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Spatial interactions between saithe (*Pollachius virens*) and hake (*Merluccius merluccius*) in the North Sea

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Abstract:

Spatial interactions between saithe (*Pollachius virens*) and hake (*Merluccius merluccius*) were investigated in the North Sea. Saithe is a well-established species in the North Sea, while occurrence of the less common hake has recently increased in the area. Spatial dynamics of these two species and their potential spatial interactions were explored using binomial generalized linear models (GLM) applied to the International Bottom Trawl Survey (IBTS) data from 1991 to 2012. Models included different types of variables: (i) abiotic variables including sediment types, temperature, and bathymetry; (ii) biotic variables including potential competitors and potential preys presence; and (iii) spatial variables. The models were reduced and used to predict and map probable habitats of saithe, hake but also, for the first time in the North Sea, the distribution of the spatial overlap between these two species. Changes in distribution patterns of these two species and of their overlap were also investigated by comparing species' presence and overlap probabilities predicted over an early (1991–1996) and a late period (2007–2012). The results show an increase in the probability over time of the overlap between saithe and hake along with an expansion towards the southwest and Scottish waters. These shifts follow trends observed in temperature data and might be indirectly induced by climate changes. Saithe, hake, and their overlap are positively influenced by potential preys and/or competitors, which confirms spatial co-occurrence of the species concerned and leads to the questions of predator–prey relationships and competition. Finally, the present study provides robust predictions concerning the spatial distribution of saithe, hake, and of their overlap in the North Sea, which may be of interest for fishery managers.

Keywords: biotic interactions ; Competition ; generalized linear models ; hake ; North Sea ; Overlap ; predator–prey relationship ; saithe ; species distribution modelling

1 Introduction

Spatial distributions of fish species shifted in the North Sea over the past twenty years as a result of environmental and ecosystem changes (Perry *et al.*, 2005; ICES, 2008; Reid and Valdés, 2011; Loots *et al.*, 2011). Importantly, shifts in species distribution may alter the nature of biological interactions, through changes in the spatial overlap between predators, their competitors and their preys, which may consequently affect fisheries through changes in catch composition. In the case of mixed fisheries, these rearrangements may lead to an increase in bycatch (Jones *et al.*, 2013), but also of discarding, when fishing vessels do not have a sufficient catch quota provision to match these bycatch. In a fluctuating environment context (Boyd *et al.*, 2014), it appears essential to better understand the interactions between commercial species through, for example, their spatial overlap. The related changes need to be quantified in order to improve fisheries management strategies under sustainable exploitation regimes.

In this context, this study focuses on two widely distributed gadiform species of the Northeast Atlantic: saithe (*Pollachius virens*) and hake (*Merluccius merluccius*). Because of their importance for European fisheries, saithe and hake are mainly managed through single-stock Total Allowable Catch (TAC), the setting of which depends to a large extent on the outcomes of stock assessments carried out by the International Council for the Exploration of the Sea (ICES). The North Sea saithe stock covers the North Sea, the Skagerrak, the Kattegat and Western Scotland (ICES, 2013a). The northern hake stock covers, as for saithe, the North Sea, the Skagerrak, the Kattegat and Western Scotland but also the Celtic Seas, the Channel and the Bay of Biscay where the bulk of its distribution is located (ICES, 2013b). On the one hand, North Sea saithe, mainly landed by Norway, France and Germany, has been exploited at around Maximum Sustainable Yield (MSY) level for several years. However its Spawning Stock Biomass (SSB) began to decline most recently. On the other hand, the SSB of northern hake, mainly landed by France and Spain, increased dramatically since the late 2000's (Figure 1). During the same period, North Sea saithe fisheries reported a substantial increase in their hake bycatch. These fisheries have a very limited hake quota and therefore may be forced to discard this species, which could affect them economically (Baudron and Fernandes, in press) but also adversely affect the perception of stock status (Jones *et al.*, 2013). Therefore the study of the overlap between saithe and hake, referring from now to the component of these two species stocks covering the North Sea, the Skagerrak and the Kattegat, is timely to inform fisheries managers and stock assessment scientists.

Saithe and hake are found at depths ranging from 37 to 364 meters, and 70 to 200 meters, respectively (Scott and Scott, 1988; Kacher and Amara, 2005). These two species are generally considered as demersal but have both pelagic behaviour (Scott and Scott, 1988; Cohen *et al.*, 1990; Bergstad, 1991a), particularly regarding feeding (Cohen *et al.*, 1990; Homrum *et al.*, 2013). In addition to the top-down pressure exerted by fisheries, the populations of these two top-predators may importantly be controlled by bottom-up processes, through *e.g.* forage fishes availability (Frederiksen *et al.*, 2006). Saithe and hake present diet similarities, particularly concerning fish preys and seasonal patterns (Bergstad, 1991b; Du Buit, 1991, 1996), which may lead to competition for food (Link and Auster, 2013). However, the spatial overlap and subsequently the trophic interactions between hake and saithe were very limited in the North Sea, until the late 2000's, since the abundance of northern hake was low compared to saithe (Figure 1) and its distribution was mostly concentrated in the Celtic Seas (Baudron and Fernandes, in press). Northern hake was therefore barely studied in the North Sea area and its relative abundance was never considered as a potential issue for the North Sea mixed demersal fisheries until very recently (Baudron and Fernandes, in press). Given their recent biomass trends, it appears critical to investigate saithe and hake spatial overlap in the North Sea, in order to understand their potential effects on saithe fisheries but also on saithe population, through *e.g.* competitive interactions.

While saithe and hake are both included in the ICES North Sea atlas, FishMap, available online (http://www.ices.dk/marine-data/maps/Pages/ICES-FishMap.aspx), the information concerning their spatial distribution in the North Sea region is scarce and their overlap was never studied. Bergstad (1991a) mapped saithe and hake spatial distribution in the Norwegian Deep from trawl data and highlighted seasonal differences of occurrence and abundance of the two species, particularly in relation to depth. More recently, Perry *et al.* (2005) and Jones *et al.* (2013) studied spatial distribution shifts of a number of North Sea species, including saithe and hake, in relation to climate change. Concerning saithe, the results obtained differ as Perry *et al.* (2005) did not found any shift while Jones *et al.* (2013) highlighted a northward shift of saithe spatial distribution related to temperature increase. Homrum *et al.* (2013) used tagging experiment to study migration and distribution of saithe in the Northeast Atlantic, including Icelandic, Faroese and Norwegian waters. The authors highlighted migration patterns from Norwegian to Icelandic and Faroese waters that might reflect feeding migration of saithe pursuing fish preys like herring (*Clupeus harengus*). Also, Baudron and Fernandes (in press) used survey and commercial data to study changes in abundance of northern hake in the different areas occupied, including the North Sea and the Skagerrak. The authors showed a large increase in hake abundance in the North Sea reflecting the trends of the overall stock (Figure 1) but also an expansion of the area historically occupied by hake which they related to the availability of suitable habitat under density-dependent pressure.

In this context, the study of saithe and hake relative habitats appears indispensable to better understand the spatial interactions between these two species. However, the definition of habitats "must surely be among the least rigorous of any in science" (Mitchell, 2005). Kearney (2006) redefined the habitat, as a function of its abiotic and biotic features, without including explicit mechanisms affecting the fitness of the species of interest. These biotic features may allow the inclusion of biotic interactions, like predator-prey relationships and/or competition. Although many studies highlighted the need of including biotic features in habitat models (Guisan and Zimmermann, 2000; Ciannelli *et al.*, 2007; Planque *et al.*, 2011; Robinson *et al.*, 2011), abiotic features are always preferred at large spatial scales (Johnson *et al.*, 2013). The paucity of habitat modelling studies including biotic interactions at large scales might result from the common assumption that biotic interactions take place at small spatial scales while abiotic features are the overall drivers of species distribution. Another reason why habitat studies have often focused almost solely on abiotic features might be a lack of information on non-commercial species abundance and/or a lack of knowledge on biotic interactions (Johnson *et al.*, 2013). For Northeast Atlantic marine ecosystems, there are only few examples of species distribution modelling including prey abundance through explanatory variables *e.g.* Wright and Begg (1997), Sveegaard *et al.* (2012) and Hjermann *et al.* (2013), who all noted the importance of prey to model predators spatial distribution. Prey abundance was also integrated in a study on demersal fishes distribution in the Balearic Islands (Johnson *et al.*, 2012) but no significant relationship was found between the distribution of hake abundance and of its preys.

Dormann (2007) considered that neglecting biotic interactions could induce spatial autocorrelation in species distribution models. Because the probability of presence of a species in an area may be more similar in its close neighbourhood than farther apart (Legendre, 1993; Quinn and Keough, 2002; Fortin and Dale, 2005) the risk of falsely rejecting the null hypothesis, or error type I might increase (Dormann *et al.*, 2007; Zuur *et al.*, 2009). In order to explore correlation between spatial distributions and changing environmental conditions, it is common to use Generalized Linear Models (GLM) which aim to reproduce the average of the species response *e.g.* species probability of presence, and allow the description and prediction of species probable habitat *i.e.* area where species may be present (Guisan and Zimmermann, 2000). The inclusion of underlying spatial structure, in order to reduce error type I, is possible including spatial eigenvectors in the GLM (Dray *et al.*, 2006; Legendre and Legendre, 2012). However this method is recent and was only applied twice to North Sea fish species (Loots *et al.*, 2010, 2011).

The specific goals of this study were (i) to investigate the distribution of saithe and hake in the North Sea; (ii) to define their probable habitat including both abiotic and biotic features; (iii) to analyse their spatial overlap and (iv) to compare the different distributions over an early (1991-1996) and recent period (2007-2012).

2 Materials and methods

2.1 Study coverage and area presentation

The study covers the North Sea, the Skagerrak and the Kattegat at the spatial scale of an ICES statistical rectangle, hereby referred to as "statistical rectangle", *i.e* grid of 1° longitude × 0.5° latitude (Figure 2). This area is covered by the International Bottom Trawl Survey which has been operated since 1991 both in summer and in winter. In the North Sea, bathymetry is positively correlated with latitude (Knijn *et al.*, 1993). The North Sea is characterised by two different temperature gradients. In the northern region, temperatures decrease towards south because of the entrance of the relatively warmer North Atlantic Current (Reid and Valdés, 2011). In the southern region, temperatures increase with latitude in winter while gradient is reverse in summer with temperature decreasing toward north (Knijn *et al.*, 1993; Janssen *et al.*, 1999).

2.2 Data

Extraction from International Council for the Exploration of the Sea (ICES) online DAtabase of TRAwling Survey (DATRAS) of Catch Per Unit Effort (CPUE) per length per statistical rectangle was undertaken for six trophically-related species (Bergstad, 1991b; Du Buit, 1991), of which saithe (*Pollachius virens*), hake (*Merluccius merluccius*) and cod (*Gadus morhua*) were considered as potential competitors and Norway pout (*Trisopterus esmarkii*), blue whiting (*Micromesistius poutassou*) and herring (*Clupeus harengus*) as potential preys. Fixed length-at-maturity were used as a threshold to separate each species in two length groups characterising juveniles and adult: 55.4 cm for saithe, 50 cm for hake, 70 cm for cod, 18.5 cm for Norway pout, 25 cm for blue whiting and 23 cm for herring. Data were aggregated by year, season, statistical rectangle, species and length group and species abundance (CPUE) were transformed into presence/absence data. To study the overlap between saithe and hake, an extra column was created coding 1 for combination of year, season and statistical rectangle where both species could be found together, and 0 otherwise.

Abiotic data, extracted from ICES Oceanographic online database (OCEAN), were averaged by year, season and statistical rectangle and merged with biotic data. Seabed sediment types were previously extracted (Larsonneur *et al.*, 1982; Augris *et al.*, 1995; Schlüter and Jerosch, 2009). They were reclassified into five broad categories: mud, fine sand, coarse sand, gravel and pebbles by Carpentier *et al.* (2009) in the Channel Habitat Atlas for marine Resource Management (CHARM). Land coverage was specified as a sixth category in addition to the five sediment types in order to account for areas including islands. Proportions of sediment type coverage per statistical rectangle (including land) were calculated. A polynomial function of third degree was added for temperature (here sea surface temperature) and bathymetry in order to improve the fit. Indeed, data exploration plots suggested that these two descriptor-response relationships were following a cubic polynomial. The average temperatures observed were mapped at different periods and seasons (Figure S1).

Seasonal subsets were created, winter data covered January, February and March while summer data covered July, August and September. Also, for model development, seasonal datasets were split into two subsets exhibiting similar range of the different variables and spatial autocorrelation: *datafit* included years 1991, 1992, 1995, 1996, 1999, 2000, 2003, 2004, 2007, 2008, 2011 and 2012 and *datapred* included years 1993, 1994, 1997, 1998, 2001, 2002, 2005, 2006, 2009 and 2010.

2.3 Model formulation

2.3.1 Conceptual framework

A correlative approach based on presence/absence data was chosen to fulfil the study objectives concerning saithe, hake and their spatial overlap distributions. Assuming a binomial distribution of the binary data under investigation, Generalized Linear Models (GLM) (McCullagh and Nelder, 1989) may be considered as the most parsimonious approach (Guisan *et al.*, 2002) and therefore was used for this study. A logistic multiple regression was applied to relate occurrence or probability of presence (pp) to explanatory variables or predictors (x) by fitting data to a logistic curve (Quinn and Keough, 2002):

$$pp(x_1, x_2, ..., x_n) = \frac{e^{\beta_0+\beta_1\cdot x_1+\beta_2\cdot x_2+...+\beta_n\cdot x_n}}{1 + e^{\beta_0+\beta_1\cdot x_1+\beta_2\cdot x_2+...+\beta_n\cdot x_n}} \tag{1}$$

where β are the regression parameters or coefficients.

2.3.2 Environmental models

Three environmental models per season were created, one for each species and a third one for the overlap. All models initially included all biotic and abiotic variables presented in previous section (2.2). Both types of variable were tested for collinearity (Dormann *et al.*, 2013) and separation, which is an outcome of binary model fitting (Albert and Anderson, 1984). In order to limit the collinearity of independent variables, Spearman correlation coefficient and Variance Inflation Factor (VIF) were analysed, with thresholds set to 0.85 and 2.5, respectively. Concerning model potential convergence problems through infinite estimates of one or several coefficients β, separation of the data was tested using R package {brglm} (Kosmidis, 2013).

Concerning biotic variables, saithe, hake, Norway pout and blue whiting presented a high positive correlation (over 0.85) between total presence (irrespective of length groups) and at least one of the length group (juveniles and adult). Following the parsimony principle, only total presence of these four species were conserved. For cod and herring, the two length groups contrasted enough so that total presence were discarded in order to discriminate length groups of these two species in the analysis. The VIF analysis did not suggest to discard any biotic variables. For the abiotic ones, Spearman coefficients were all below the chosen threshold $(0,85)$ but the VIF analysis led to discard mud proportion. The separation test depended on the response studied and led to discard coarse sand proportion from the overlap models.

Table 1 presents the explanatory variables with their description, their units and their sources while Equations (2) to (4) present the final formulas of the environmental models including (i) potential competitors presence, (ii) potential preys presence, (iii) sediment types, (iv) temperature and (v) bathymetry:

Saithe occurrence environmental model:

$$\begin{aligned} \text{S.Tot} \sim\ & \text{H.Tot} + \text{C.Adu} + \text{C.Juv} + \text{NP.Tot} + \text{BW.Tot} + \text{HG.Juv} + \text{HG.Adu} \\ & + \text{CSpp} + \text{FSpp} + \text{Gpp} + \text{Ppp} + \text{Lpp} + \text{Temp} + \text{Temp2} + \text{Temp3} \\ & + \text{Depth} + \text{Depth2} + \text{Depth3} \end{aligned} \tag{2}$$

Hake occurrence environmental model:

$$\begin{aligned} \text{H.Tot} \sim\ & \text{S.Tot} + \text{C.Adu} + \text{C.Juv} + \text{NP.Tot} + \text{BW.Tot} + \text{HG.Juv} + \text{HG.Adu} \\ & + \text{CSpp} + \text{FSpp} + \text{Gpp} + \text{Ppp} + \text{Lpp} + \text{Temp} + \text{Temp2} + \text{Temp3} \\ & + \text{Depth} + \text{Depth2} + \text{Depth3} \end{aligned} \tag{3}$$

Overlap environmental model:

$$\begin{aligned} \text{Overlap} \sim\ & + \text{C.Adu} + \text{C.Juv} + \text{NP.Tot} + \text{BW.Tot} + \text{HG.Juv} + \text{HG.Adu} \\ & + \text{FSpp} + \text{Gpp} + \text{Ppp} + \text{Lpp} + \text{Temp} + \text{Temp2} + \text{Temp3} \\ & + \text{Depth} + \text{Depth2} + \text{Depth3} \end{aligned} \tag{4}$$

2.3.3 Spatial models

In order to accomodate the independence assumption (Zuur *et al.*, 2009; Legendre and Legendre, 2012) and to capture spatial patterns at different scales, the Moran's Eigen-Vectors (MEV) mapping method was chosen. This method allows the translation of the spatial arrangement of the data directly into explanatory variables through the eigenvector decomposition of data coordinate connectivity matrix (Dormann *et al.*, 2007; Dray, 2008; Legendre and Legendre, 2012).

MEV were extracted from the connectivity matrix based on relative neighbourhood (Toussaint, 1980) and weighted as a function of the inverse of Euclidian distance calculated from the scaled and centred latitudes and corrected longitudes (cos(latitude × $\pi/180$)) of statistical rectangle central points (Borcard *et al.*, 2011). This was undertaken using R package {spdep} (Bivand *et al.*, 2013). MEV were computed and their Moran's index was calculated using 999 permutations and {spacemakeR} (Dray, 2013). Significant ($p < 0.01$) and positive MEV were selected. MEV significance relative to the detrended response was tested by forward selection with double criteria (Dormann *et al.*, 2007; Borcard *et al.*, 2011). The forward selection was performed using {packfor} (Dray *et al.*, 2013) with significance level (α) and cumulated coefficient determination (R^2_{more}) set both to 0.001. The forward selection stopped when either the R^2 of the last variable added was lower than R^2_{more} or when its significance level was higher than α. The residuals obtained after fitting responses to a second-order polynomial ($X + X^2 + X \times Y + Y + Y^2$) based on corrected longitude (X) and latitude (Y) were used as detendred responses. At the end of the process, the number of spatial variables (*i.e.* MEV) selected depended on the response. 7, 13 and 8 spatial variables were added to winter environmental models and 6, 7 and 6 to summer ones, completing Equations (2) to (4), respectively.

2.4 Model calibration

Model calibration was realised using *datafit* dataset described earlier. Model reduction started from the six initial full models: three environmental-only models and three spatial models that included environmental variables and spatial ones (*i.e.* MEV). Environmental variables were eliminated by forward, backward and both stepwise selection using three common criteria: Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and Chi squared (χ^2). MEV were selected *a priori* as described in the previous section (2.3.3) and these were not changed (Dormann *et al.*, 2007). Consequently for spatial models, minimum or null models included all (and only) MEV *a priori* selected and reduction operated only on environmental variables. This procedure, similar to the one presented by Lelièvre *et al.* (2014), resulted (including initial full models) in twenty models per response and per season *i.e.* ten environmental-only models and ten spatial ones.

2.5 Model selection

Model selection was based on the predictive abilities of the different models (Planque *et al.*, 2011; Lelièvre *et al.*, 2014) using the True Positive Rate (TPR), or sensitivity. Sensitivity represents the prediction rate of observed presence. It was preferred to the, more commonly used, receiver operating characteristic because of false absence which often characterise marine ecosystem sampling (Hirzel *et al.*, 2002). Predictions of presence probability (ranging from 0 to 1) were made based on *datapred* dataset described earlier and transformed into observation predictions (absence, 0 or presence, 1) using a threshold value. This threshold was calculated for each model in order to maximise the sensitivity (Jimenez-Valverde and Lobo, 2007). Each model sensitivity was then calculated and the different values were compared: models with sensitivity values closer to 1 indicate a better ability to predict presence. When sensitivity was not discriminant, *i.e* difference of sensitivity < 0.05, variables were counted and the most parsimonious models were selected. Six models per season were selected for evaluation (three environmental-only models and three spatial ones) which is a total of twelve models.

2.6 Model evaluation

Spatial autocorrelation was checked for detrended residuals of selected models using Moran's I coefficient and correlograms (Fortin and Dale, 2005; Borcard *et al.*, 2011; Legendre and Legendre, 2012). Moran's I coefficient characterises spatial autocorrelation going from -1 to 1 with values close to 0 characterising random arrangement, *i.e.* few or no spatial autocorrelation. Correlograms are a graphical tool used to visualise spatial correlation by plotting Moran's I coefficient by spatial lags, here ten lags separated by 75 ± 10 kilometres each. Moran's I coefficient, their significance and associate correlograms were computed using {`spdep`} (Bivand *et al.*, 2013). The final six least spatially autocorrelated models, three per season, were selected for further evaluation. Goodness-of-Fit (GoF) was evaluated using the adjusted coefficient of determination (adjR^2) and the dispersion parameter (φ). Descriptor coefficients were calculated, tested using χ^2 test and the percentage of deviance explained by each of them was examined. Finally, maps of absolute fitting error (absolute Student residuals) were produced to complete the evaluation.

2.7 Model prediction

After evaluation, the six final models were used to predict seasonal probable habitat and overlap of saithe and hake within the modelled area. Predictions were made following Equation (1), using values of predictors x and associated regression parameters β calculated during calibration (section 2.4). In order to study the changes of probable habitat and overlap between the two species, predictions were averaged on two time periods: 1991-1996, the early period, and 2007-2012, the recent one. The early period averaged predictions were then subtracted to the recent ones in order to provide an overview of the changes of the different responses over the last twenty years. The results were mapped using R version 2.15.3.

3 Results

3.1 Environmental predictors

A comparison of environmental-only and spatial models variable significance and estimated coefficients is presented in the supplementary material (Tables S1 to S3). However, only the outputs of spatial models, which explicitly account for spatial autocorrelation were further investigated (Tables 2 and 3).

For each of the selected models, there are differences in explanatory variable selection and in the contribution of these selected variables to the total deviance explained by the model. These differences depend on the response variable and on the season (Tables 2 and 3). However, the signs of the models estimated coefficients are consistent for all response variables and seasons. When they are significant, saithe (*Pollachius virens*), hake (*Merluccius merluccius*) and overlap response variables are always positively influenced by the presence of potential preys, Norway pout (*Trisopterus esmarkii*), blue whiting (*Micromesistius poutassou*) and adult herring (*Clupeus harengus*), potential competitors, saithe, hake and adult cod (*Gadus morhua*), temperature (polynom) and bathymetry (polynom). In contrast, these response variables are always negatively influenced by the presence of juvenile herring and the percentage cover of fine sand or pebbles (Table 2). Abiotic and biotic variables have the highest contribution to explain saithe and overlap occurrences while spatial variables have the lowest one. Only hake presence variations are generally much better explained by adding spatial variables (9.78% of deviance explained in winter and 11.48% in summer) than by using only biotic and abiotic ones (Table 3).

Concerning abiotic variables, temperature and bathymetry are the most important in terms of deviance explained. However, the importance of these two variables varies depending on the models and once again hake models differ from the two others. Indeed, hake presence variations are generally less explained by bathymetry with only 1.02% of deviance explained in summer and 19.26% in winter. This contrasts with the bathymetry explanatory power ranging from 25.18% for overlap winter model to 40.84% for saithe summer one. The relationship with temperature is more important for hake presence than for saithe (not selected at all) or overlap (selected only in summer), particularly in summer where it is the most important abiotic variable with 5.04% of deviance explained.

Concerning biotic variables, both species presence are positively influenced by potential preys presence (Norway pout, blue whiting and adult herring), particularly in winter. The mutual relationship with Norway pout explaining 1.35% and 0.35% of saithe and hake winter presence variations, respectively, is consistent with the relation between overlap and Norway pout presence (1.30% of deviance explained in winter and 1.13% in summer). The relation between saithe and hake presence is independent of the season and saithe presence explains 10.89% of hake presence in summer. In addition, for saithe and overlap models, adult cod presence is, independently of the season, the most important biotic variable in terms of response presence variation with 2.59% and 3.96% of deviance explained in winter and 1.67% and 2.98% in summer, respectively.

3.2 Predicted distributions

An increase of presence probabilities of saithe, hake and of their overlap is generally observed in the regions above the line hereby termed as Dogger Bank Line (DBL), irrespective of the seasons. This increase occurs generally in association with a south-west expansion of the distribution towards Scottish and English waters (Figures 3 to 5). However, seasonal and period-related differences are revealed when each distribution is more thoroughly investigated.

Saithe is mainly found in the northern region of the North Sea and the Skagerrak. However, seasonal differences can be noted, particularly in the early period distributions. In winter (Figure 3a), saithe distribution is concentrated above 57.5° of latitude. This region indicates high probabilities of presence (pp) ranging from 0.6 to 0.9 at its northern boundary. In the early period and in summer (Figure 3b), presence probabilities are even higher in this area ($0.8 < pp < 1$) and distribution expands to the Central North Sea above the DBL where saithe can be found at medium presence probabilities ($pp > 0.4$). In the most recent years (Figures 3c and 3d), a notable increase in presence probabilities is observed in the northern region with positive differences in presence probabilities ($dpp > 0.1$) along with a south-west expansion of the distribution, particularly in winter.

Hake is mainly found in the northern region of the North Sea, in the Skagerrak and in the Kattegat. However, compared to saithe, hake is more widely spread and has a lower presence probability in the area where both species are present *i.e.* above 57.5° of latitude. In winter and during the early period (Figure 4a) hake is intermediately present in the area with medium presence probabilities ranging from 0.4 to 0.8. In summer and during the early period (Figure 4b), hake presence probabilities above the DBL are higher ($0.6 < pp < 1$) and its northern distribution expands towards south-west and the Scottish waters. There is also medium presence probabilities in the south-east region, below the DBL ($0.4 < pp < 0.8$). Regarding the most recent years, hake winter area of distribution (Figure 4c) did not change much except for a slight expansion towards the English waters and an increase of presence probabilities in the region where hake was already present during the early period ($ddp > 0.2$). In the most recent years and in summer (Figure 4d), a decrease of presence probabilities is observed in the Skagerrak, the Kattegat and the region south of the DBL ($dpp < -0.1$) while in the region above the DBL, an increase of presence probabilities ($ddp > 0.1$) and a south-west expansion towards English waters is notable.

The two species mainly overlap in the Northern North Sea, above 57.5° of latitude.

Overlap distribution in winter and during the early period (Figure 5a), indicates medium overlap probabilities in the central part of the Northern North Sea, the Skagerrak and also along the Norwegian coast ($0.3 < pp < 0.7$). In summer and during the early period (Figure 5b), the area is similar in terms of latitude but wider in terms of longitude ranges, and it is characterised by generally higher overlap probabilities ($0.4 < pp < 0.9$). The southern boundary of the overlap distribution is, generally, consistent with saithe distribution patterns. In the most recent years, a notable increase of winter overlap (Figure 4c), is observed at the edges of the northern region (Norwegian and Scottish coast) and in the Skagerrak ($ddp > 0.2$) along with a slight expansion towards south-west. Similar trends are observed in summer (Figure 4d) with the increase of overlap probabilities in the northern region and the persistence of the south-west expansion towards the Scottish and English waters.

3.3 Evaluation

Models evaluation reveals, first, that there is only few spatial autocorrelation left in the detrended residuals of spatial models (Figure 6) in comparison to environmental-only models (Figure S2). The number of significant spatially correlated lags ranges from 0 to 1, with a maximum Moran's I coefficient absolute value equal to 0.05 in hake summer model. These results mean that only very small arrangement patterns are detected in radius of 75 ± 10 kilometres and validate the selection of spatial models in order to reduce the chances of falsely rejecting the null hypothesis (no effect of one variable), also called error type I. However, the results also show that the coefficients estimated with the hake models are more biased than for the saithe and overlap ones (Tables S1 to S3), due to higher spatial autocorrelation remaining in the residuals and therefore that their selected variables are more subject to error type I than those selected for saithe and overlap models. Second, all models satisfy the Goodness-of-Fit (GoF) with value ranging from a minimum adjusted coefficient of determination (adjR^2) of 0.31 and a maximum of 0.59; dispersion parameter φ close to 1 for every model and True Positive Rate (TPR), or sensitivity, ranging from 0.74 to 0.84 (Table 4). Finally, fitting error (fe) maps indicates a very good ability of the models to predict absence ($fe < 0.25$) but a more uncertain presence prediction ($0.25 < fe < 1$) (Figure S3).

4 Discussion

4.1 Ecological aspects

Saithe (*Pollachius virens*) suitable habitat in the North Sea is determined by relatively deep waters (> 50 meters). Saithe distribution has slightly expanded towards southwest over the last twenty years which might be linked to an increase of temperature in the North Sea (ICES, 2008; Reid and Valdés, 2011). Indeed, in the recent period, warmer temperatures are found further south and in the Scottish waters. Hake (*Merluccius merluccius*) suitable habitat in the North Sea is determined by temperatures ranging from 7°C to 15°C. Bathymetry seems less important as hake can be found in a wide spectrum of depth ranges. The strong relationship of hake distribution with temperature indicates that overall warming (Boyd *et al.*, 2014) could make the North Sea a more suitable habitat for this species. Temperature effect is confirmed by an increase of presence probabilities over the last twenty years in the northern area which has warmed up both in winter (+0.6°C) and summer (+0.9°C). In summer, the disappearance of the southern patch (below the Dogger Bank Line (DBL)) is consistent with temperatures exceeding 15°C in the recent years. If depth is not overly restrictive within the models, a limiting temperature factor might exist around 15°C. Applied to hake, this limit could be related to reproduction as spawning occurs in temperatures of up to 15°C with an optimum between 10°C and 12.5°C (Ibaibarriaga *et al.*, 2007). The study of the overlap between saithe and hake shows highest occurrences of the two species together in the Northern North Sea with a major importance of bathymetry but also an effect of temperature in summer. There is a consistent spatial trend of increasing overlap probabilities above 57.5° of latitude along with an expansion towards southwest and the Scottish waters. These trends are consistent with saithe and hake spatial distributions changes but also with changes observed in temperature patterns. In the Northern North Sea, temperature and bathymetry are strongly correlated and present similar gradients: temperature and depth decrease with latitude (Knijn *et al.*, 1993; Reid and Valdés, 2011). Therefore, disentangling the respective effects of these two variables is a challenge.

The seasonal differences and the relations with depth and temperature are consistent with Bergstad (1991a) and Jones *et al.* (2013). The direction of the shifts in the North Sea, towards south-west, differs from Perry *et al.* (2005) who found no shift at all and Jones *et al.* (2013) who predicted a northwards shift. However, the authors focused on global long-term climate change effects and covered large temporal scale compared to the twenty years investigated here. In addition, the southeastern region of the North Sea (below the DBL) presents inverse gradients of temperature in winter and summer. This area might be too cold in winter and too warm in summer which might the limited expansion towards south-west in the Scottish and English waters. Baudron and Fernandes (in press) noted an eastward shift for hake and rejected the hypothesis of a climate-induced change on the basis of the absence of latitude centroids shifts in the other areas occupied by northern hake. The authors suggested that hake expansion may result from density-dependent pressure due to hake recent increase of abundance. They related this increase of abundance to fishery management decisions applied in 2004. Indirect climate-induced changes through *e.g* changes in marine communities (Beaugrand *et al.*, 2003; Beaugrand, 2004; Perry *et al.*, 2005) might explain the changes in habitat suitability of the Scottish and English waters, as they could affect prey availability and therefore may supplement density-dependent induced changes assumption (Baudron and Fernandes, in press).

The present study considers potential competitors and preys occurrence in modelling saithe, hake and their overlap spatial distributions. Species occurrence have been used to describe biotic interactions. Norway pout (*Trisopterus esmarkii*), blue whiting (*Micromesistius poutassou*), herring (*Clupeus harengus*) and juvenile cod (*Gadus morhua*) were considered as potential preys while saithe, hake and adult cod were considered as potential competitors (Bergstad, 1991b; Du Buit, 1991, 1996). The positive relationships between potential competitors highlighted in the present study agrees with Baudron and Fernandes (in press) assumption concerning an impact of fishery management restriction adopted in 2004 within the Northern hake recovery plan. The same year, cod recovery plan was adopted in the North Sea which substantially reduced Total Allowable Catch (TAC) for cod. The resulting economical impacts for demersal mixed fisheries could lead to an avoidance of cod presence areas by these fleets and therefore induced side-effects on other species abundance. This is consistent with the relative importance of adult cod in almost all the models. Link and Auster (2013) suggested that competitors feeding on the same resource are likely to be found in the same areas, which would be characterised by positive relationships at the population scale. Therefore, potential competitive interactions of saithe and hake with cod but also potential competition between saithe and hake assumptions are strengthen by their mutual positive relationships.

Interspecific positive relationships indicate spatial co-occurrence of the different species but do not imply any causal relationship. They could reflect a covariate of major importance missing (Guisan and Thuiller, 2005) and thus they might illustrate indirect biotic effects. Based on the current knowledge concerning saithe and hake diet and the results obtained here, the assumption of predator-prey relationships with Norway pout, blue whiting and adult herring appears reasonable. The percentages of deviance explained by these different species occurrences are consistent with Bergstad (1991b), Du Buit (1991) and Du Buit (1996) who recorded Norway pout and blue whiting as major preys for saithe and hake, respectively. These authors also noted a seasonal diet difference with an increased importance of fish-based diet in winter while saithe and hake fed mostly on zooplankton in summer. This is consistent with the non-selection of fish preys in the models for this season. Johnson *et al.* (2012) did not find prey abundance as significant while studying hake abundance in the Balearic Islands but highlighted an importance of prey size. In order to increase the meaningfulness of the estimated coefficients and improve the interpretation of the relationships, the integration of size groups for potential preys could be of interest, particularly regarding hake. The positive relationships of the overlap with Norway pout, blue whiting, juvenile cod and adult herring confirm the assumption that both saithe and hake feed on these preys.

The present study supplements Baudron and Fernandes (in press) results and suggests that the North Sea warming may have had direct and indirect effects on saithe and hake distribution as well as on their overlap. The similarities between saithe and hake relationships with the different explanatory variables (abiotic and biotic ones) strengthen the assumption that spatial overlap between the two species could keep increasing in the future years. In order to investigate direct effects of climate changes, the study could benefit from the use of global indices representing warming processes better than the average temperatures used here. Indirect effects may be trophically related. Perry *et al.* (2005) showed a southwards shift of Norway pout distribution in relation to the North Sea warming. Therefore, the positive relationship between Norway pout presence and the presence of saithe, hake as well as their overlap supports the hypothesis of trophically-related changes and is consistent with Homrum *et al.* (2013) who highlighted feeding migration behaviour of saithe. As a result, the importance of integrating biotic variables at large scale for species distribution modelling is confirmed by the present study which suggest a participation of other species presence in habitat suitability. The substantial amount of information brought by the biotic variables confirms the importance of integrating potential competitors and preys occurrence in predators habitat models (Torres *et al.*, 2008; Schick and Lutcavage, 2009). The inclusion of biotic features, through other species presence/absence, also increase the robustness of the predictions with spatial autocorrelation quantitative bias far smaller than the 25% assessed by Dormann (2007) in environmental-only models (see supplementary material for detailed comparison of coefficients).

The interspecific positive relationships provide a first step towards the study of potential bottom-up processes involved in predators spatial distribution through an estimation of their relations with potential preys. In order to confirm these assumptions, it is essential to investigate saithe and hake respective diets in the North Sea as they are currently lacking. The outcomes of diet analyses would in particular allow defining different group sizes for preys, but also modelling species by length groups based on potential diet differences as length-at-maturity used in this study was not discriminant. Ontogenetic variation are not considered in this study because of the high correlation between the total presence of both saithe and hake (juveniles and adult mixed) and at least one of the related length group. This lack of consideration might cause misinterpretation of the results particularly concerning hake. Indeed, juveniles saithe stay in deep waters along the Norwegian coast till they reach maturity which might explain the high correlation between total presence and adult group. For hake, the lack of knowledge concerning maturation in the North Sea but also concerning the presence (or not) of nursery ground in the area are aspects which need to be further investigated. Diet analysis and interspecific comparison would also facilitate the investigation of these two species potential competition. Indeed, even if it could be part of long-term natural fluctuations, the opposite abundance trends of saithe and hake in the North Sea (ICES, 2013a; Baudron and Fernandes, in press) fulfil the first requirement to demonstrate competition in a large marine ecosystem between two marine species according to Link and Auster (2013). The second requirement these authors suggested concerned spatial overlap which has been established in the present study.

4.2 Modelling aspects

Hake emergence in the North Sea and its potential impacts on commercial species and related fisheries could be further investigated. Hake's spatial distribution is currently expanding and this species could in the future years populate areas where it is currently absent (Baudron and Fernandes, in press). This is consistent with the particular results obtained for hake models concerning the importance of spatial autocorrelation and spatial variables. Quantiles regression techniques may supplement the results obtained here by determining hake potential habitat *i.e* area with suitable conditions for species to be present (Vaz *et al.*, 2008) and give a better overview of hake potential future distribution in the North Sea. Also, modelling the early and late period separately could be of interest in order to compare the importance of the different variables at the two periods. Concerning potential preys, this is particularly interesting for opportunistic feeders which is generally the case of gadiforms fishes in the North Sea. Finally, the study of hake's models performance in a new area, presenting similar range of predictor variables like for example West-Scotland, could also provide an external validation (Guisan *et al.*, 2006; Robinson *et al.*, 2011). Alternatively, the inclusion of West-Scotland data in model calibration could potentially improve the understanding of spatial interactions between saithe and hake in all the area of distribution of North Sea saithe.

5 Conclusion

The increasing interest on the effects of global warming (Boyd *et al.*, 2014) lead to a large number of studies which undertook species spatial distribution shifts in the North Sea (Beaugrand, 2004; Perry *et al.*, 2005; Reid and Valdés, 2011; Jones *et al.*, 2013). However, the potential new interactions resulting from these shifts were less examined. In addition, the lack of biotic features used in species distribution modelling (Johnson *et al.*, 2013) may lead to an incomplete view of the situation and to poor predictions (Guisan and Zimmermann, 2000; Mitchell, 2005; Dormann, 2007; Planque *et al.*, 2011; Robinson *et al.*, 2011), which may become a problem for fishery management (Johnson *et al.*, 2013). In this context, the present study investigated saithe and hake spatial distribution in the North Sea, defined their probable habitat and addressed hake recent emergence in the North Sea in relation with saithe through the study of their spatial overlap. This investigation was undertaken through the exploration of the different species presence relationships with abiotic features like temperature and bathymetry. However the novelty of the method was to also include biotic interactions into saithe and hake distribution models through the presence/absence of other species recorded in the literature as potential competitors or preys.

An increasing overlap between saithe and hake over time has been established, which could be induced by climate and trophic changes. These results provide a solid basis to further investigate competition between saithe and hake in the North Sea. In addition, the important contribution of biotic features in the models confirms the importance of including such variables while modelling species distribution at the population scale. The relations between predator occurrence and prey availability were statistically estimated. The results obtained increase our understanding of interspecific interactions and more particularly of bottom-up processes and are of interest in a climate change context. These results would valuably be complemented by a thorough comparative analysis of saithe and hake respective diets. Finally, the present study provided robust predictions concerning saithe and hake spatial distribution in the North Sea. In a context of multi-specific fisheries management, these results may be considered by managers in their decisions (*e.g.* setting of the TACs) concerning saithe, hake and their related fisheries in the area.

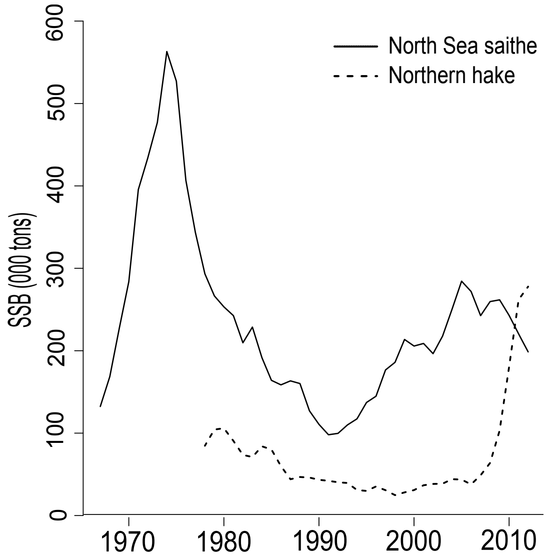


Figure 1: Historical trends of Spawning Stock Biomass of North Sea saithe and northern hake from 1967 to 2012. (ICES, 2013b,a)

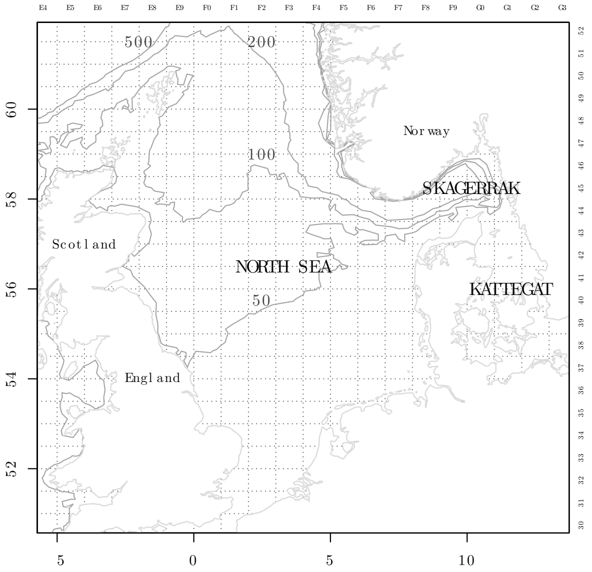
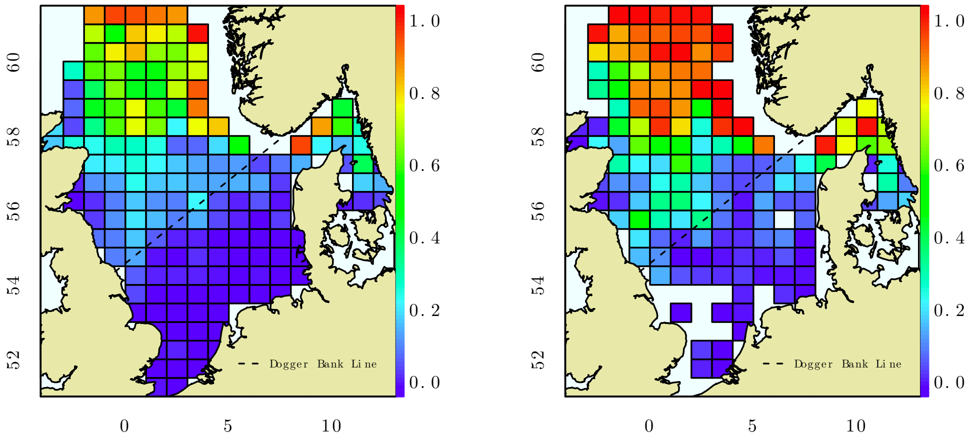


Figure 2: Map of the study area. In upper case, maritime area names and in lower case country names. Grey lines represent depth contours accompanied by their corresponding depth value in meters. The dotted grid in the background represents the ICES statistical rectangle grid.

(a) Winter, early period, *pp* (b) Summer, early period, *pp*



(c) Winter, difference with recent period, *dpp* (d) Summer, difference with recent period, *dpp*

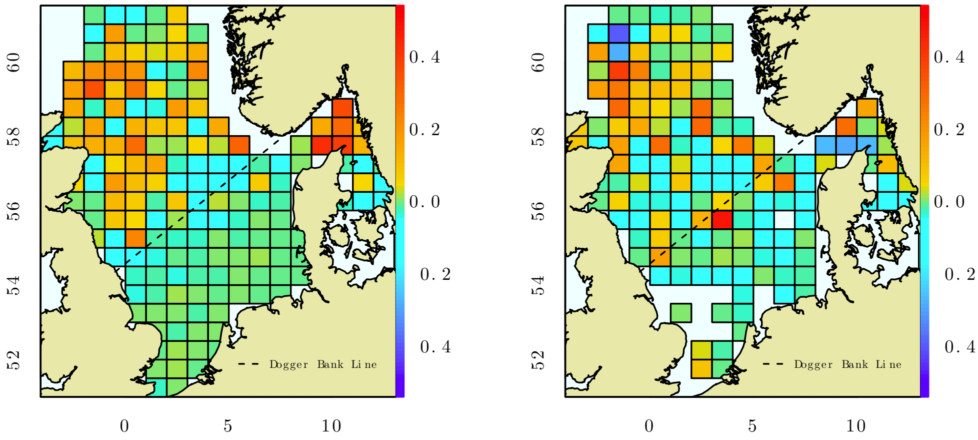
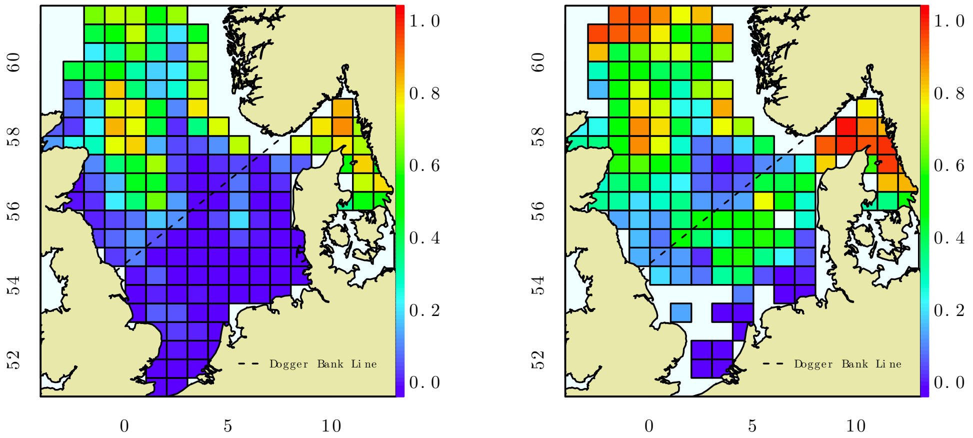
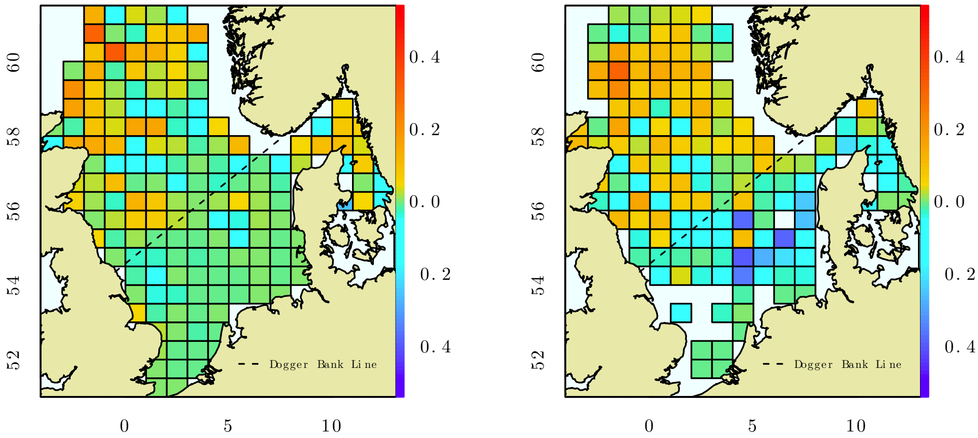


Figure 3: Saithe presence probabilities, *pp*, predictions maps for the early period, 1991-1996, in (a) winter and in (b) summer. Changes in saithe distributions over the last twenty years resulting from the difference between recent, 2007-2012, and early period in (c) winter and in (d) summer. Note the difference of scale for (c) and (d) where the colour gradient displays a difference of presence probabilities, *dpp*.



(a) Winter, early period, *pp*

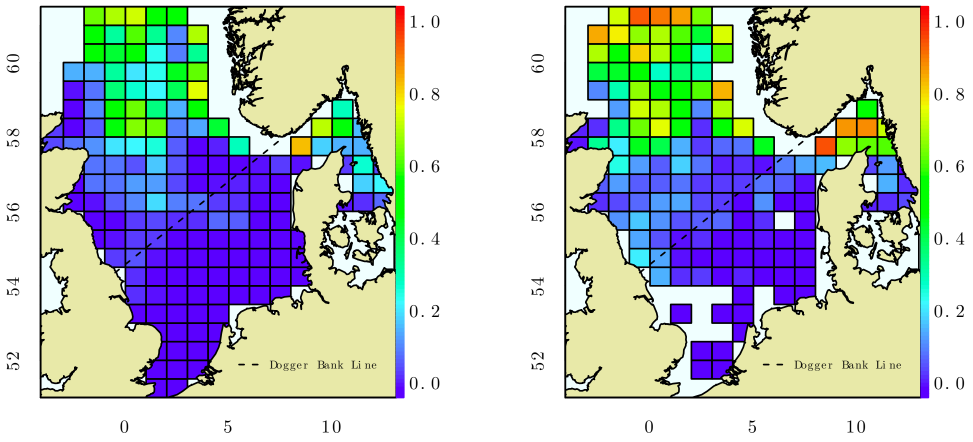
(b) Summer, early period, *pp*



(c) Winter, difference with recent period, *dpp*

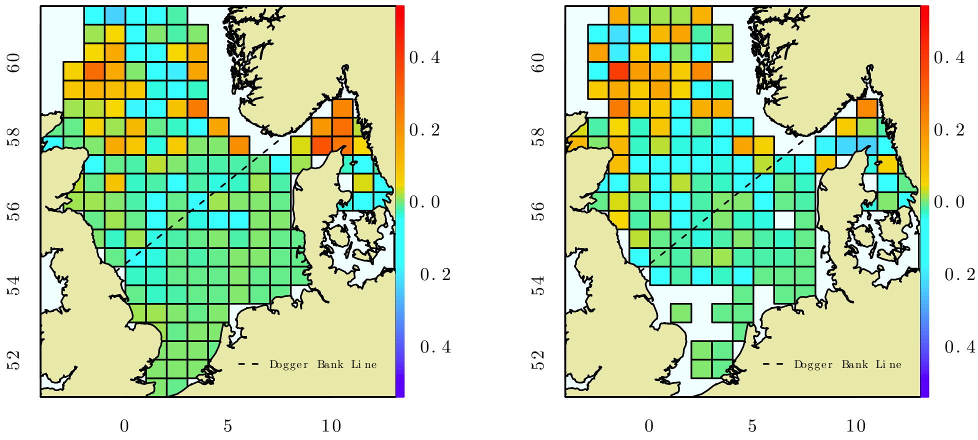
(d) Summer, difference with recent period, *dpp*

Figure 4: Hake presence probabilities, *pp*, predictions maps for the early period, 1991-1996, in (a) winter and in (b) summer. Changes in hake distributions over the last twenty years resulting from the difference between recent, 2007-2012, and early period in (c) winter and in (d) summer. Note the difference of scale for (c) and (d) where the colour gradient displays a difference of presence probabilities, *dpp*.



(a) Winter, early period, *pp*

(b) Summer, early period, *pp*

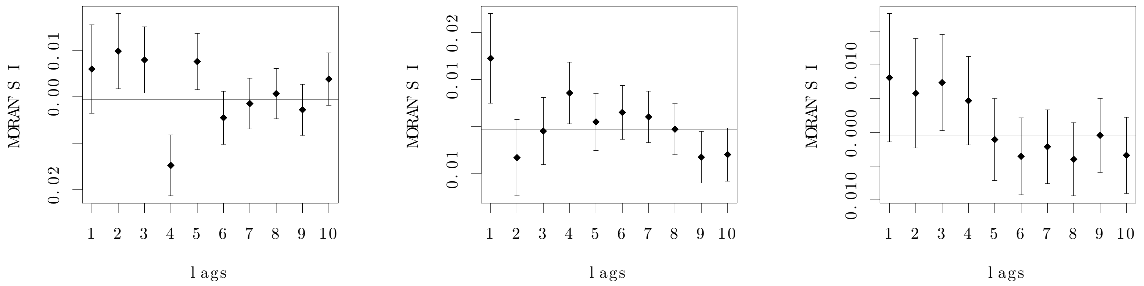


(c) Winter, difference with recent period, *dpp*

(d) Summer, difference with recent period, *dpp*

Figure 5: Overlap between saithe and hake probabilities, *pp*, predictions maps for the early period, 1991-1996, in (a) winter and in (b) summer. Changes in overlap over the last twenty years resulting from the difference between recent, 2007-2012, and early period in (c) winter and in (d) summer. Note the difference of scale for (c) and (d) where the colour gradient displays a difference of presence probabilities, *dpp*.

(a) Saithe, winter (b) Hake, winter (c) Overlap, winter



(d) Saithe, summer (e) Hake, summer (f) Overlap, summer

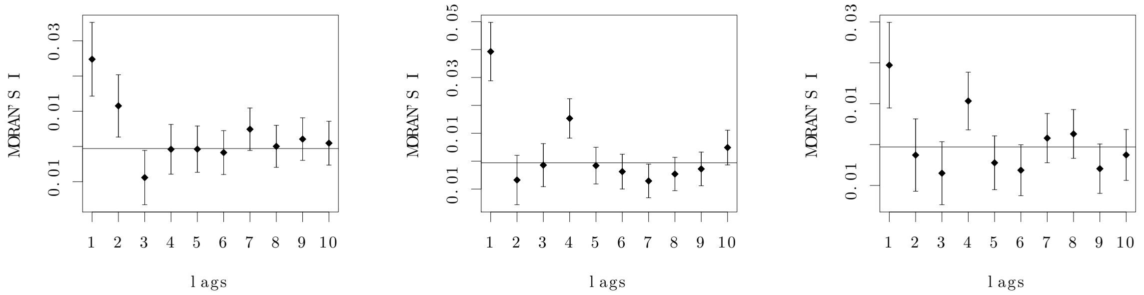


Figure 6: Correlograms of detrended residuals of selected models for saithe (first column), hake (second column) and their overlap (third column) at winter (first line) and summer (second line). Moran's *I* coefficients depending on different spatial lags, spaced by 75 ± 10 kilometres.

Table 1: Biotic and abiotic variables used to build saithe, hake and overlap models during winter and summer period. Total presence and overlap include both juvenile and adult individuals.
Comp.: potential competitors; Preys: potential preys; Sedi.: sediment type; Temp.: temperature; Bathy.: bathymetry.
cm: centimeter; –: no units; %: percentage; °C: degree Celsius; m: meter.

Type		Name	Description	Units	Source
Biotic	Comp.	S.Tot	Total presence saithe	–	DATRAS
		H.Tot	Total presence hake	–	DATRAS
		Overlap	Presence of both saithe and hake	–	DATRAS
		C.Adu	Presence of adult cod (≥ 70cm)	–	DATRAS
	Preys	C.Juv	Presence of juvenile cod (< 70cm)	–	DATRAS
		NP.Tot	Total presence Norway pout	–	DATRAS
		BW.Tot	Total presence blue whiting	–	DATRAS
		HG.Adu	Presence of adult herring (≥ 23cm)	–	DATRAS
		HG.Juv	Presence of juvenile herring (< 23cm)	–	DATRAS
Abiotic	Sedi.	CSpp	Proportion of coarse sand coverage	%	CHARM
		FSpp	Proportion of fine sand coverage	%	CHARM
		Gpp	Proportion of gravel coverage	%	CHARM
		Ppp	Proportion of pebble coverage	%	CHARM
		Lpp	Proportion of land coverage	%	CHARM
	Temp.	Temp	Average temperature	°C	OCEAN
		Temp2	Average squared temperature	°C	OCEAN
		Temp3	Average cubic temperature	°C	OCEAN
	Bathy.	Depth	Average bottom depth	m	OCEAN
		Depth2	Average squared depth	m	OCEAN
		Depth3	Average cubic depth	m	OCEAN

Table 2: Estimated coefficient β signs for selected variables for saithe, hake and their overlap final models in the two seasons. W: winter. S: summer. See Table 1 for environmental variables description.

			Saithe		Hake		Overlap	
			W	S	W	S	W	S
Biotic	Comp.	S.Tot			+	+		
		H.Tot	+	+				
		C.Adu	+	+		+	+	+
	Preys	C.Juv		+				+
		NP.Tot	+		+		+	+
		BW.Tot			+			+
		HG.Adu			+		+	
		HG.Juv	−	−			−	−
Abiotic	Sedi.	CSpp				−		
		FSpp		−	−	−	−	−
		Gpp	+	+		+		
		Ppp			−	−		
		Lpp		+				
	Temp.	Temp				+		+
		Temp2			−			−
		Temp3			+	−		
	Bathy.	Depth	+	+	+	+	+	+
		Depth2			−		−	−
		Depth3	−	−	+			+

Table 3: Deviance explained (%) for selected variable for saithe, hake and their overlap final models in the two seasons. W: winter. S: summer. MEV : Moran's EigenVectors. See Table 1 for environmental variables description.

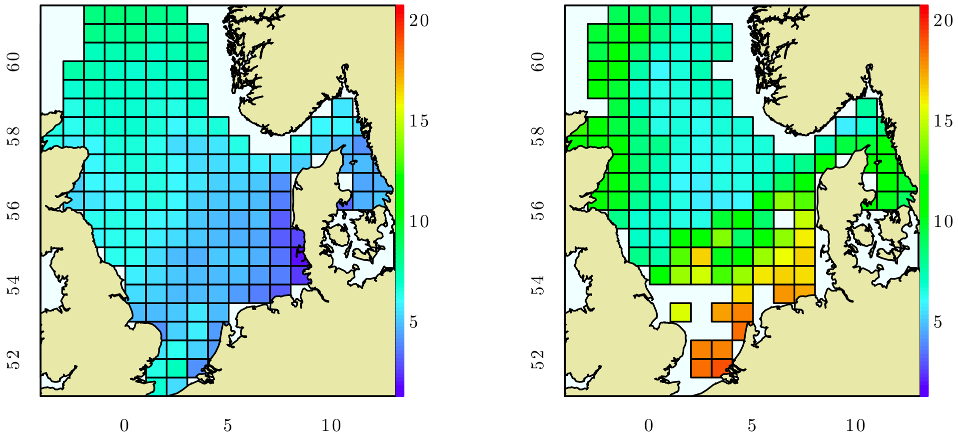
			Saithe		Hake		Overlap	
			W	S	W	S	W	S
Biotic	Comp.	S.Tot			1.61	10.89		
		H.Tot	1.60	1.96				
		C.Adu	2.59	3.96		0.99	1.67	2.98
	Preys	C.Juv		1.41				0.47
		NP.Tot	1.35		0.35		1.30	1.13
		BW.Tot			0.59			0.63
		HG.Adu			0.91		0.85	
		HG.Juv	1.25	1.10			1.03	1.36
Subtotal			6.79	8.43	3.46	11.88	4.85	6.57
Abiotic	Sedi.	CSpp				0.46		
		FSpp		0.53	4.00	0.40	0.94	0.76
		Gpp	0.53	0.56		0.57		
		Ppp			1.75	0.37		
		Lpp		0.37				
	Temp.	Temp				3.54		0.40
		Temp2			0.44			1.63
		Temp3			1.13	1.50		
	Bathy.	Depth	31.35	38.99	14.18	1.02	21.91	24.62
		Depth2			3.48		3.27	3.59
		Depth3	0.68	1.85	1.60			0.40
Subtotal			32.56	42.3	26.58	7.86	26.12	31.4
Spatial	MEV		2.66	2.84	9.78	11.48	3.79	4.83
TOTAL			42.01	53.57	39.82	31.22	34.76	42.80

Table 4: Goodness-of-Fit and predictive power according to different parameters of final models for saithe, hake and their overlap in the two seasons. W: winter. S: summer. adjR^2: adjusted coefficient of determination, TPR: True Positive Rate, or sensitivity

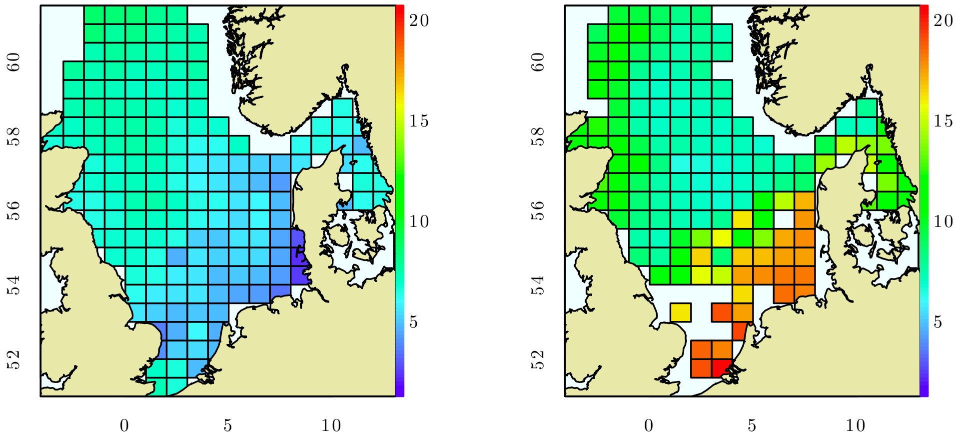
		adjR^2	dispersion (φ)	threshold	TPR
Saithe	W	0.47	1.06	0.20	0.83
	S	0.59	1.15	0.31	0.84
Hake	W	0.42	1.00	0.37	0.84
	S	0.36	1.02	0.44	0.74
Overlap	W	0.31	0.97	0.11	0.83
	S	0.46	0.97	0.26	0.81

Supplementary material

Supplementary materials presenting maps of temperatures in the area of interest (Figure S1), correlograms of non-selected environmental-only models (Figure S2) and absolute models fitting errors from early period (Figure S3) are available at the *ICES Journal of Marine Science* online version of the paper. In addition, the supplementary material includes three regression parameters tables (Tables S1 to S3), for saithe, hake and their overlap, respectively, allowing the comparison between non-selected environmental-only models and selected spatial ones.

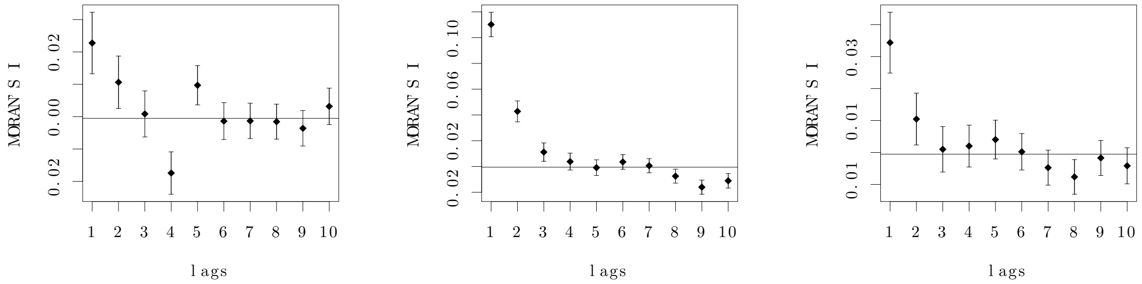

(a) Winter, early period

(b) Summer, early period


(c) Winter, recent period

(d) Summer, recent period

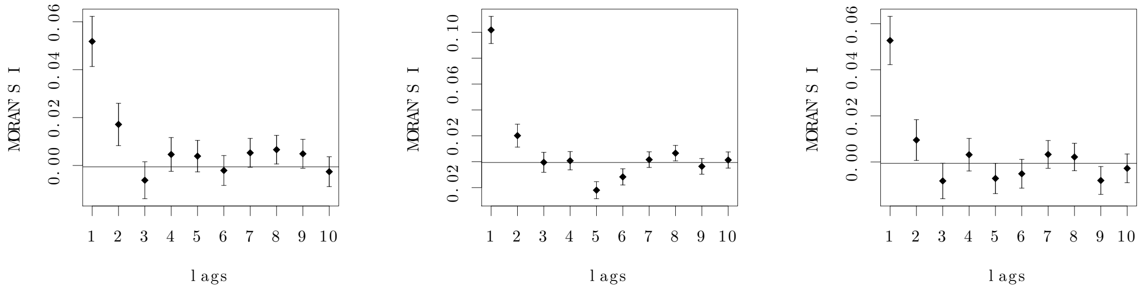
Figure S1: Temperature observation maps (in degree Celsius) for the early period (1991-1996), in (a) winter and in (b) summer and for the recent period (2007-2012) in (c) winter and in (d) summer.



(a) Saithe, winter

(b) Hake, winter

(c) Overlap, winter

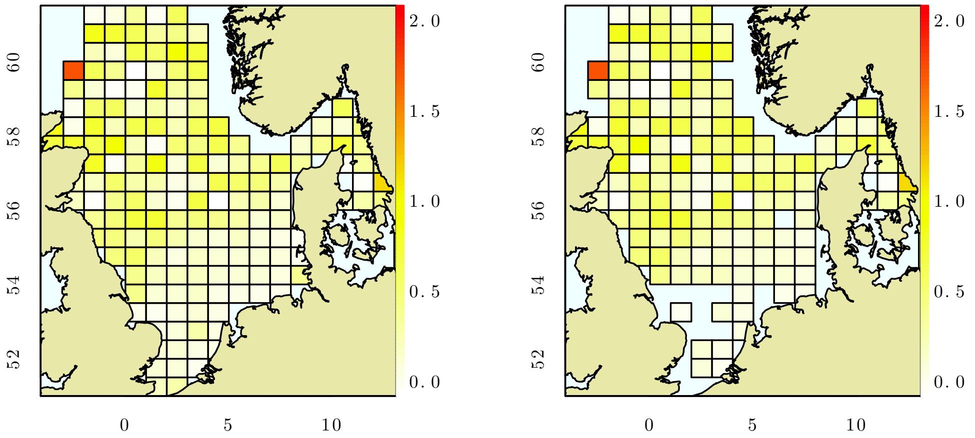


(d) Saithe, summer

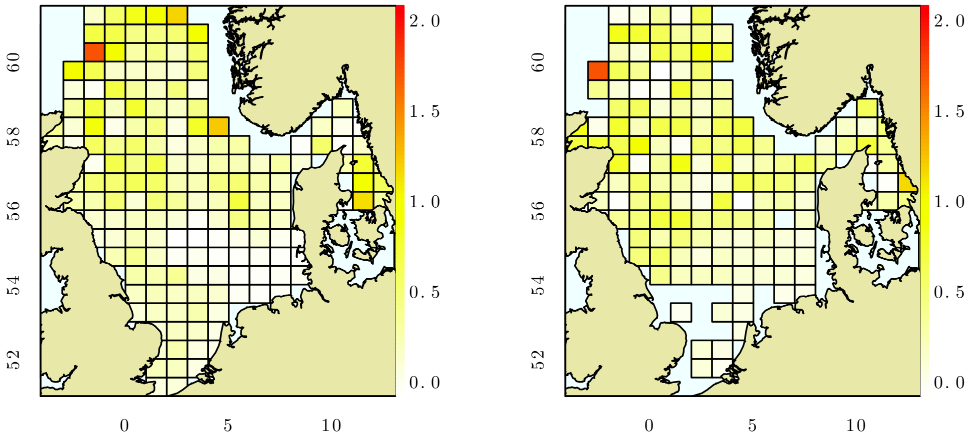
(e) Hake, summer

(f) Overlap, summer

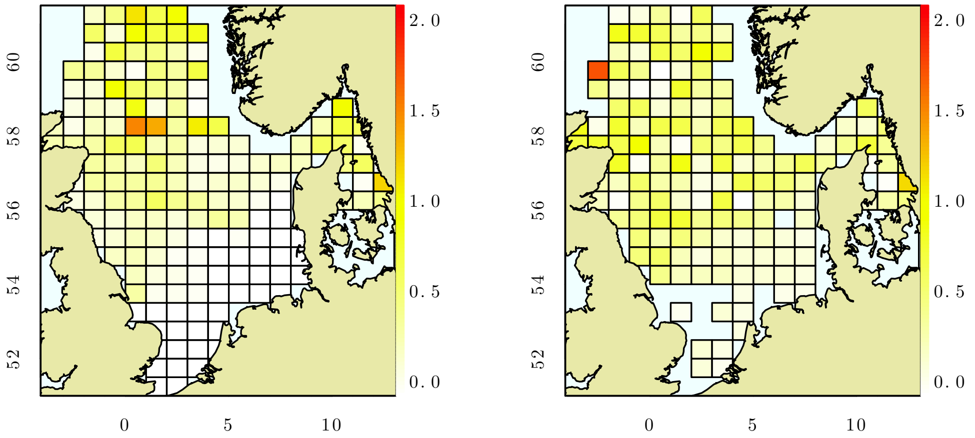
Figure S2: Correlograms of detrended residuals of environmental-only models for saithe (first column), hake (second column) and their overlap (third column) at winter (first line) and summer (second line). Moran's I coefficients depending on different spatial lags, spaced by 75 ± 10 kilometres.


(a) Saithe, winter, early period

(b) Saithe, summer, early period


(c) Hake, winter, early period

(d) Hake, summer, early period


(e) Overlap, winter, early period

(f) Overlap, summer, early period

Figure S3: Maps of spatial models absolute fitting error, error between observations and predictions, calculated for the early period (1991-1996) for saithe (a) in winter and (b) in summer; for hake (c) in winter and (d) in summer; for overlap (e) in winter and (f) in summer.

Table S1: Environmental-only and spatial saithe distribution models parameters β per variables (Table 1) and for each season. All coefficients are significant with $p < 0.001$, except for those marked with a letter as exposant. ^{a}: $p < 0.01$.

	Winter		Summer	
	ENV	ENV+SP	ENV	ENV+SP
H.Tot	7.92×10^{-1}	7.89×10^{-1}	9.57×10^{-1}	9.22×10^{-1}
C.Adu	1.05	1.05	1.02	1.09
C.Juv			1.58	1.61
NP.Tot	1.18	1.18		
BW.Tot				
HG.Adu				
HG.Juv	-8.29×10^{-1}	-8.46×10^{-1}	-1.02	-9.04×10^{-1}
CSpp				
FSpp			-1.13	-9.77×10^{-1}
Gpp	3.96^a	4.23	5.71	6.60
Ppp				
Lpp				3.72×10^{1a}
Temp				
Temp2				
Temp3				
Depth	2.84×10^{-2}	2.83×10^{-2}	6.27×10^{-2}	4.77×10^{-2}
Depth2			-1.09×10^{-4}	
Depth3	-6.98×10^{-8}	-6.52×10^{-8}		-1.66×10^{-7}

Table S2: Environmental-only and spatial hake distribution models parameters β per variables (Table 1) and for each season. All coefficients are significant with $p < 0.001$, except for those marked with a letter as exposant. ^{a}: $p < 0.01$; ^{b}: $p < 0.05$.

	Winter		Summer	
	ENV	ENV+SP	ENV	ENV+SP
S.Tot	6.10×10^{-1}	7.86×10^{-1}	1.02	1.09
C.Adu			5.01×10^{-1}	4.40×10^{-1a}
C.Juv				
NP.Tot	9.89×10^{-1}	7.82×10^{-1a}		
BW.Tot	7.85×10^{-1}	7.76×10^{-1}	6.47×10^{-1a}	
HG.Adu	1.31	1.25		
HG.Juv				
CSpp				$-1.97\ ^{a}$
FSpp	-2.92	-2.75	-1.13	-8.60×10^{-1}
Gpp				5.17
Ppp	-3.28	-4.62	-2.71	-2.43
Lpp				
Temp	5.07^{b}		1.13	1.06
Temp2	$-1.01\ ^{a}$	-1.56×10^{-1}		
Temp3	6.41×10^{-2a}	1.79×10^{-2}	-2.79×10^{-3}	-2.57×10^{-3}
Depth	4.04×10^{-2}	4.37×10^{-2}	6.76×10^{-3}	7.87×10^{-3}
Depth2	-2.07×10^{-4}	-2.09×10^{-4}		
Depth3	2.73×10^{-7}	2.59×10^{-7}		

Table S3: Environmental-only and spatial overlap models parameters β per variables (Table 1) and for each season. All coefficients are significant with $p < 0.001$, except for those marked with a letter as exposant. ^{a}: $p < 0.01$.

	Winter		Summer	
	ENV	ENV+SP	ENV	ENV+SP
C.Adu	7.24×10^{-1}	7.73×10^{-1}	1.02	9.80×10^{-1}
C.Juv			8.81×10^{-1a}	9.37×10^{-1a}
NP.Tot	1.17^a	1.41	9.37×10^{-1a}	9.51×10^{-1a}
BW.Tot			7.64×10^{-1}	7.12×10^{-1}
HG.Adu	1.33	1.28		
HG.Juv	-7.94×10^{-1}	-1.11	-8.23×10^{-1}	-9.16×10^{-1}
FSpp	-1.54	-1.02	-1.34	-1.09
Gpp				
Ppp				
Lpp				
Temp	1.07×10^{1a}		1.63	1.65
Temp2	$-1.91\ ^a$		-7.04×10^{-2}	-7.19×10^{-2}
Temp3	1.08×10^{-1}			
Depth	5.53×10^{-2}	2.75×10^{-2}	6.78×10^{-2}	6.03×10^{-2}
Depth2	-2.00×10^{-4}	-3.88×10^{-5}	-2.53×10^{-4}	-2.12×10^{-4}
Depth3	2.31×10^{-7a}		2.91×10^{-7}	2.32×10^{-7a}

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