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

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Abstract:

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

Introduction

Plaice is a flatfish heavily exploited in the North Sea (Rijnsdorp and Millner, 1996). The state of the stock has been evaluated by quantitative stock assessment and is available for the period 1957-2007 (ICES, 2008). Its spawning distribution has been mainly studied through the spatial distribution of eggs (Harding *et al.*, 1978; ICES, 2005), however little attention has been paid to the distribution of spawning adults (but see Cushing, 1990; Hunter *et al.*, 2004; Metcalfe, 2006).

Many processes play a role in the control of population spatial distribution. Environmental control finds its ecological basis through the ecological niche theory of Hutchinson which is delimited by a hypervolume of *n* dimensions, each of them being an environmental factor limiting the species survival, growth and/or reproduction (Hutchinson, 1957). Spawning populations have ecological preferences for particular environmental ranges and because the environment displays positive spatial autocorrelation, i.e. it is more similar in nearby than in distant locations (Legendre, 1993; Fortin and Dale, 2005), the distribution of the spawners is also autocorrelated. Fish distribution is also affected by attractive or repulsive interactions like during the spawning period when males and females tend to concentrate at relatively small spatial scale to minimise gamete loss and maximize reproductive success. This conspecific attraction may also leads to the distribution of fish being autocorrelated in space.

Internal controls of the spawning distribution are related to the state of the population, mainly its size and demography. Differences in spatial location of the preferred spawning grounds can exist between young and old spawning individuals (Rijnsdorp, 1989). One can therefore reasonably expect that spatial distribution of spawning may then fluctuate depending on the demographic structure of the adult population. Population size can affect the spatial distribution through spatial density dependence. This was formalised by Fretwell and Lucas (1970), Sutherland (1983) and McCall (1990) using the ideal free distribution concept. Under the ideal free distribution, individuals possess a complete knowledge of their surrounding environment and are able to select their habitat in an ideal way in order to maximise their fitness. In the density dependent habitat selection (Rosenzweig, 1991; Marshall and Frank, 1995; Shepherd and Litvak, 2004), fish contract their distribution to their basic suitable areas defined by their environmental preferences at low level of population size and extend their distribution to less suitable areas at high level of population size. This phenomenon can lead to a species abundance-area relationship (Swain and Morin, 1996; Fisher and Frank, 2004; Blanchard *et al.*, 2005). Finally, the spatial distribution of fish populations tends to have a degree of persistence over years and recurrent spawning grounds are common for many fish stocks (Hunter *et al.*, 2003; Solmundsson *et al.*, 2005). The maintenance of spatial population pattern across years and across generations is likely driven by conservatism at the 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 which include: environmental conditions, spatial dependency, density-dependent habitat selection, demographic structure, population conservatism and site attachment.

Investigating on 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 theory approach as prescribed by Hilborn and Mangel (1997), Burnham and Anderson (2002), Johnson and Omland (2004), Stephens *et al.* (2007) and Diniz-Filho *et al.* (2008). In this approach, several models, reflecting various hypotheses of control are compared on the basis of a distance metrics between model predictions and observations. The selection procedure can result in several models being reasonably good candidates for 'best model'.

Hypotheses contained in these models can thus be inferred to influence the spatio-temporal variability of the population distribution pattern.

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

Material and methods

The international bottom trawl survey

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 data necessary for the stock assessment of several important demersal fishes (ICES, 2007; ICES, 2008). The sampling network is designed according to statistical rectangles of 1° of longitude by 0.5° of latitude (Figure 1) designed by the International Council for the Exploration of the Sea (ICES). Each rectangle is visited by two different countries which perform a standardised trawl of 30 min using a 36/47 GOV-trawl. Trawl locations are randomly chosen by the country among a pre-defined set of three or four sites inside the rectangle. This results in a minimum of two trawls per rectangle each year. For each trawl, all the specimens are sorted by species and counted. Length measurements, otolith sampling and determination of sexual maturity are performed, for several key species, on a proportion of fish for seven standard “roundfish” areas (ICES, 2004, Figure 1). Individuals are classified into four stages of maturity, stage 3 corresponds to spawning individuals with fluent gonads (ICES, 2004). From 1980 to 2007, 11 343 bottom trawls have been performed which represents an average of 405 bottom trawls per year. These data are available through DATRAS

(DATRAS Trawl Survey data, http://datras.ices.dk/Home/Default.aspx) coordinated by the ICES.

Biological response

Abundance data of plaice spawning adults from the first quarter of the IBTS (January-March) from 1981 to 2007 were used. These abundances have been computed from the available proportion of spawning adults within any given length class (Figure 2). Because the determination of sexual maturity of plaice has been performed only since 2001, there were insufficient data to estimate the proportion of spawning adults within each size class for each year and each area. Therefore, data on the sexual maturity from 2001 to 2007 were pooled together to calculate these proportions for northwest areas pooled together (2, 3 and 4) and southeast areas pooled together (5, 6 and 7). No data on the sexual maturity of plaice in area 1 was available. Males and females were also merged together as there was not enough data to calculate proportions of spawning adults for each sex. This reduced the total number of trawling stations available to 7317 (Figure 1). For each of these stations, total abundance of spawning adults were calculated from the product of the total abundance within each size class and the corresponding proportions of spawning adults inside that size class.

Hypotheses of control

Ten possible control factors were modelled: persistent and non-persistent environment, three scales of spatial dependency, population size, annual and spatial age structure, geographic location and population memory. Persistent environment are the environmental factors that are spatially structured but have not changed during the study period (depth, mean annual bottom shear stress and sediment type at each location). Non-persistent environment are the environmental conditions that are also spatially structured and have changed during the study period (bottom temperature and salinity). Spatial dependency (also termed spatial autocorrelation) describes the spatial structure present in the spatial distribution of plaice. This structure may potentially be shared by other controls like persistent and non-persistent environment. Population size is the size of the population estimated each year, in biomass as well as the total number of individuals in the population. Annual age structure (referred as annual demography) is the proportions of each cohort in each year whereas spatial age structure (referred as spatial demography) is the spatial distribution of each cohort at each trawling station for each year. Geographic location corresponds to absolute coordinates (latitude and longitude) and population memory depicts the degree of persistence of plaice distribution from one year to the next. Geographic location supposes that plaice returns to the same spawning site every year whereas population memory reflects that current spatial distribution depends upon past distribution.

Five environmental variables were used in the analysis: depth (m), bottom temperature (°C) and salinity, seabed stress ($N.m^{-2}$) and sediment type. Depth, bottom temperature and salinity were measured at each trawl location from 1981 to 2007. Salinity was transformed using the equation $\exp(Salinity)/10^{15}$, 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 2D hydrodynamic model (Aldridge and Davies, 1993) from the Proudman Oceanographic Laboratory (POL), and running on a regular grid of 1/8° of longitude by 1/12° 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 1 km^2 resolution. 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 summarised 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 corresponding maps at trawl location using ArcMap's Hawth's Analysis Tools extension (Beyer, 2004). Depth, seabed stress and sediment type were grouped to represent persistent environment, i.e. environment that did not vary during the period of study, whereas bottom temperature and salinity were kept to represent non-persistent environment.

Spatial dependency in the spatial distribution of spawning plaice was modelled using principal coordinates of neighbour matrices (PCNM). PCNM are especially 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 PCNM has been 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 $(longitude \times \cos((latitude \times \pi)/180))$ transforms decimal degrees of longitude into decimal degrees of latitude which are of constant distance using a Mercator like projection formula. The resulting distance matrix was then truncated by recoding all the distances above a particular threshold to four times this threshold. The threshold was taken as the maximum distance between two neighbouring stations in order to keep all the stations connected together. A principal coordinate analysis was then performed on this truncated distance matrix leading to 7317 potential PCNM from which only positive PCNM (eigenvectors with positive eigenvalues) were kept.

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

Spatial scale of these PCNM 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 which represents the spatial scale described by each PCNM. The eigenvalue of each PCNM were plotted versus their range (Figure 3) to group PCNM describing equivalent spatial scale into three sub-models : broad, medium and fine scale sub-model (Bellier *et al.*, 2007). These sub-models were used as three distinct hypotheses of control. The R free software combined to the

PrCoord Tool 1.0 of CANOCO 4.5 software (ter Braak and Smilauer, 2002) were used for PCNM extraction. The ‘forward.sel’ function of the ‘packfor’ package (Dray *et al.*, 2007) was used for the forward selection of the PCNM. Experimental and theoretical variograms were calculated using the geoR package (Ribeiro Jr and Diggle, 2001).

Control through demography was expressed trough both spatial (at each trawl) and annual (at each year) demography using percentage of each cohort from 1 to 5 years old. These are provided each year as estimations since 1957 by the ICES Working Group (ICES, 2007) that is in charge of stock assessment using the Virtual Population Analysis (VPA) method. The proportion of each age for each size class was applied to the total number of individuals of each trawl.

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

Spatial persistence of population distribution over years was expressed using geographical location and population memory. The identity of the ICES statistical rectangles was used as a categorical variable to represent the geographical location. Memory of the population was expressed through the observed abundance of spawning adults of the previous year. Each trawling stations was allocated the observed abundance of the previous year using the spatial joining tools of ArcMap 9.1. For trawling positions for which there was no observation the previous years owing to a lack of time or poor weather, the observed abundance of the closest location was used. This reduced the total available number of trawling stations to 6313 from 1981 to 2007.

Model structure

Generalised additive models (GAM, Hastie and Tibshirani, 1990; Guisan *et al.*, 2002) have been used for building the models. They allow relating, in a non-linear way, a biological response to several explanatory variables using smoothing functions. As often with ecological data, the abundances 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 built respectively on presence-absence and non-null log-transformed abundances. For the binomial model, the various hypotheses of control were tested: geography, persistent and non-persistent environment, the three spatial sub-models, annual demography, population size and memory. For the Gaussian model, the spatial demography was also added.

Model adjustment and prediction

Models were fitted (adjusted) on one part of the dataset and applied for prediction on another part of the dataset to see the effect of the dataset on models and hypotheses selection. In strategy (a) ‘Predict 2000s’, models were fitted to data from the beginning of the study period (1981-1999) and applied to predict on the spatial distribution of plaice for the later part of the study period (2000-2007). A total of 4410 and 3190 trawl sets were used to fit binomial and Gaussian models, respectively, and 1088 and 843 trawl sets, for binomial models and Gaussian models respectively, were used for prediction. In strategy (b) ‘Predict 1980s’, models were fitted on the end of the study period (1990-2007) and applied for prediction to the beginning of the study period (1981-1989). In this instance, 4268 and 3229 trawl sets were used to fit binomial and Gaussian models respectively, while 962 and 647 trawl sets were used for prediction.

Degrees of smoothing were adjusted simultaneously on the corresponding fitting period for all the variable of the same hypothesis (Table 1). Finally, for each class of model (either binomial or Gaussian), all the combinations of the hypotheses were calculated resulting in 2^n-1 candidate models (with *n*, the number of hypotheses). Models were implemented using the R free software (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 predict the spatial distribution of plaice. Models were compared based on their goodness of fit using the Akaike Information Criteria (AIC) (Akaike, 1974) and AIC differences (Burnham and Anderson, 2002; Johnson and Omland, 2004) which are calculated according to the following formulas :

$$(1)\quad AIC_i = -2 \times \log L_i + 2 \times p_i$$

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

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

where Δ_i is the AIC difference for the model i^{th} model and $AIC_{\min}$ is the lower AIC over all candidate models (the AIC of the "best" model).

In the binomial model, the log-likelihood of formula (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) :

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

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) :

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

with Y the vector of observed non-null abundances, $\hat{Y}_i$ the vector of predicted abundances of the i^{th} model, σ^2 the residuals sum of square between predicted and observed abundances, j the number of observations and C a constant.

According to formulas (1) and (2), the best among all candidate models is the one 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 Δ_i. Only binomial and Gaussian models with Δ_i less than 10 were selected as models with higher Δ_i are unlikely to include the best model (Burnham and Anderson, 2002).

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

$$LRT_i = -2 \times (\log L_i - \log L_{\max})$$

with LRT_i the likelihood ratio test of model i and $\log L_{\max}$ the log-likelihood of the best model (with thus a LRT equal to 0).

Models were ranked according to their LRT from smallest to largest. The same selection threshold of 10 as for Δ_i was used in order to keep only a reduced set of selected models.

The AIC has been calculated with the AIC function of the ‘stats’ package in R (R Development Core Team, 2008). The log-likelihood has been calculated using the ‘dbinom’ and ‘dnorm’ functions respectively in R (Bolker, pers. com., 2008).

<u>Model Evaluation</u>

Binomial and Gaussian models selected based on the likelihood ratio test were re-applied to the corresponding prediction dataset of each strategy within the same range that have been used to fit Gaussian models (more restrictive as based on lesser observations). Predicted probabilities of presence and predicted log-transformed abundances were then combined in a delta approach where they are multiplied to each other (Stefánsson, 1996) to predict spatial distribution. This resulted in several predicted distributions by combination of binomial and Gaussian models. Predicted distribution were graphically compared to observed distribution by the mean of a Taylor diagram (Taylor, 2001), through the use of three similarity indices. These were the standard deviation, the root mean squared error (RMSE) and the Spearman correlation coefficient. Plot of the standard deviation allows to establish if 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 quantifying the correspondence between the observed and predicted patterns. Delta-model predictions were compared to observations over all the studied period 1981-2007. Also, predictions from a pure environmental delta-model and a control delta-model (combination of the worst determined binomial and Gaussian models) were also plotted for comparison with selected models. The Taylor diagram has been computed using the 'plotrix' package (Lemon *et al.*, 2008) in R.

Results

PCNM extraction and selection

PCNM were used to depict spatial dependency in the spatial distribution of spawning plaice. A threshold of 1.13 (decimal degrees of latitude) was used to truncate the distance matrix between stations. Overall, 2965 positive PCNM were extracted from the principal correspondence analysis and 23 were determined as significant by the forward selection (p < 0.001; adjusted-r^2 = 0.26). From these 23 PCNM, three sub-models representing 3 spatial scales were identified (Figure 5) : broad scale (111-233 km), medium scale (55-111 km) and fine scale (< 55 km). Six PCNM 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, a total number of 41 models were selected (Table 2). Selected models were not the same depending on the selection criteria which means that 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). Selected models were also not the same according to the strategy and type of model (Table 2); binomial models were less complex compared to Gaussian models (Figure 6).

Frequencies of each hypothesis within the set of selected models were estimated (Table 3). Three hypotheses dominated: population size, population memory and spatial demography. Persistent environment and broad and medium scale sub-models were also important but less frequent. Geography, non-persistent environment, fine scale sub-model and annual demography were the less frequent hypotheses and those that show strong differences in 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-persistent environment and fine scale sub-model 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 models 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 2000-2007 period which resulted in 32 predicted distributions. For strategy (b) ‘Predict 1980s’, combinations of the unique binomial model with the 12 Gaussian models, selected from prediction, where reapplied on the 1981-1989 period which resulted in 12 predicted distributions. The Taylor diagram comparing these predicted distributions to observed distribution is presented in Figure 7. 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-persistent environment and annual demography and the Gaussian model containing annual demography. For strategy (b) ‘Predict 1980s’, it is the combination of geography, non-persistent environment, medium and fine scale sub-models and annual demography with the annual demography. Maps of corresponding predicted distribution are presented in Figure 8.

Selected models were clearly distinct from the pure environmental model and the control model. Predictions from selected models have higher correlation, higher standard deviation and lower RMSE with observations than the environmental and control model, confirming that the selected models have a greater predictive power. Predicted distribution pattern from the best model are more similar to the observed distribution relative to the others (Figure 8). Selected models had similar correlations, standard deviation and RMSE which make them hard to distinguish using the Taylor diagram. Selected models of strategy (a) ‘Predict 2000s’ and (b) ‘Predict 1980s’can be distinguished on the diagram even though they have similar values of correlation (R^2 close to 0.7), RMSE (around 0.7) and standard deviation (between 0.75 and 0.80).

Discussion

Influence of the selection procedure

Selection procedure either based on fitting (measured using the AIC) or prediction (based on LRT) performances had an impact on model selection. Models selected on the basis of their fitting performances were usually more complex than those selected on their prediction performances. This suggests that selection based on the AIC tends to promote more complex models that are possibly over-fitted to the data. This may arise because data are autocorrelated in both space and time with the true number of independent observation being smaller than the number of empirical ones. Such phenomenon would artificially inflate the weight of the first term of the AIC (the model adjustment) compared to the second term (the parsimony of the model), thereby 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 problem of autocorrelation for model selection. Burnham and Anderson (2002) did not exclude the possibility that the AIC based selection may results in over-fitted model. They advised to avoid “models with a great many parameters” more than is thought to be really needed. To alleviate an unreasonable number of competing models (Diniz-Filho *et al.*, 2008), models were constructed as the combination of hypotheses rather than individual explanatory variables. Moreover, all degree of smoothing were not considered but were determined before the combination of the various hypotheses, this also limits the final number of competing models.

Model over-fitting resulting from AIC-selection is a critical issue. It can lead to inappropriate promotion of complex hypotheses which contain many variables. Such models may display a good adjustment to the data but a low predictive power. This is illustrated by the fine scale sub-model hypothesis (containing 8 variables) which was retained in AIC-selection but rejected when selection is performed of model predictive performance. Inversely, this can lead to undervaluing some hypothesis such as pure geography. When categorical factors are used, each category is counted as 1 parameter in the model. Here, geographical models based on 114 statistical rectangles treated as factors are strongly penalised because their AIC value is highly inflated. Conversely, when selection procedure is based on prediction, the number of variables is not taken into account in the likelihood ratio test and thus the geography is not penalised more than other hypotheses. For these reasons, we argue that model selection based on prediction is more relevant to infer the role of the various hypotheses of control on the spatial distribution of spawning plaice.

Influence of datasets on model and hypothesis selection

The present study reveals that selected models are not the same according to the time period on which they are adjusted and applied. This approach has proven to be informative as it has shown that these differences in selected models reflect that some hypotheses have not the same relevance according to the time period considered. The non-persistent environment for the beginning of the period (1980s and 1990s) was more relevant to explaining plaice distribution that was observed in the 2000s. However, when models are defined from the environmental conditions of 1990s and 2000s to explain what is observed in the 1980s, the non-persistent environment is no longer relevant. Conversely, geography and annual demography were determined as more relevant hypotheses to predict the spatial distribution in 1980s than during the 1990s and 2000s. These aspects will be further discussed in following sections addressing the role of each hypothesis on the spatial distribution of plaice.

Control of 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 determined to be important (present in more than 50% of selected models) to determine presence/absence of spawning plaice population: persistent environment, broad and medium scale and population size and memory. Geographical location and population demography (both annual and spatial demography) appear to be additional factors for the control of abundance.

The importance of persistent environment to determining the spatial distribution of both presence/absence and abundance of spawning plaice means that its spatial distribution is primarily controlled by geographical variation in depth, seabed stress and sediment type. Whereas non-persistent environment was present in most of selected models, we think that it is not a relevant hypothesis to explain the spatial distribution of spawning plaice. We argue that the difference of frequency of both geographical location and non-permanent environment according to the time period considered reflects an overlapping effect in the 1980s between them on the spatial distribution of plaice. In the 1980s, the effect of geography was embedded in non-persistent environment and, although the non-persistent environment changed in the later period, the spatial distribution of plaice did not really change, revealing the importance of geography. This means that it is more the spatial structure of the non-permanent environment (highlighted by the importance of the geographical location) that is important rather than the pure environmental effect of non-persistent 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-permanent environment is in contrast with results of most of the studies based on habitat modelling (Koubbi *et al.*, 2003; Koubbi *et al.*, 2006; Planque *et al.*, 2007; Loots *et al.*, 2007; Vaz *et al.*, 2008). In those models, environment was generally the only hypothesis tested. As a result, one or several environmental variables are often kept in the final habitat model as they explained some variation in the distribution. The present study shows that when control by fluctuating environment is confronted to other hypotheses, it may not be as important based on prior expectations. This means that non-persistent environment may not directly control the spatial distribution of a population, particularly during the reproduction season, but can be spatially correlated 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 hypotheses inference because it reveals that classical habitat modelling may attribute too much importance to non-permanent factors only because they only consider the environmental hypothesis. The low importance of non-permanent environment compared to other factors may reflect 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 population were within the tolerance range of plaice. Also, as 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 everywhere for plaice reproduction and that temperature and salinity are not as important to the distribution of spawning adults as much as they may be for the successful survival of eggs and larvae.

Combined to persistent environment, control through the size of the population suggests a density dependent effect of the spatial distribution of plaice population during its reproduction time. For small population size, individuals contract their distribution to preferred areas which can be characterised mostly by their persistent environmental characteristics. At high population size, fishes tend to expand their distribution. The fact that persistent environment and population size control both the presence and abundance of plaice suggests a basin type model (McCall, 1990). In the basin model, the size of the area occupied (Shepherd and Litvak, 2004) as well as the level of abundance vary according to the size of the population. Population size was slightly more important in determining the areas of high abundance of plaice population than its areas of presence. This could reflect that variations in population size was not sufficient to fully detect its effect on the occupation of the spawning areas. Therefore, these results reveal that temporal variations in the size of the population are an important feature to explain temporal variations in the spatial distribution of spawning plaice.

We argue that the low frequency of the annual demography hypothesis during the 2000s only reflects the low diversity in the age structure at this time. This is supported by the fact that when the age structure is more diverse (during the 1980s the size of the population was greater than in the 2000s), the role of the annual demography becomes evident trough its frequency in selected models. For this reason, we argue that both the annual and spatial demography are important hypotheses to explain temporal variations in the spawning plaice distribution. Moreover, population demography seems to be more relevant in controlling level of abundances 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 that are present in the stock each year. The use of the "old" and "young individuals" terminology is relative for plaice as only a small part of the natural age-pyramid is represented. The current heavily exploited population is dominated by younger ages (1 to 8 years, ICES, 2008) whereas plaice may live up to 20-30 years old (Froese and Pauly, 2009). This may have caused us to underestimate the full role of the population age structure in determining the presence of spawning plaice. Despite the current truncated age structure, both annual and spatial population demography seem to be important to explain temporal variations in the spatial distribution of abundances. Young and old individuals of plaice are not occurring in the same areas. The older ones are usually distributed more offshore compared to youngest ones more near to the coast (Cushing, 1990). There is also a difference in time spent on the spawning grounds according to the age of the individuals. Old individuals arrive first on spawning grounds and stay longer compared to young individuals (Rijnsdorp, 1989). This implies that, depending on the annual age structure of the population observed in different years, several areas will be more or less occupied, which will lead to substantial variations in the observed distribution pattern from one year to another year.

Of the three spatial scales we detected in the distribution of spawning plaice, when confronted to other hypotheses, two are important: the broad and medium scales. Broad scale is more important to characterise the areas of presence whereas medium scale is more important to characterise the areas of high abundances. This suggests that areas of presence are wider than areas of high abundances and thus not fully occupied. Moreover, the lower ability of the broad scale to explain the distribution at the beginning of the time period relative to the end suggests a difference in the extent in the distribution between the two periods. Patterns of presence were much wide spread at the beginning of the time period when population abundance was much greater than at the end. This also confirms what was previously stated about the control by the size of the population through density-dependent effect. Finally, because the fine scale features (55 km) are similar to that of the surveys, the absence of control of the fine scale sub-model could simply results from the sampling strategy. The actual design of the survey (both sampling strategy and gear) is not suitable to explore processes at scales smaller than 55km.

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

Both presence and abundance of spawning plaice also depends on the memory hypothesis. High concentrations of spawning adults were mainly located in the south-eastern North Sea and along the east coast of United Kingdom. Spawning adults were not abundant in the central and Northern part of the North Sea. These areas of high abundance coincide with the spawning grounds described in the literature based on ichthyoplankton surveys (Harding *et al.*, 1978). These spawning grounds were occupied by distinct sub-population that have been identified using tag experiment (Hunter *et al.*, 2004). Three main sub-populations have been identified, one in the western part, one in the south-eastern part and one more in the northern part of the North Sea. A hypothesis for the existence of a fourth sub-population in the Moray Firth region has also been advanced. The three sub-populations of the southern part of the North Sea are located on distinct feeding grounds during summer and mix on southern spawning grounds during winter (Hunter *et al.*, 2004). Northern and eastern sub-populations migrate predominantly to the German Bight and Transition areas whereas the western sub-population migrate to the Flamborough Head region, Southern Bight area and the eastern English Channel (Hunter *et al.*, 2003). This migration pattern seems to be repeated each year (Hunter *et al.*, 2003) which explains why several studies have shown from egg surveys that location of the spawning grounds did not vary a lot during the 20th century (ICES, 2003). Site fidelity for spawning areas has also been demonstrated in Icelandic plaice (Solmundsson *et al.*, 2005).

Conservatism has been proposed to explain the ability of a population to maintain its spawning location in time (Corten, 2002). It implies that fish have learned a certain behaviour that have transformed into a habit and that has been transmitted across generations. Whereas conservatism has been suggested for several pelagic species (McQuinn, 1997; Corten, 2002; Petitgas *et al.*, 2006), one can ask if this concept can be valid for a demersal species. In the case of plaice, the habit corresponds to the annual migration from northern summer feeding grounds to southern winter spawning grounds. Whereas the habit formation part of conservatism could be favoured by using external clues such as physical characteristics of migrations routes and tidal current (Hunter *et al.*, 2003), orientation mechanisms implied in plaice migration remain unclear. Corten (2002) argues that to prove the existence of habit formation, it must be demonstrated that (1) the same fish visit the same location in successive years, (2) that this behaviour is not genetically determined and (3) that the return of the fish is not simply as a result of environmental constraints. Point (1) is supported by the fact that tagging experiments have shown that the different sub-populations of North Sea plaice tend to return to their specific spawning grounds from one year to another (Hunter *et al.*, 2004). The present study allows us to validate point (3) as it has proved that space, persistent environment and population memory are the key factors and that non-persistent environment is not as important because the observed distribution does not appear to follow its changes. We believe that because the permanent environment is spatially structured but does not vary in time, it acts more like a spatial constraint rather than like a pure environmental constraint (i.e. in the sense of direct physiological effect that temperature and salinity may have on spatial distribution). For this reason, we argue that the importance of permanent 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 encounter between first time spawners and spawning adults on spawning or nursery grounds (Cushing, 1990) could be a preliminary supportive evidence for the existence of tradition (*sensu* Corten, 2002).

Three principal circumstances may alter the habits associated with conservatism (Corten, 2002). First, if environmental conditions reach physiological extremes (Rindorf and Lewy, 2006). During our study period, we found no evidence of dramatic changes in the main pattern of spawning distribution because spawning plaice are still located in the western and southern part of the North Sea. This could suggest that until now plaice did not experience strong enough environmental changes to modify their spawning behaviour. However, this view can be biased by the fact that conservatism creates a certain inertia in the spawning behaviour which can result in a time lag between the environmental change and the change in fish migration (Corten, 2002). It is highly probable that current distribution of North Sea plaice reflects the environmental conditions of the past rather than those at present. Then, traditional habits may also change following a collapse of the stock. North Sea plaice has been evaluated since 1957 (ICES, 2008) and no stock collapse has been observed, which may also explain why the distribution pattern has been maintained successfully across generations. Finally, the last explanation of change in traditional habits is an abnormal distribution of the recruiting year-class or a scarcity of older individuals. In both instances, older individuals are not sufficiently abundant to affect the behaviour of all younger individuals, which could lead to the loss of a part of the population recruits that could potentially colonise past or new spawning areas. As Rijnsdorp (1989) noted, age and size at maturity in plaice has decreased since the beginning of the century. The fact that all individuals do not become mature at the same age greatly limits the risk of non-entrainment and lost of a part of the first time spawners. This is true only under the condition that older individuals are still numerous enough to entrain young individuals even in the case of a small pool of recruits. In the case of plaice, several important recruitments to spawning population have been noticed since 1957 (ICES, 2008). If conservatism in plaice is true, the fact that spawning tradition has been maintained across generations could suggest that the pool of older individuals has always been sufficient to entrain the majority of young individuals onto the spawning grounds. However, as it has been previously said, the term “old” is relative for plaice and we have to consider that reproduction in plaice is nowadays predominantly ensured by younger individuals. In the context of global warming, this can have strong impact on the future distribution of North Sea spawning plaice population if, as Corten (2002) suggested, young individuals are expected to respond more directly to environmental change than older ones.

Conclusion

Although considered as simple, multiple-regression approach is an elegant way to model single hypotheses using simple explanatory variables and to combine them in order to construct models of increasing complexity. This method has also revealed itself useful in confronting and selecting models that are best able to reproduce the observed distribution of spawning plaice. Present study has pointed out some discrepancies between selected models depending on the selection criteria and it has been deduced that inference on the various hypotheses of control should be based on models selected from prediction rather than from calibration. If this method offers a valuable alternative, the time period considered as well as the data variability it encompasses is also an important feature to evaluate the importance of the various hypotheses, as applying models on a wide range of ecological variability can reveal hidden effect between collinear variables. Some key questions raised in this study deal with the size of the prediction dataset. In this study, the calibration dataset was much larger than the prediction dataset which can lead to more complex models 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 correctly reproduce the observed pattern whatever the number of years considered. For plaice, it was unfortunately impossible to build a larger prediction dataset that would include all the range of variability of the calibration dataset. However, this particular aspect should also be further studied 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 makes it possible to separate what controls the presence/absence of plaice to what controls their abundance. From the models selected from prediction, we deduced that a greater number of factors intervene in the control of the distribution of abundances of spawning plaice than in the control of its presence/absence. The present study confirms the high fidelity of North Sea plaice to its spawning areas through the importance of the hypotheses of geographical attachment, population memory and spatial dependency. If the spatial structure of persistent environment seems to be a key factor in determining the spatial distribution of plaice, temporal variations in population size and demography govern changes in the spatial pattern of plaice distribution. In this context, inter-annual variability of environmental factors like temperature and salinity are poorly related to inter-annual variations of spawning areas of plaice. For the time being, the North Sea seems to still offer good enough environmental conditions for plaice reproduction. However, as the observed distribution is restricted to particular areas, it may suggest that the actual distribution should be the pertinent conformation to ensure the successful end up of plaice life cycle rather than a response to environmental constraint. However, this may not be the case in the future context of global warming due to the strong reliance on young individuals to ensure reproduction success.

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Figure 1 : Map of the North Sea. Trawling stations of the first quarter (January-March) of the International Bottom Trawl Survey from 1980 to 2007, for which abundances of spawning adults of North Sea plaice are available, are indicated. Countries involved in the IBTS, ICES statistical rectangles, standard roundfish areas and main locations are also indicated.

Figure 2 : Proportions of adults of stage 3 (spawning adults) of North Sea plaice per size class. Left : areas 2, 3 and 4 pooled together. Right : areas 5, 6 and 7 pooled together. No data is available for area 1. Symbols represent the observed proportions and dotted lines correspond to the adjusted proportions using a smoothing spline for missing size class.

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Figure 7 : Plot of the Taylor diagram. Only the positive correlation part is represented. Observations and predictions of selected (square), environmental (triangle) and control (circle) models are compared for strategy (a) ‘Predict 2000s’ (black symbols) and strategy (b) ‘Predict 1980s’ (open symbols) using the standard deviation, the root mean square error (RMSE) and the Spearman correlation. Observations are symbolised as a point called the reference point and are normalised so that the standard deviation is equal to 1, the correlation equal to 1 (the correlation between the observations and themselves) and the

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Figure 8 : Maps of spawning adults distribution. Maps for the best selected model, the environmental model and the control model were computed from predicted values of these models for the year 2004 (strategy (a) ‘Predict 2000s’) and year 1985 (strategy (b) ‘Predict 1980s’). Corresponding maps of observed distribution of spawning adults for these two years are also represented.

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Table 1 : Hypotheses formulas. Explanatory variables of each hypothesis for binomial and Gaussian models were fitted on the corresponding fitting period for strategy (a) ‘Predict 2000s’ and (b) ‘Predict 1980s’. “s” means that a smoothing function has been used and the corresponding degree of smoothing is indicated in bracket. PCNMs are denoted by the “Ax” term. Hypotheses : G = geography, Ep = persistent environment, Enp = non-persistent environment, Bs = broad scale sub-model, Ms = medium scale sub-model, Fs = fine scale sub-model, Ps = population size, Da = annual demography, Ds = spatial demography, M = population memory.

Table 2 : Formulas of selected models. Models were selected according to their capability to fit (Δ_i) and predict (LRT) the observed distribution. Models selected from fitting are those with a Δ_i lower than 10 and models selected from prediction are those with a LRT

lower than 10. In the case of selection based on fitting, the LRT is also given as an informative value as well as the Δ_i in the case of selection based on prediction. In both cases, Δ_i and LRT values are higher than 10 which shows that models that fit the best are not those that predict the best. Formulas are given for selected binomial and Gaussian models for strategy (a) ‘Predict 2000s’ and strategy (b) ‘Predict 1980s’. Hypotheses : G = geography, Ep = persistent environment, Enp = non-persistent environment, Bs = broad scale sub-model, Ms = medium scale sub-model, Fs = fine scale sub-model, Ps = population size, Da = annual demography, Ds = spatial demography, M = population memory.

Table 3 : Frequencies of the different hypotheses. They give the percentage of model in which each hypothesis is present. They were recoded according to five levels : 0 (absence), + (<25%), ++ (25-50%), +++ (50-75%), ++++ (75-100%). For each selection procedure, they are indicated for the whole set of selected models and according to the model class (binomial or Gaussian) and strategy (a ‘Predict 2000s’ and b ‘Predict 1980s’). Hypotheses : G = geography, Ep = persistent environment, Enp = non-persistent environment, Bs = broad scale sub-model, Ms = medium scale sub-model, Fs = fine scale sub-model, Ps = population size, Da = annual demography, Ds = spatial demography, M = population memory.

Strategy (a) 'Predict 2000s'

HYPOTHESES	BINOMIAL MODELS	GAUSSIAN MODELS
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'

HYPOTHESES	BINOMIAL MODELS	GAUSSIAN MODELS
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,) + 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)

Strategy (a) 'Predict 2000s'

SELECTION PROCEDURE	MODEL FORMULAS	Δi	LRT
FITTING (n=6)	***Binomial (n=4)***		
	Ep + Enp + Bs + Ms + Ps + Da + M	0	40.9
	Ep + Enp + Bs + Ms + Da + M	0.7	71.6
	Ep + Bs + Ms + Ps + Da + M	3.9	39.7
	Ep + Bs + Ms + Da + M	8.9	103.5
	Gaussian (n=2)		
	Ep + Enp + Bs + Ms + Ps + Da + Ds + M	0	157.3
	Enp + Bs + Ms + Ps + Da + Ds + M	7.5	153.6
PREDICTION (n=13)	***Binomial (n=9)***		
	Ep + Enp + Bs + Ps + M	130.3	0
	Ep + Enp + Bs + M	149.4	1.2
	Ep + Enp + Bs + Fs + Ps + M	128.3	3.6
	Ep + Enp + Bs + Fs + M	148.2	4.6
	Enp + Bs + Ms + Ps + M	74.3	8.2
	Enp + Bs + Ms + M	97.5	8.6
	Ep + Enp + Bs + Ms + Ps + M	56.3	9.1
	Ep + Enp + Bs + Ms + M	81.2	9.5
	Enp + Bs + Ms + Fs + Ps + M	87.1	9.6
	Gaussian (n=4)		
	Bs + Ms + Fs + Ps + Ds + M	55.2	0
	Ep + Bs + Ms + Fs + Ps + Ds + M	50.6	1.5
	Bs + Ms + Ps + Ds + M	45.5	4.9
	Ep + Bs + Ms + Ps + Ds + M	38.1	6.0
	Bs + Ms + Ps + Da + Ds + M	45.1	8.9
	Ep + Bs + Ps + Da + Ds + M	51.1	9.6

Strategy (b) 'Predict 1980s'

SELECTION PROCEDURE	MODEL FORMULAS	Δi	LRT
FITTING (n=9)	***Binomial (n=5)***		
	Ep + Enp + Bs + Ms + Ps + M	0	61.4
	Ep + Bs + Ms + Ps + M	2.3	79
	Ep + Enp + Bs + Ms + Fs + Ps + M	6.6	66.3
	Ep + Bs + Ms + Fs + Ps + M	7.8	83.2
	Ep + Bs + Ms + Ps + Da + M	8.9	40.5
	Gaussian (n=4)		
	Ep + Enp + Bs + Ms + Fs + Ps + Da + Ds + M	0	28
	Ep + Bs + Ms + Fs + Ps + Da + Ds + M	3	13.3
	Ep + Enp + Bs + Ms + Fs + Ps + Ds + M	3.8	31.4
	Ep + Bs + Ms + Fs + Ps + Ds + M	6.8	18.5
PREDICTION (n=13)	***Binomial (n=1)***		
	Ep + Ms + Fs + Ps + Da + M	149.7	0
	Gaussian (n=12)		
	G + Ep + Ms + Ps + Da + Ds + M	105.5	0
	G + Ms + Ps + Da + Ds + M	109.7	2
	Ep + Bs + Ms + Ps + Da + Ds + M	23.4	3.3
	G + Ep + Ps + Da + Ds + M	82.6	4.7
	G + Ep + Bs + Ms + Ps + Da + Ds + M	118.3	4.7
	G + Bs + Ms + Ps + Da + Ds + M	120.1	6.8
	G + Ep + Bs + Ps + Da + Ds + M	83.8	7
	G + Ep + Ms + Ps + Ds + M	106.8	7.3
	G + Ep + Ms + Ps + Da + Ds	157.9	7.8
	G + Ps + Da + Ds + M	88.1	8.2
	Bs + Ms + Ps + Da + Ds + M	45.1	8.9
	Ep + Bs + Ps + Da + Ds + M	51.1	9.6

Fitting based selection

HYPOTHESES	ALL MODELS	STRATEGY (a) 'PREDICT 2000s'	STRATEGY (b) 'PREDICT 1980s'	BINOMIAL MODELS	GAUSSIAN MODELS
G	0	0	0	0	0
Ep	++++	++++	++++	++++	++++
Enp	+++	+++	++	++	+++
Bs	++++	++++	++++	++++	++++
Ms	++++	++++	++++	++++	++++
Fs	++	0	+++	+	+++
Ps	++++	+++	++++	++++	++++
Da	+++	++++	++	+++	+++
Ds	++++	++++	++++	-	++++
M	++++	++++	++++	++++	++++

Prediction based selection

HYPOTHESES	ALL MODELS	STRATEGY (a) 'PREDICT 2000s'	STRATEGY (b) 'PREDICT 1980s'	BINOMIAL MODELS	GAUSSIAN MODELS
G	++	0	+++	0	+++
Ep	+++	+++	+++	+++	+++
Enp	++	+++	0	++++	0
Bs	+++	++++	++	++++	+++
Ms	+++	+++	+++	+++	++++
Fs	+	++	0	++	+
Ps	++++	+++	++++	+++	++++
Da	++	0	++++	+	+++
Ds	++++	++++	++++	-	++++
M	++++	++++	++++	++++	++++

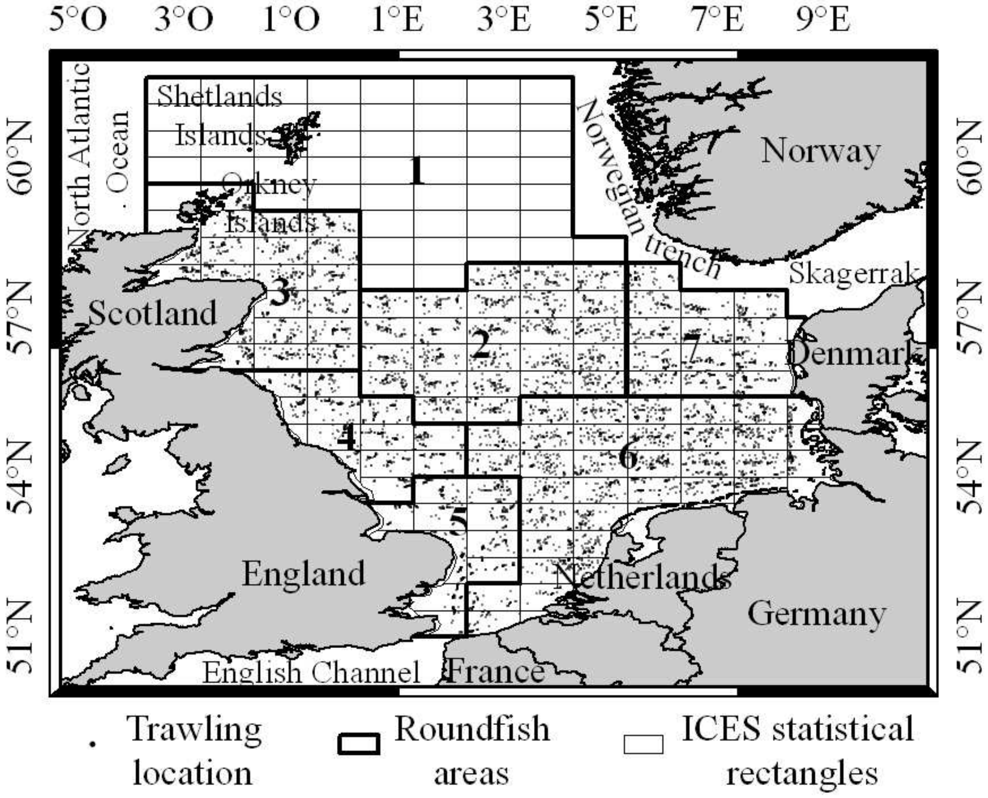

Figure 1 : Map of the North Sea. Trawling stations of the first quarter (January-March) of the International Bottom Trawl Survey from 1980 to 2007, for which abundances of spawning adults of North Sea plaice are available, are indicated. Countries involved in the IBTS, ICES statistical rectangles, standard roundfish areas and main locations are also indicated.
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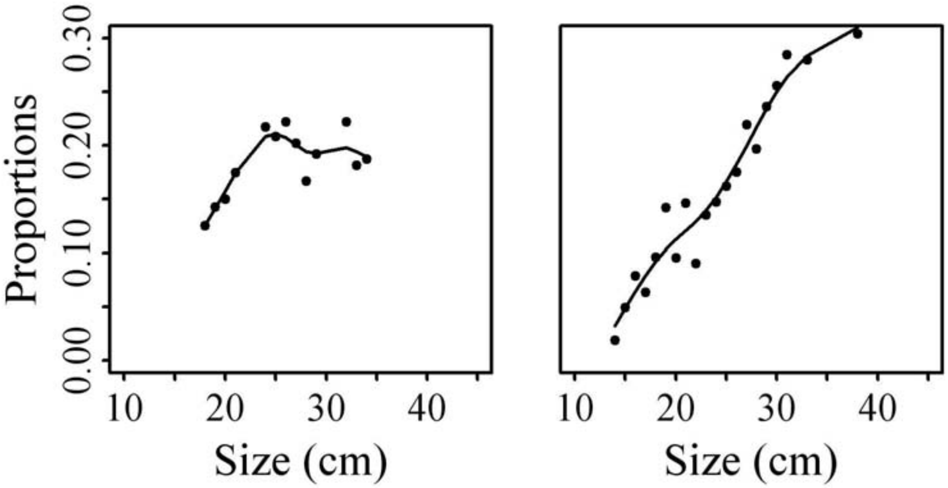

Figure 2 : Proportions of adults of stage 3 (spawning adults) of North Sea plaice per size class. Left : areas 2, 3 and 4 pooled together. Right : areas 5, 6 and 7 pooled together. No data is available for area 1. Symbols represent the observed proportions and dotted lines correspond to the adjusted proportions using a smoothing spline for missing size class.
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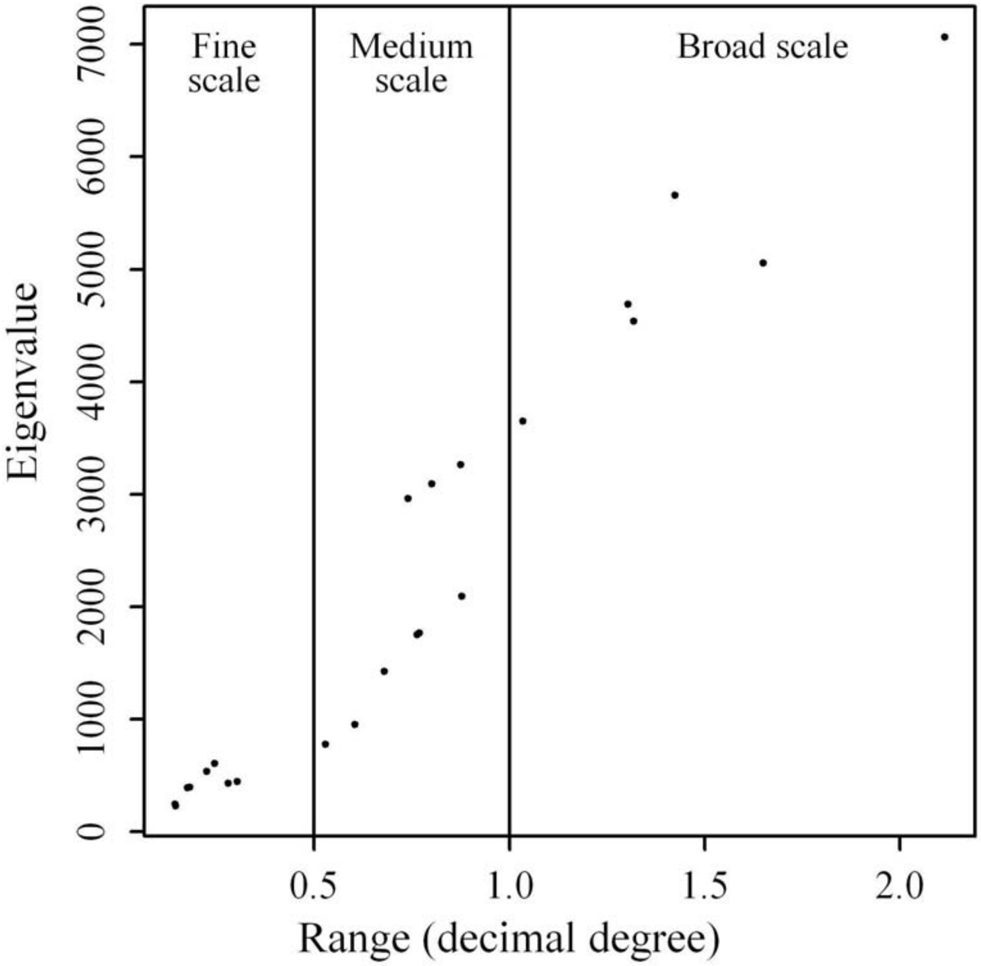

Figure 3 : Plot of the range values of the 23 selected PCNM against their eigenvalue. Ranges were obtained by fitting a Gaussian model as a theoretical variogram on each spatial predictor. Three scales were determined. Broad scale : eigenvectors with a range between 111 and 233 km (1 to 2.1 decimal degrees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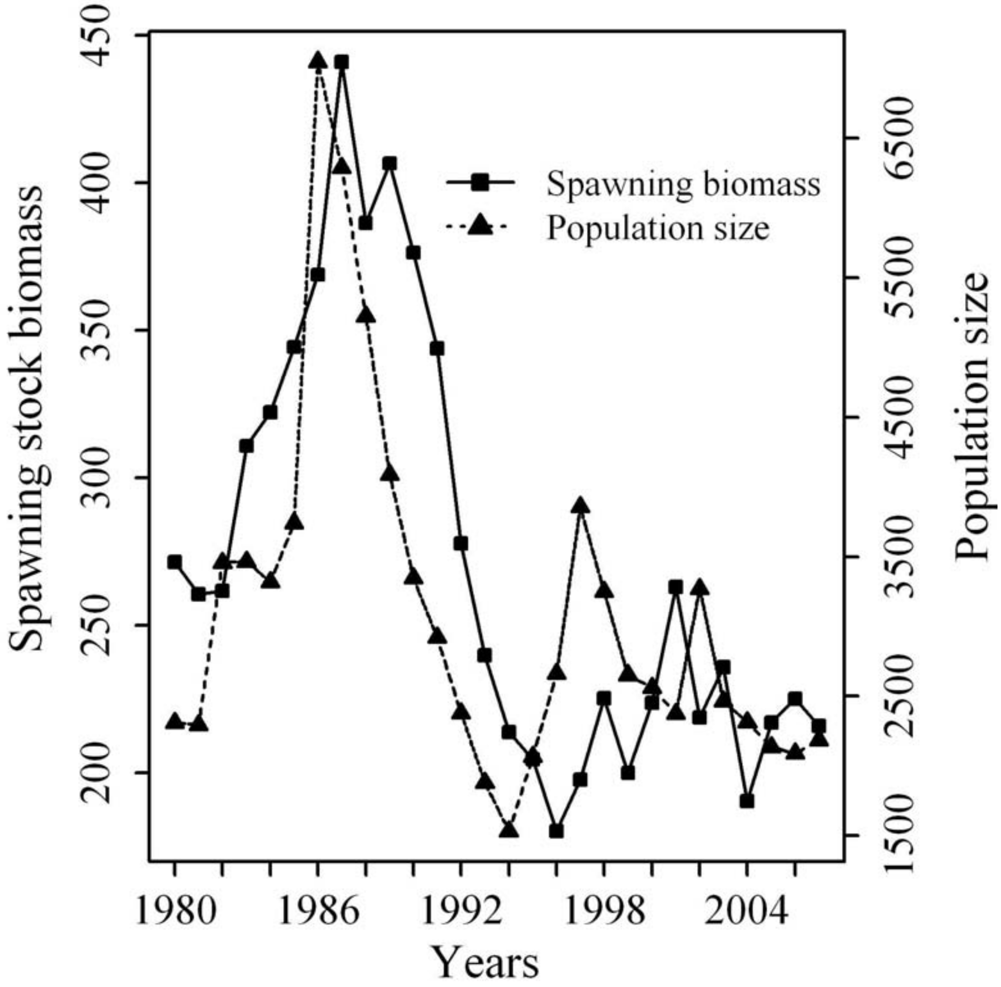

Figure 4 : ICES estimation (IBTS Working Group) of population size (thousands of individuals) and spawning stock biomass (thousands of tons) of North Sea plaice from 1980 to 2007.
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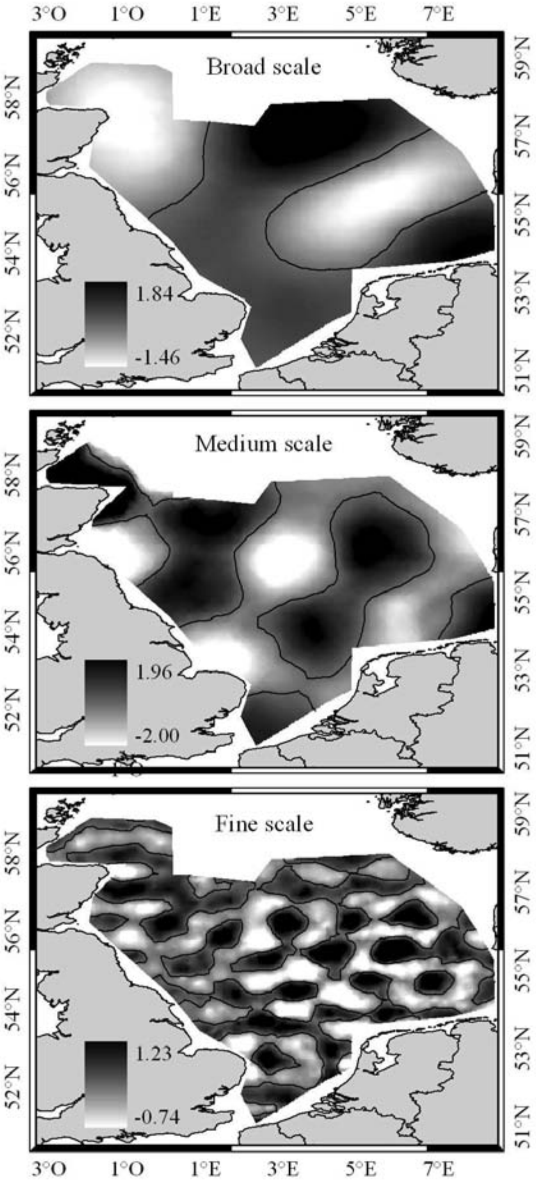

Figure 5 : PCNM spatial sub-models (arbitrary unit). Left : broad scale sub-models; middle: medium scale sub-models; right: fine scale sub-models. Black lines denote the zero value. See also figure 3 for more details on the scales of the sub-models.
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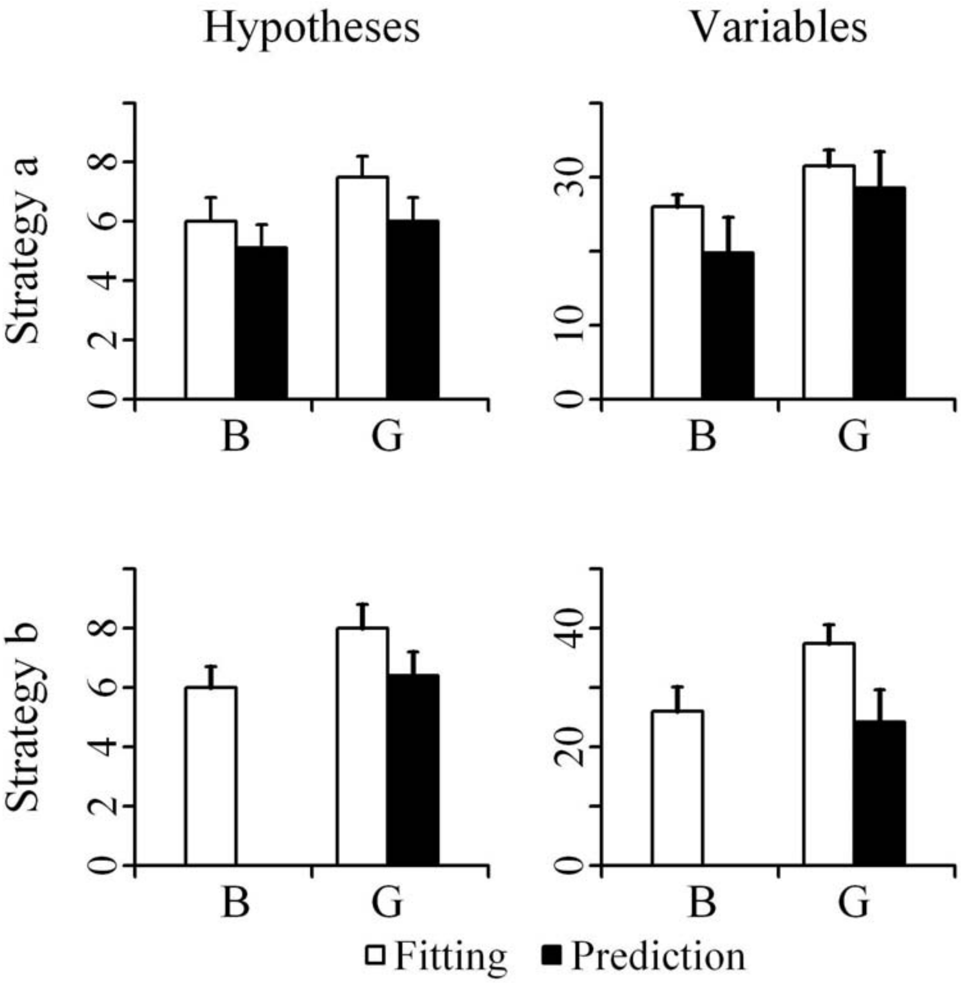

Figure 6 : Complexity of selected binomial and Gaussian models. Complexity is represented by the mean number of hypotheses and explanatory variables in models retained. Mean and standard deviation of the number of hypotheses and explanatory variables are given for strategy (a) 'Predict 2000s' and strategy (b) 'Predict 1980s', for binomial and Gaussian models and for the two selection procedures. No value has been calculated for binomial model from prediction of strategy (b) as only 1 model was selected.
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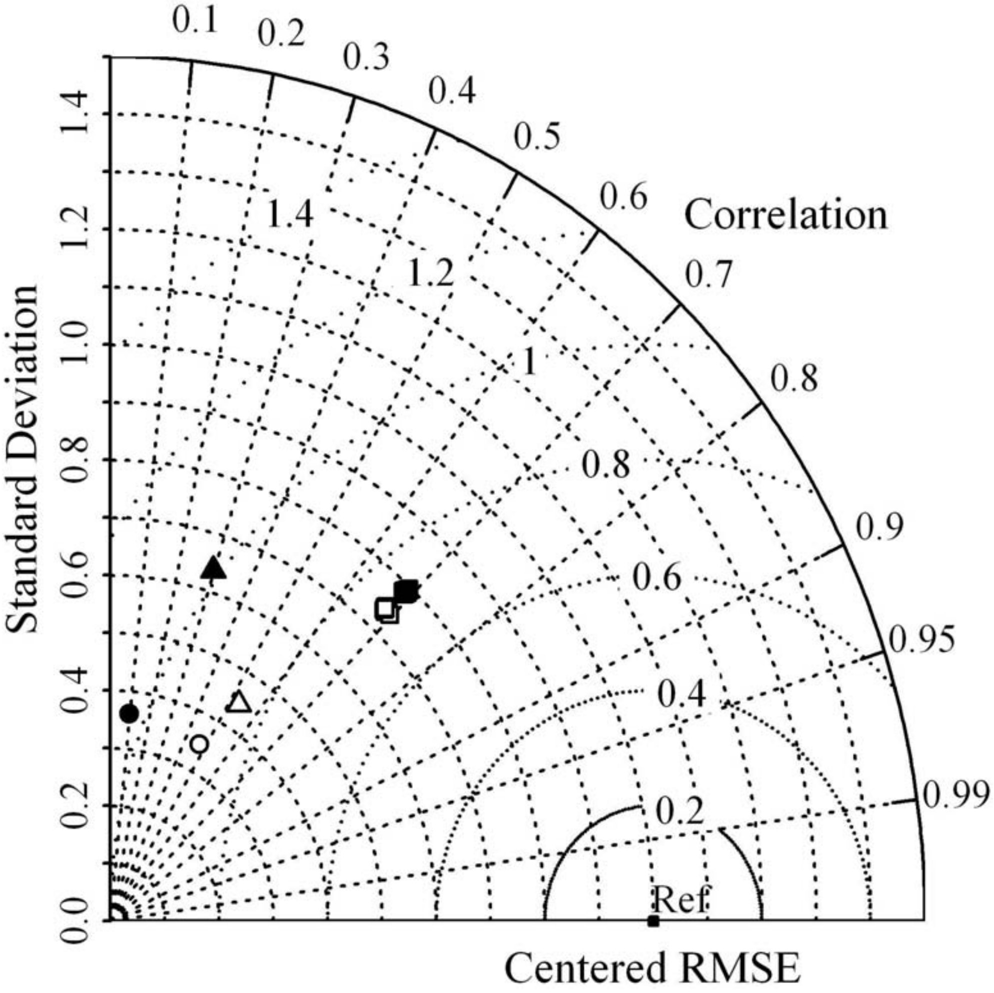

Figure 7 : Plot of the Taylor diagram. Only the positive correlation part is represented. Observations and predictions of selected (square), environmental (triangle) and control (circle) models are compared for strategy (a) ‘Predict 2000s’ (black symbols) and strategy (b) ‘Predict 1980s’ (open symbols) using the standard deviation, the root mean square error (RMSE) and the Spearman correlation. Observations are symbolised as a point called the reference point and are normalised so that the standard deviation is equal to 1, the correlation equal to 1 (the correlation between the observations and themselves) and the root mean squared error equal to 0 (the difference between the observations and themselves). Values of the indexes for the predictions are plotted with the standard deviation on the y-axis, the correlation on the radials of the circle and the RMSE on concentric circles around the reference point.
74x74mm (600 x 600 DPI)

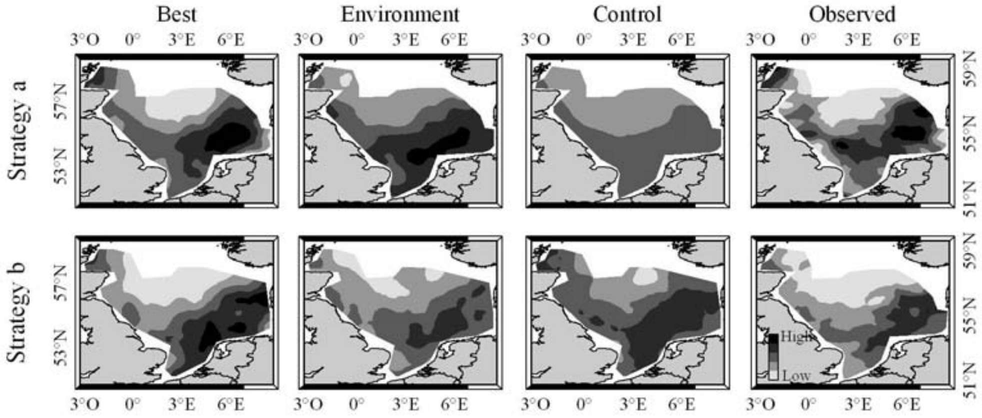

Figure 8 : Maps of spawning adults distribution. Maps for the best selected model, the environmental model and the control model were computed from predicted values of these models for the year 2004 (strategy (a) 'Predict 2000s') and year 1985 (strategy (b) 'Predict 1980s'). Corresponding maps of observed distribution of spawning adults for these two years are also represented.
155x65mm (300 x 300 DPI)