial distribution of a population, particularly during the reproductive season, but it can be correlated spatially with other more direct factors that are not (or not adequately) taken into account in habitat modelling studies. This is a critical issue in the context of hypothesis inference because it reveals that classical habitat modelling may attribute too much importance to non-persistent factors simply because they consider just the environmental hypothesis. The lesser importance of non-persistence of the environment compared with factors may reflect the fact that this study focuses on the spatial distribution of a population and not on that of the species. This implies that the spatial scale involved is not the same and suggests that the temporal variations in temperature and salinity experienced by the North Sea plaice population were within the tolerance range of the species. Also, because the present study is restricted to the particular phase of spawning in the plaice life cycle, this may also suggest that the North Sea provides suitable hydrographic conditions throughout for plaice reproduction and that temperature and salinity are not as important to the distribution of spawning adults as they may be for the survival of eggs and larvae.

Combined with persistence of the environment, control through the size of the population suggests a density-dependent effect on the spatial distribution of the plaice population during its reproductive period. At a small population size, individuals contract their distribution to preferred areas characterized mostly by their persistent environmental characteristics. At large population sizes, fish tend to expand their distribution. The fact that persistence of the environment and population size control both the presence and abundance of plaice suggests a basin-type model (MacCall, 1990). In the basin model, the size of the area occupied (Shepherd and Litvak, 2004), as well as abundance, vary according to the size of the population. Population size was slightly more important in determining the areas of greater abundance of plaice than the species' areas of presence. This could intimate that the variations in population size were not sufficient to detect its effect on plaice occupation of spawning areas fully. Therefore, the results reveal that temporal variations in the size of the population are an important feature in explaining temporal variations in the spatial distribution of spawning plaice.

We believe that the low frequency of the annual demography hypothesis during the 2000s only reflects the limited diversity in age structure then. This suggestion is supported by the fact that

when the age structure is more diverse (during the 1980s, the size of the population was greater than that in the 2000s), the role of annual demography becomes evident through its frequency in selected models. For this reason, we argue that both the annual and the spatial demography are important hypotheses in explaining temporal variations in the distribution of spawning plaice. Moreover, population demography seems to be more relevant in controlling the abundance of spawning plaice than it is in controlling their presence/absence. This implies that with the actual age structure of the population, spawning areas are occupied whatever the proportion of old or young adults present in the stock each year. The use of the "old" and "young individuals" terminology is relative for plaice because only a small part of the natural age pyramid is represented. The current heavily exploited population is dominated by younger ages (1–8 years; ICES, 2008), whereas plaice may live up to 20–30 years (Froese and Pauly, 2009). This situation may have caused us to underestimate the overall role of the population age structure in determining the distribution of spawning plaice. Despite the current truncated age structure, both annual and spatial population demography seem to be important in explaining temporal variations in the spatial distribution of abundance. Young and old plaice are not found in the same areas; older fish are generally farther offshore than younger fish (Cushing, 1990). There is also a difference in the time spent on spawning grounds by plaice of different age. Old fish arrive at the spawning grounds first, then stay longer than young plaice (Rijnsdorp, 1989). This implies that, depending on the annual age structure of the population observed in different years, several areas will be occupied more or less, leading to substantial variations in the distribution pattern from one year to the next.

Of the three spatial scales we detected in the distribution of spawning plaice, when confronted with other hypotheses, two are important: the broad and the medium scales. The broad scale is more important in characterizing the areas of presence, whereas a medium scale is more important in characterizing areas of greater abundance. This suggests that the areas of presence are wider than the areas of great abundance, so are not fully occupied. Moreover, the lesser ability of the broad scale to explain the distribution at the beginning of the period relative to the end of the period suggests a difference in distribution between the two periods. Patterns of presence were much wider towards the start of the dataserie, when population abundance was much greater than it was at the end. This finding also confirms what has previously been stated about the control by the size of the population through density-dependent effects. Finally, because fine-scale features (55 km) are similar to the scale of the surveys, the absence of control of the fine-scale submodel could simply result from the sampling strategy. The actual design of the survey (both sampling strategy and gear) is not suitable for exploring processes at scales <55 km.

### **The role of population memory: evidence of conservatism in plaice?**

Both the presence and the abundance of spawning plaice depend too on the memory hypothesis. Spawning adults were abundant mainly in the southeastern North Sea and along the east coast of the UK, and not in the central or northern part of the North Sea. The areas of abundance coincide with the spawning grounds described in the literature based on ichthyoplankton surveys (Harding *et al.*, 1978), spawning grounds occupied by a

distinct subpopulation identified using tags (Hunter *et al.*, 2004). Three main subpopulations have been identified, one in the western part, one in the southeastern part, and another in the northern part of the North Sea. There is also a hypothesis for the existence of a fourth subpopulation near the Moray Firth. The three subpopulations in the southern part of the North Sea are located on distinct feeding grounds during summer, then mix on the southern spawning grounds in winter (Hunter *et al.*, 2004). Northern and eastern subpopulations migrate predominantly to the German Bight and the Transition Area, whereas the western subpopulation migrates to the Flamborough Head region, the Southern Bight, and the eastern English Channel (Hunter *et al.*, 2003). This migration pattern seems to be repeated annually (Hunter *et al.*, 2003), explaining why several studies have demonstrated from egg surveys a consistency of spawning grounds during the 20th century (ICES, 2003). Site fidelity of spawning plaice has also been demonstrated for the Icelandic stock (Solmundsson *et al.*, 2005).

Conservatism has been proposed as an explanation of why a population maintains its spawning location over time (Corten, 2002). The theory implies that fish have learned a behaviour that has been transformed into a habit, which is then transmitted across generations. Whereas conservatism has been suggested for several pelagic species (McQuinn, 1997; Corten, 2002; Petitgas *et al.*, 2006), the concept may not be so easily advanced for demersal species. For plaice, the habit has become the annual migration from northern summer feeding grounds to southern winter spawning grounds. Whereas the habit-forming portion of conservatism could be explained by the use of external clues such as physical characteristics of migrations routes and tidal currents (Hunter *et al.*, 2003), the orientation mechanisms implied in plaice migration remain unclear. Corten (2002) argues that to prove the existence of habit formation, it must be demonstrated that (i) the same fish visit the same location in successive years, (ii) this behaviour is not genetically determined, and (iii) the return of the fish is not simply a consequence of environmental constraints. Point (i) is supported for plaice by the fact that tagging experiments have shown that the different subpopulations of the North Sea stock tend to return to their same spawning grounds from one year to the next (Hunter *et al.*, 2004). The results of this study allow us to validate point (iii), because they have proved that space, persistence of the environment, and population memory are the key factors and that non-persistence of the environment is not as critical because the distribution does not appear to follow any changes in the environment. We believe that because the persistence of the environment is spatially structured but does not vary in time, it acts more as a spatial constraint than a pure environmental constraint (i.e. in the sense of the direct physiological effect that temperature and salinity may have on spatial distribution). For this reason, we argue that the importance of persistence of the environment does not call into question the role that conservatism may play in the spatial stability of North Sea plaice spawning areas. The mechanism of transmission of this habit between generations still remains unclear for plaice, but the meeting of first-time spawners and spawning adults on spawning or nursery grounds (Cushing, 1990) could be preliminary supporting evidence for the existence of tradition (*sensu* Corten, 2002).

Three main circumstances may alter the habits associated with conservatism (Corten, 2002). The first is if the environmental conditions result physiological extremes for the fish (Rindorf and

Lewy, 2006). During our study period, we found no evidence of dramatic change in the main pattern of spawning distribution because spawning plaice are still found in the western and southern part of the North Sea. This could suggest that up to now, plaice have not experienced sufficiently disruptive environmental change to modify spawning behaviour. However, this view can be biased by the fact that conservatism creates a certain inertia in spawning behaviour, which can result in a time-lag between environmental change and the change in fish migration (Corten, 2002). It is highly probable that the present distribution of North Sea plaice reflects the environmental conditions of the past rather than of the present. Traditional habits may also change following the collapse of a stock. North Sea plaice have been assessed since 1957 (ICES, 2008), and there has been no stock collapse, perhaps explaining why the distribution pattern has been consistent across many generations. Finally, a change in traditional habits could follow an abnormal distribution of the recruiting year class or a scarcity of older individuals. However, older individuals are not sufficiently abundant to influence the behaviour of all the younger fish, which would lead to the loss of a part of the population recruitment that could colonize past or new spawning areas. As Rijnsdorp (1989) noted, plaice age and size at maturity have decreased since the beginning of the 20th century. The fact that all fish do not mature at the same age greatly limits the risk of non-entrainment and the loss of a portion of first-time spawners. This statement is true only under the condition that older fish are still sufficiently numerous to entrain young ones even in the situation where recruitment is low. For plaice, several important recruitment events to the spawning population have been documented since 1957 (ICES, 2008). If conservatism in plaice is a true theory, the fact that spawning tradition has been maintained across generations could suggest that the pool of older individuals has always been sufficient to entrain most young fish onto the spawning grounds. However, as said above, the term "old" is relative for plaice, and the plaice spawning stock is nowadays dominated by younger fish. In the context of global warming, this can have a major impact on the future distribution of North Sea spawning plaice population if, as Corten (2002) suggested, young fish are expected to respond more directly to environmental change than older ones.

## Conclusions

Although considered simple, a multiple-regression approach is an elegant way to model single hypotheses using explanatory variables, then to combine them to construct models of increasing complexity. The method has also revealed itself to be useful in confronting and selecting models that are best able to reproduce the observed distribution of spawning plaice. The results of the present study have shown some discrepancies between selected models depending on the selection criteria, and it has been said that inference of the various hypotheses of control should be based on models selected from prediction rather than from calibration. If this method is taken further, the period considered as well as the data variability encompassed are crucial features in evaluating the importance of the hypotheses because applying models across a wide range of ecological variability can reveal a hidden effect between collinear variables. Some key questions raised in the study deal with the size of the predictive dataset. Here, the calibration dataset was much larger than the prediction dataset, which can lead to more complex models being needed to fit the data. However, we believe that determining the hypotheses of control



should not depend on the size of the dataset. Processes that control the distribution of a species should be able to reproduce an observed pattern whatever the number of years. For plaice, it proved impossible to build a larger predictive dataset that would include the whole range of variability of the calibration dataset. However, that particular aspect should be studied further to verify the stability of the selected set of hypotheses.

Although the use of binomial and Gaussian models may appear to be *a priori* restrictive, the approach does make it possible to separate what controls the presence/absence of plaice from what controls its abundance. From the predictive models selected, we have demonstrated that more factors intervene in the control of the abundance of spawning plaice than in the control of its presence/absence. Our results confirm the fidelity of North Sea plaice to its traditional spawning areas through the importance of the hypotheses of geographic attachment, population memory, and spatial dependence. If the spatial structure of a persistent environment seems to be a key factor in determining the spatial distribution of plaice, variations in population size and demography govern the changes in the spatial pattern of plaice distribution over time. In this context, interannual variability in environmental factors such as temperature and salinity are poorly related to the interannual variations in the spawning areas of plaice. For now at least, the North Sea seems to offer a reasonable environment for plaice spawning. However, because the distribution of spawning plaice is restricted to known areas, the distribution itself is the driving feature for the life cycle rather than a response to environmental constraints. However, this may not be the case in the future context of global warming owing to the strong reliance on young fish to ensure reproductive success.

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