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Spawning distribution of North Sea plaice and whiting from 1980 to 2007

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ABSTRACT: The spatial distributions of spawning population of North Sea plaice and whiting were studied using geostatistical analyses. Variograms were computed each year since 1980 on abundance data of spawning adults using the first quarter data from the International Bottom Trawl Survey. Maps of spatial distribution of spawning adults were produced using kriging interpolation. For both species, distributions of spawning adults were in agreement with historical spawning grounds previously described from location of their eggs. This showed that spawning adults' distribution may be used to infer the distribution of both plaice during its spawning peak and whiting at the beginning of its spawning period. Both species were strongly spatially structured with abundances of spawning adults located in particular areas. Spawning plaice was mainly located in the southern North Sea and along the east coast of the United Kingdom whereas it was virtually absent in the central part of the North Sea. For whiting, recurrent spawning sites were found both to the north and south of the Dogger Bank whereas the central and eastern parts of the North Sea were less suitable for spawning. Although this pattern of distribution remained stable in the last thirty years at the scale of the North Sea, multivariate analysis revealed a shift in the centre of distribution of spawning adults for both species. Changes in the extent of plaice spawning areas may be explained by temporal evolution of its spawning biomass. However, for whiting, the mechanisms responsible for the observed variations remain unclear.

KEY WORDS: spatial distribution, plaice, whiting, North Sea, inter-annual variability, spawning adults.

Introduction

Plaice (*Pleuronectes platessa*) and whiting (*Merlangius merlangus*) are both key species in demersal fish assemblages of the North Sea (Greenstreet & Hall, 1996; Rijnsdorp et al., 1996; Serchuk et al., 1996). Moreover, they have a high economical value as plaice is one of the most exploited flatfish (Rijnsdorp & Millner, 1996) and whiting is the third most exploited gadoid fish after cod and haddock (Stratoudakis et al., 1999). Plaice and whiting are both demersal spawners with pelagic eggs. Plaice spawns during winter (January-April) and mainly during the night (Nichols, 1989). Whiting is one of the North Sea species with the longest spawning period extending from February to June. Spawning distribution of North Sea plaice and whiting has been mainly described trough the distribution of eggs (Harding et al., 1978; Coull et al., 1998; ICES, 2005) and less through the distribution of spawning adults (Zheng et al., 2001; Zheng et al., 2002; Hunter et al., 2004). Moreover, Daan et al. (1990) emphasized that “little has been published about the extent and distribution of the spawning grounds” and that “it would be interesting to map the extent and duration of the spawning of all species throughout the North Sea”.

Spatial structures can be identified and described quantitatively using geostatistics (Petitgas, 1993; Petitgas, 2001; Mello & Rose, 2005; Woillez et al., 2007). Geostatistical methods embody a suite of methods for analysing spatial data using the variogram and allow the estimation of the values of a variable of interest at unsampled locations using interpolation by ‘kriging’ (Webster & Oliver, 2001). The variogram is a function that measures the relation between pairs of observations a certain distance apart. It summarises the way in which the variance of a variable changes as the distance and direction separating any two points varies. Typically, for spatially structured data, the variance is small at short lags and increases with larger separating distance. Based on the variogram, kriging interpolation produces optimal unbiased estimates that can be used for mapping to predict the values at unsampled locations.

The aim of this study is to describe the distribution of spawning population of North Sea plaice and whiting from 1980 to 2007. Geostatistical analyses combined to a geographical information system (GIS) were performed on abundances of spawning adults to map their spawning distribution. Moreover, interpolated abundances for each year were used to explore the inter-annual variability through multivariate analyses.

Material and methods

The International Bottom Trawl Survey

The first annual quarter International Bottom Trawl Survey (IBTS) has been carried out each year (since 1980) in the North Sea, from January to March, to collect data necessary to 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 (Fig. 1) defined by the International Council for the Exploration of the Sea (ICES). Each rectangle is visited by two different countries which each perform one standardised 30 min trawl using a 36/47 GOV (Grande Ouverture Verticale) bottom trawl. Trawling locations are randomly chosen by the country among a pre-defined set of three or four trawling locations inside the rectangle. This results in a minimum of two trawl hauls per rectangle per survey quarter. All specimens in each trawl sample are sorted by species and counted. Length measurements, otolith sampling and sexual maturity staging are performed for several key species, on a representative sample of individuals within seven standard "roundfish" areas (ICES, 2004, Fig. 1).

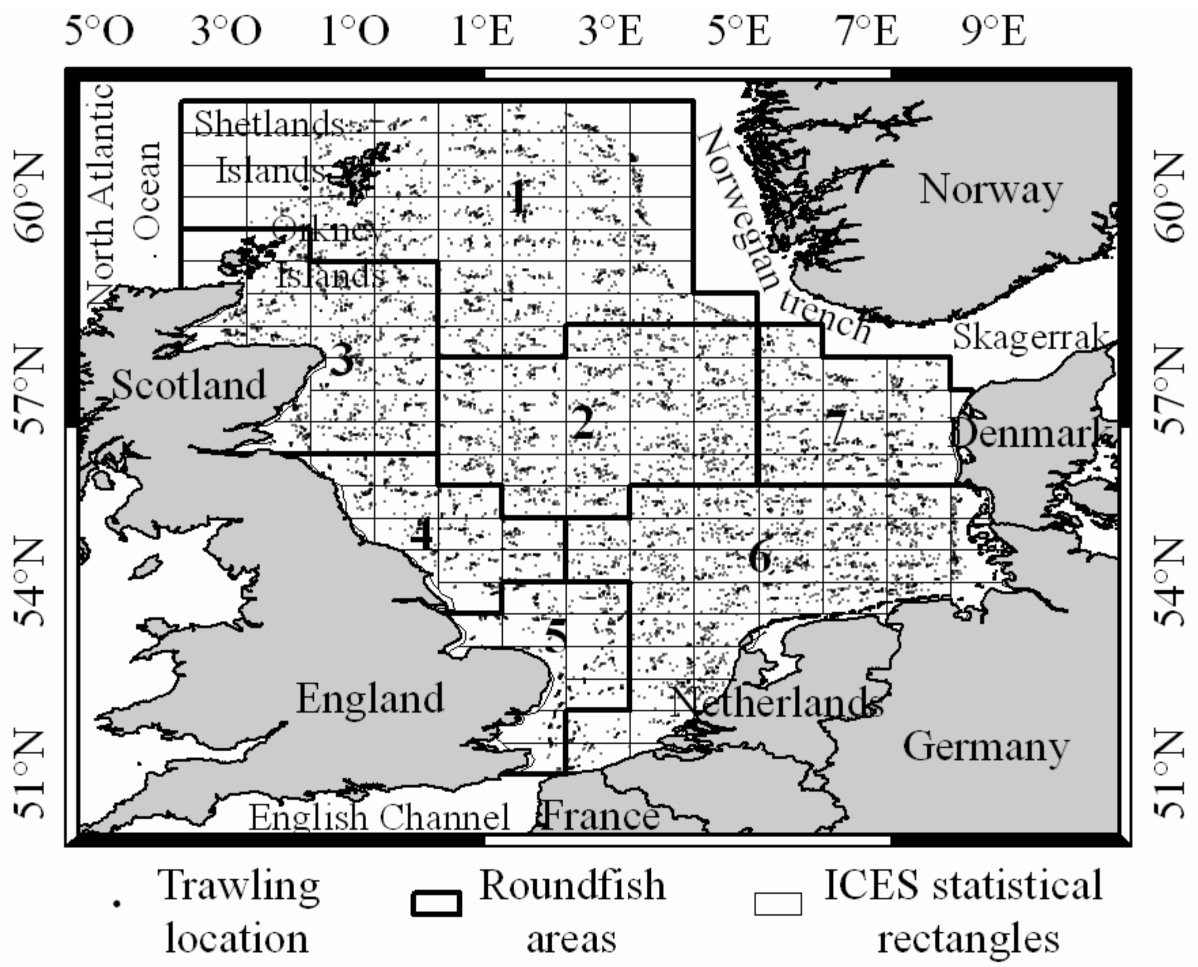

Figure 1: The North Sea International Bottom Trawl Surveys (IBTS). Black dots indicate the location of bottom trawls for the first quarter (January-March) of the IBTS since 1980. Countries involved in the IBTS, ICES statistical rectangles and the seven roundfish areas are also indicated.

Individuals are classified into four stages of maturity, from 1 to 4, with stage 3 corresponding to spawning individuals with fluent gonads (ICES, 2004). From 1980 to 2007, 11 343 bottom trawls were performed, which represent an average of 405 bottom trawl hauls per year. These data are available through the DATRAS database (DAtabase of TRAwl Surveys, http://datras.ices.dk/Home/Default.aspx) coordinated by ICES.

Abundance of spawning adults

Abundance data of spawning adults from the first annual quarter of IBTS (January-March), were computed from the available proportion of spawning adults within any given length class. For whiting, these proportions were calculated for each of the seven standard roundfish areas (Fig. 1), by pooling together maturity data available from 1990 to 2007. For plaice, the determination of sexual maturity has only been carried out since 2001, so there was not enough data to calculate the proportion of stage 3 adults within each length class and for each year and roundfish area. Consequently, data on sexual maturity from 2001 to 2007 were merged to calculate these proportions for northwest areas (areas 2, 3 and 4 pooled together, Fig. 1) and southeast areas (areas 5, 6 and 7 pooled together, Fig. 1). This choice was based on the time of spawning and spawning activity of plaice in each area (Daan et al., 1990). No data on the sexual maturity of plaice in area 1 was available. For both species, data on males and females were merged as there was not enough data to calculate proportions of spawning adults for each sex. This reduced the total number of trawling station, available for analyses, from 11 343 to 7 317 and 9 435, respectively for plaice and whiting (table. 1). For each of these stations, total abundance of spawning adults (in individuals.km^{-2}) were calculated from the summed product of the total abundance within each length class and the corresponding proportions of spawning adults inside that length class.

Table 1: Sampling periods of the first annual quarter of the IBTS surveys since 1980 and number of trawling stations available for each year for plaice and whiting.

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Year	Sampling Period		Number of stations		Year	Sampling Period		Number of stations	
	Start	End	Plaice	Whiting		Start	End	Plaice	Whiting
1980	22/1	6/3	270	353	**1994**	6/1	21/3	248	322
1981	21/1	5/3	180	199	**1995**	7/1	28/2	224	291
1982	28/1	13/3	234	275	**1996**	16/1	27/2	206	280
1983	1/2	10/3	265	320	**1997**	17/1	27/2	242	316
1984	26/1	10/3	306	391	**1998**	6/1	25/2	281	364
1985	28/1	5/3	334	435	**1999**	10/1	25/2	242	313
1986	11/1	17/3	340	446	**2000**	13/1	4/3	262	337
1987	24/1	22/3	356	457	**2001**	14/1	22/3	303	380
1988	24/1	2/3	288	381	**2002**	18/1	28/2	300	379
1989	24/1	2/3	285	360	**2003**	8/1	27/2	294	374
1990	21/1	24/2	248	329	**2004**	21/1	26/2	254	330
1991	7/1	28/2	224	324	**2005**	21/1	7/3	228	305
1992	13/1	26/2	256	330	**2006**	12/1	23/2	246	326
1993	17/1	1/3	222	301	**2007**	16/1	26/2	179	217

Geostatistics

Geostatistics (Webster & Oliver, 2001) were used to map the spatial distribution of spawning adults of plaice and whiting. Abundance of spawning adults were log-transformed (log (z + 1) where z is abundance) to reduce skewness. For each year and each variable, an “experimental” variogram was computed according to formula (1).

$$\gamma(h) = \frac{1}{2 \times n(h)} \times \sum \left[z(x+h) - z(x) \right]^2 \qquad (1)$$

where $\gamma(h)$ is the experimental variogram, $n(h)$ is the number of pairs of observations for the distance h, h is the distance between two locations and $z(x)$ is the observed abundance at location x (Fig. 2).

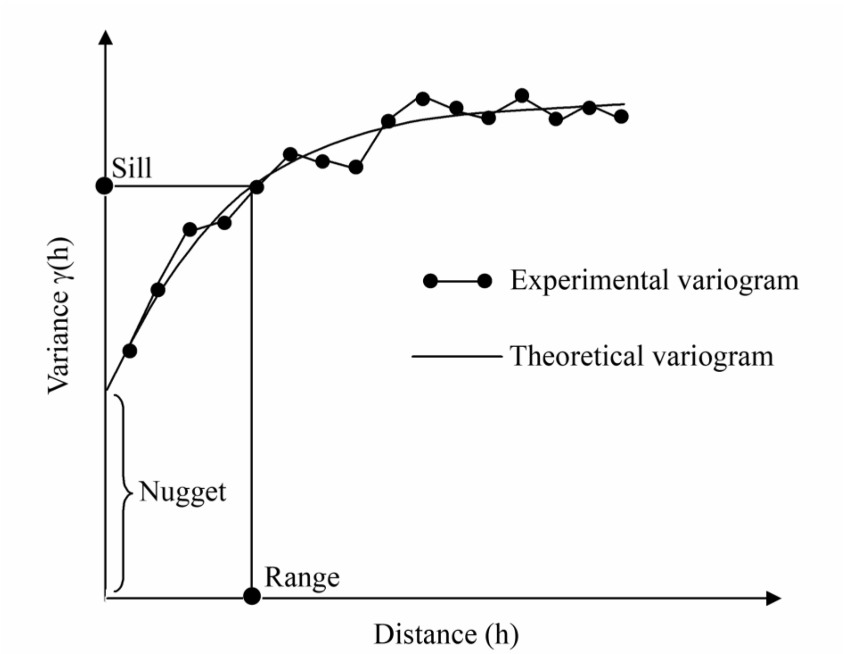

Figure 2 :: Experimental and theoretical variograms. The *nugget* is the variance between very close observations. The *range* indicates the distance after which observations are independent. At this distance, there is maximal variance which corresponds to the *sill*. Here, a combined model with a nugget effect model and an exponential model is fitted to the data and is used as the theoretical variogram, which provides a smooth variation of spatial variance as a function of distance between spatial locations

The distance h was calculated using the latitude (φ) and corrected longitude (G_φ) of the trawling location. The longitude correction (2) transforms decimal degrees of longitude (G) into decimal degrees of latitude which are of constant distance in a Mercator-like projection formula.

$$G_\varphi = G \times \cos(\frac{\varphi \times \pi}{180}) \qquad (2)$$

In case of non stationarity of $z(x)$, it can be split into two components following (3).

$$z(x) = m(x) + R(x) \qquad (3)$$

where $m(x)$ is the spatial trend and $R(x)$ are the residuals.

When accounting for more than 20% of the variation of the data, the spatial trend was modelled by fitting a low-order polynomial (linear or quadratic regression) to the spatial coordinates using the least-square regression method. The experimental variogram was then calculated on the residuals. A “theoretical” variogram was obtained as a model, chosen among exponential, circular, spherical and penta-spherical usual functions adjusted to the “experimental” variogram to determine the nugget, sill and range (Fig. 2). The four models were adjusted using the least-square regression method (Webster & Oliver, 2001) and the one with the best visual and statistical fit to the experimental variogram was retained as the chosen theoretical variogram model. This theoretical variogram was then used to estimate $z(x)$ on the mesh of a regular grid by using the ordinary kriging interpolation method, or the universal kriging when accounting for a spatial trend. A mesh size of 0.2 decimal degrees was chosen for the interpolation grid, as the mean survey resolution for IBTS was 0.16 decimal degrees. Geostatistics were implemented using Genstat (GenStat Release 7.1., 2004).

Using previously interpolated abundance, the ratio of spatial variance over temporal variance was calculated as a criteria to examine how the distribution varies in both space and time (Planque et al., 2006). The spatial variance was calculated as the mean variance between all grid cells over all years and the temporal variance as the mean variance between years over all grid cells. A ratio exceeding 1 means that the population distribution is more variable in space than in time, which indicates a spatial structure that tends to persist in time. A ratio less than 1 indicates that there is more variation in time than in space, which means that temporal variance greatly exceeds geographical difference (Planque et al., 2006).

Distribution mapping

Interpolated abundance of spawning adults was mapped in a geographical information system using ArcMap 9.1 (ESRI, 2005). Extrapolated areas (located outside of the surveyed area) were removed from the maps. The average map which summarises the average spawning area was computed as the mean of the maps between 1980 and 2007. The variability map represents the inter-annual variability in spawning and was produced by summing the standard deviation of maps between 1980 and 2007.

Preferential, occasional and unfavourable spawning sites were defined following Bellier et al. (2007) using the average and variability maps. Preferential spawning sites were characterised by a high mean and a low variance, occasional spawning sites by a high mean and a high variance and unfavourable spawning sites by a low mean and a low variance. The thresholds used to split the maps into high and low values of mean and variance were chosen visually according to their distribution histograms. The raster calculator of the Spatial Analyst extension of ArcMap 9.1 was used to combine the average and variability maps into the final map of preferential, occasional and unfavourable spawning sites.

Inter-annual variability

The inter-annual variability of spawning adult distribution was studied using a correspondence analysis performed on kriged abundance from 1980 to 2007. A contingency table of 28 years (columns) and 692 stations (lines) for plaice and 807 stations for whiting was extracted from the interpolated grid. A cluster analysis based on a Chi-square distance and using a flexible link (β= - 0.25) was performed to group similar stations together. The correspondence analysis was performed using CANOCO 4.5 (ter Braak & Smilauer, 2002) and the cluster analysis using PC-ORD 4.25 (McCune & Mefford, 1999).

Results

Proportion of spawning adults

For plaice, proportions of spawning adults are presented in figure 3. Proportions were the highest for large fish. They were also higher in areas 5, 6 and 7 than in areas 2, 3 and 4. Also, a sill of 20%, was observed for areas 2, 3 and 4 but not for other areas.

For whiting, each area presented different proportions of spawning adults (Fig. 4). Proportions were high in the southern areas (5 and 6), intermediate in the central areas (2, 4 and 7) and low in the northern areas (1 and 3). As for plaice, proportions also increased with the size of fish. They reached their maximum in area 6 with over 25% of spawning adults for sizes greater than 30 cm.

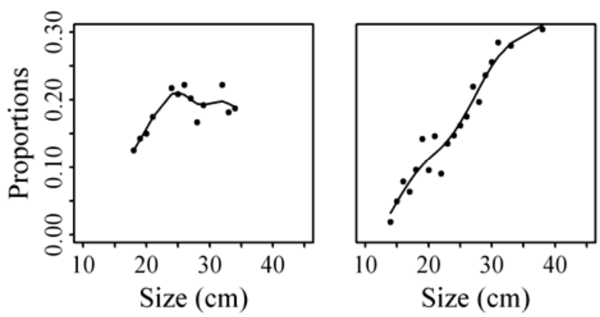

Figure. 3: Plaice: proportions of adult stage 3 (spawning adults) per size class. Left, areas 2–4 pooled. Right, areas 5–7 pooled. No data are available for area 1. The data points represent the proportions observed, and the lines the adjusted proportions using a smoothing spline for missing size classes.

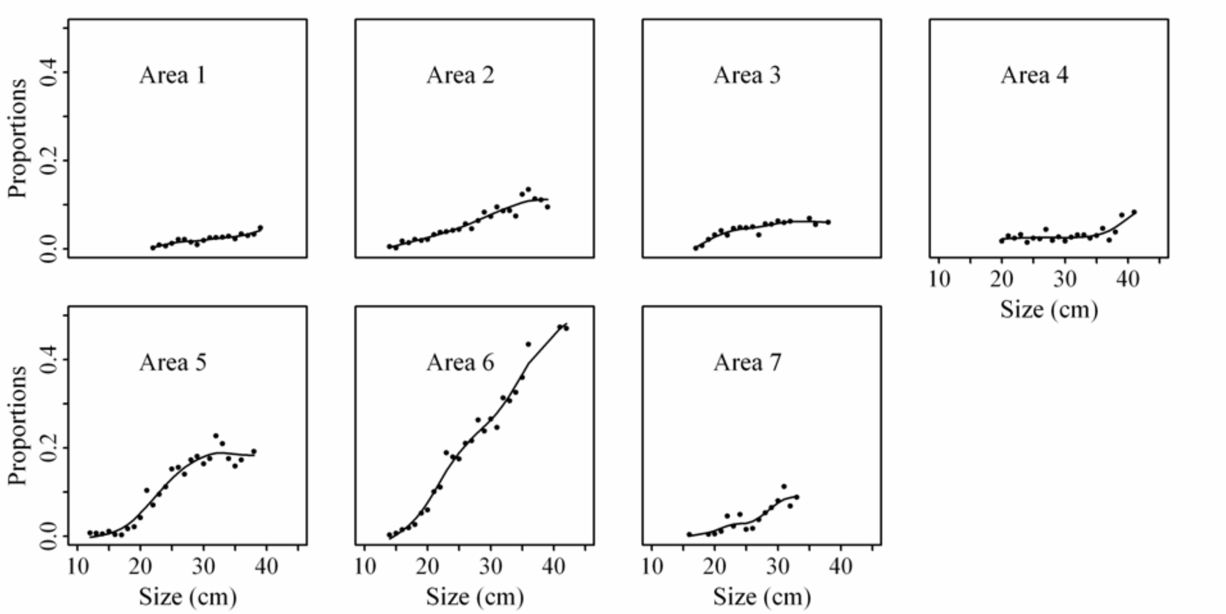

Figure 4: Whiting: Proportions of adult stage 3 (spawning adults) per size class. for each roundfish area. The data points represent the proportions observed, and the lines the adjusted proportions using a smoothing spline for missing size classes.

Geostatistics

For plaice, twenty eight variograms (one per year) were computed and adjusted. A significant quadratic trend was detected for years until 1994 (except 1982) and years 1995 and 1999 as it explained more than 20% of the variation in the data (Fig. 5). At the end of the nineties, percentage explained by the spatial trend was below 20 % and decreased until 10% in the 2000's. Percentage explained by the spatial trend showed the same variation along years as that of the spawning stock biomass (SSB, Fig. 5). There was an increase close to 450 000 t during the eighties followed by a decrease at the beginning of the nineties. Since 1994, the SSB was less variable and varied between 150 and 250 000 t.

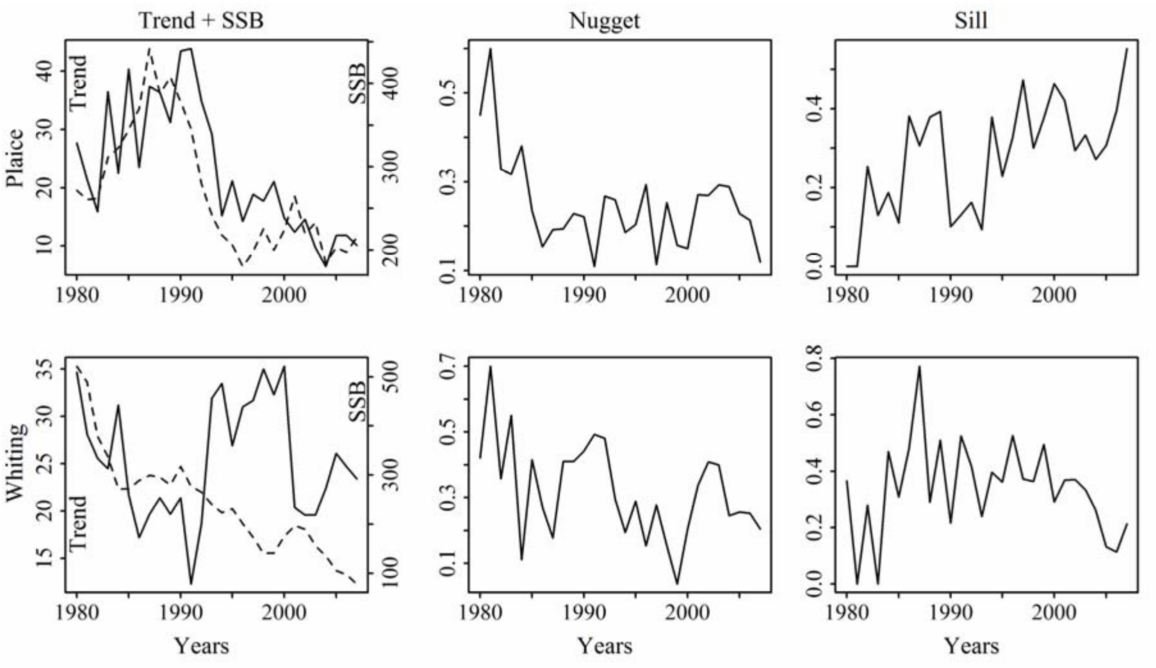

Figure 5: Parameters of the variogram. The spatial trend (percentage explained – continuous line), the nugget and the sill for plaice and whiting are plotted for each year between 1980 and 2007. ICES estimation of spawning stock biomass (SSB, 10^3 tons, ICES, 2008) are also indicated (stippled line).

For years 1980 and 1981, no spatial structure was detected in the residuals and a "pure nugget" model was used. For other years, a combined model with a nugget component and a circular component were used to adjust experimental variograms (table 2). Nugget had values between 0.3 and 0.6 for the first four years and lower ones between 0.1 and 0.3 for the later period (Fig. 5). Sill showed low values for years 1982-1985 and 1990-1993 and higher values for years 1986-1989 and 1994-2007 (Fig. 5). Range values were not directly comparable between years as they depended on whether the spatial trend was removed or not prior to variogram computation. Therefore, range values were not shown here.

For whiting, twenty eight variograms were also computed and adjusted. The percentage explained by the spatial trend (Fig. 5) decreased between 1980 and 1991 from 35 % to 12%, then increased up to about 30 % until 2000 and, after declining, remained stable between 20 and 25 % from 2001 to 2007. For years 1980-1991, the time variation of the estimation of the whiting SSB followed the variation of the percentage explained by the spatial trend. However, this was not the case for the following years where the SSB continued to decrease.

No spatial structure was detected in the residuals for years 1981 and 1983. A pure nugget model was used for these years. For other years, a combined model with a nugget component and one of the four tested model was used as the theoretical variogram. The circular model was used in more than 50 % of the theoretical variogram models (table 2). Nugget values (Fig. 5) varied strongly between years but suggested a continuous decrease. Sill values remained in the range 0.2 to 0.5 along years (Fig. 5) except for a peak in year 1987 and lower values below 0.2 at the end of the 2000's. As for plaice, range values are not shown here.

Table 2: Models used as a theoretical variogram to fit each experimental variogram, for plaice and whiting for each year from 1980 to 2007.

Year	Plaice	Whiting
1980	Pure nugget	Circular
1981	Pure nugget	Pure nugget
1982	Circular	Circular
1983	Circular	Pure nugget
1984	Circular	Exponential
1985	Circular	Circular
1986	Circular	Circular
1987	Circular	Exponential
1988	Circular	Circular
1989	Circular	Circular
1990	Circular	Circular
1991	Circular	Circular
1992	Circular	Circular
1993	Circular	Exponential
1994	Circular	Circular
1995	Circular	Circular
1996	Circular	Exponential
1997	Circular	Exponential
1998	Circular	Pentaspherical
1999	Circular	Pentaspherical
2000	Circular	Circular
2001	Circular	Pentaspherical
2002	Circular	Circular
2003	Circular	Circular
2004	Circular	Spherical
2005	Circular	Circular
2006	Circular	Circular
2007	Circular	Circular

Distribution of spawning adults

Plaice

Maps of the spatial distribution of spawning plaice (Fig. 6) indicated that areas of high abundances of adults were located in the southern part of the North Sea and along the east coast of United Kingdom. Very low abundances were found in the central part of the North Sea (Fig. 6). The ratio of the spatial variance over the temporal variance was 2.64, indicating that the pattern of distribution of spawning plaice was quite constant over time. However, there were some temporal variations, mainly in the maximal abundance observed and in the extent of areas of high abundances. Abundances were higher and occupied a wider area at the end of the eighties than in the nineties and 2000's.

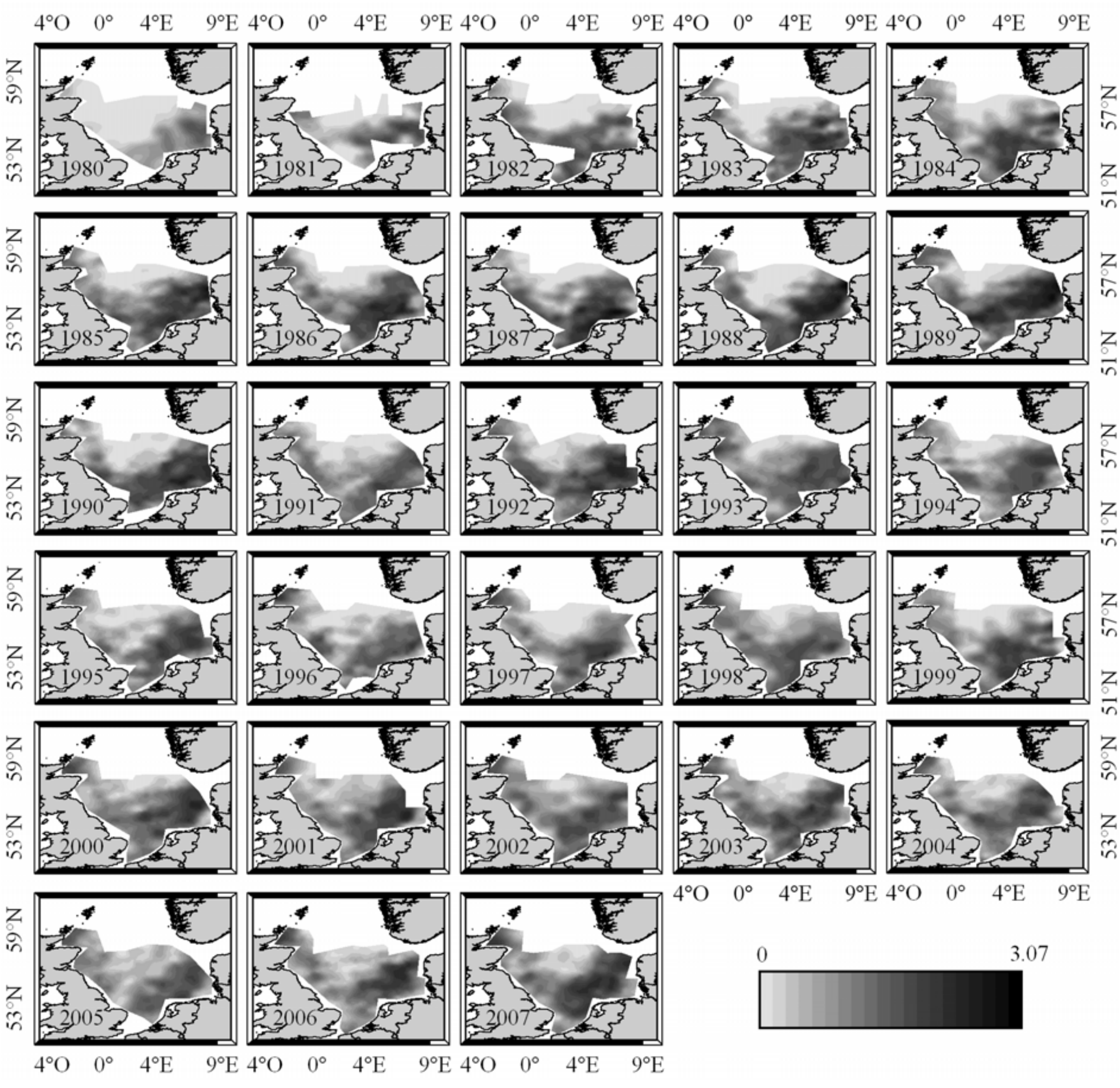

Figure 6: Spawning distribution of North Sea plaice from 1980 to 2007. Abundances of spawning adults are classified into twenty classes of equal interval from 0 to 3.07 (log-transformed).

Whiting

For whiting, maps of distribution (Fig. 7) indicated that there were two main areas of high abundances of spawning adults. One was located to the north of the Dogger Bank along the east coast of Scotland, from the south of Shetlands Islands to the Flamborough Head region. The other was located to the south of the Dogger Bank in the Southern Bight and in front of the Flamborough Head region. Very low abundances were located in the central and eastern parts of the North Sea as well as in the Firth of Forth and Moray Firth regions. For whiting, the distribution of spawning adults also varied more in space than in time with a ratio of 1.78. This indicated that the distribution pattern was constant in time. However there were temporal variations in the maximal abundance observed as well as in the extent of spawning areas. At the end of the 2000's, abundances were much lower and spawning adults were distributed in narrower areas than at the beginning of the nineties.

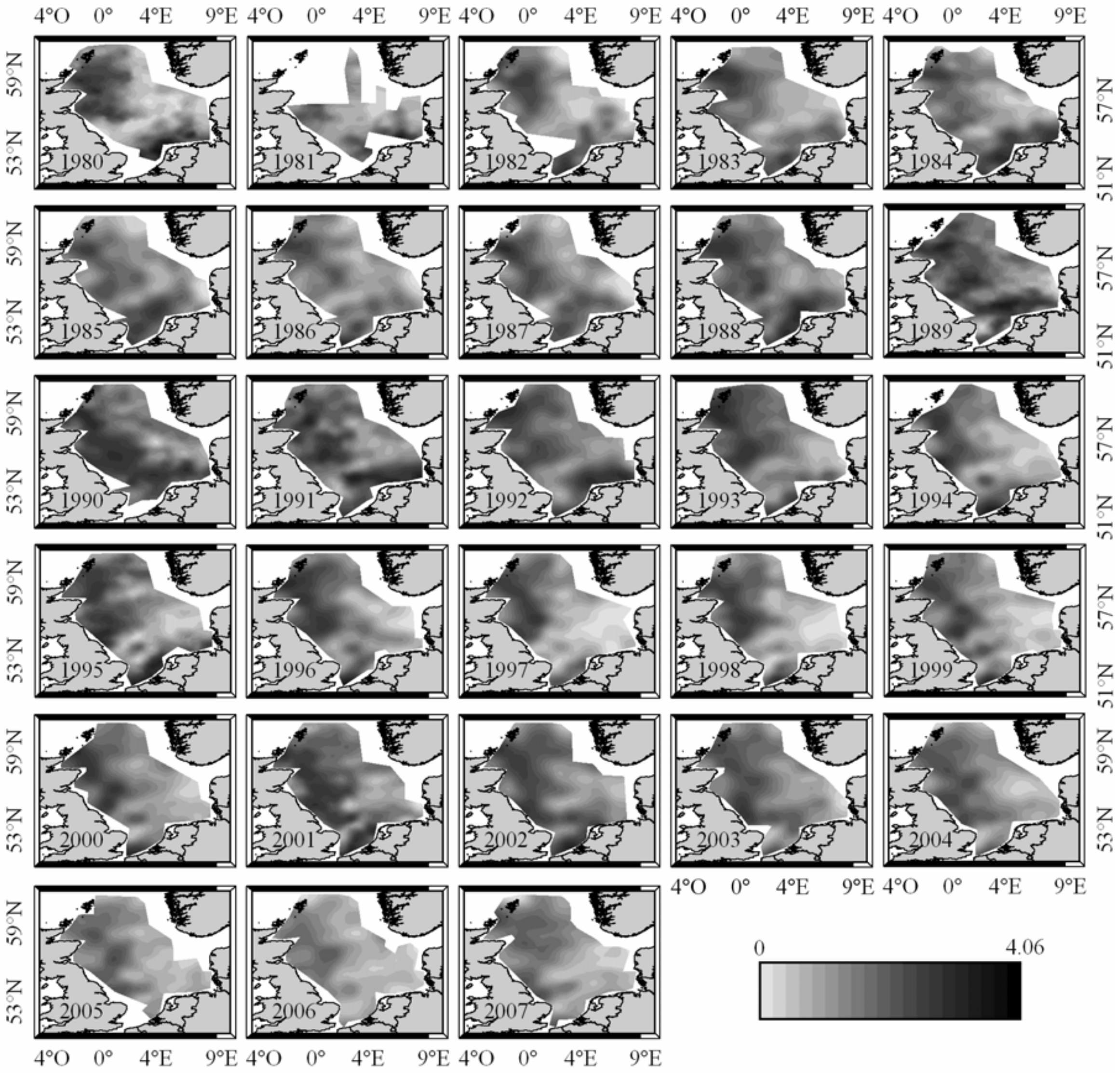

Figure 7: Spawning distribution of North Sea whiting from 1980 to 2007. Abundances of spawning adults are classified into twenty classes of equal interval from 0 to 4.06 (log-transformed).

Maps of the distribution for each year were used to define preferential, occasional and unfavourable spawning sites (Fig. 8). For plaice, preferential and occasional spawning sites were located in the southern and western part of the North Sea. Unfavourable spawning sites were located in the central part. For whiting, preferential spawning sites were located in the northern and southern part of the North Sea. Occasional sites corresponded to a small area in the Southern part whereas unfavourable areas were located in the central and eastern part of the North Sea.

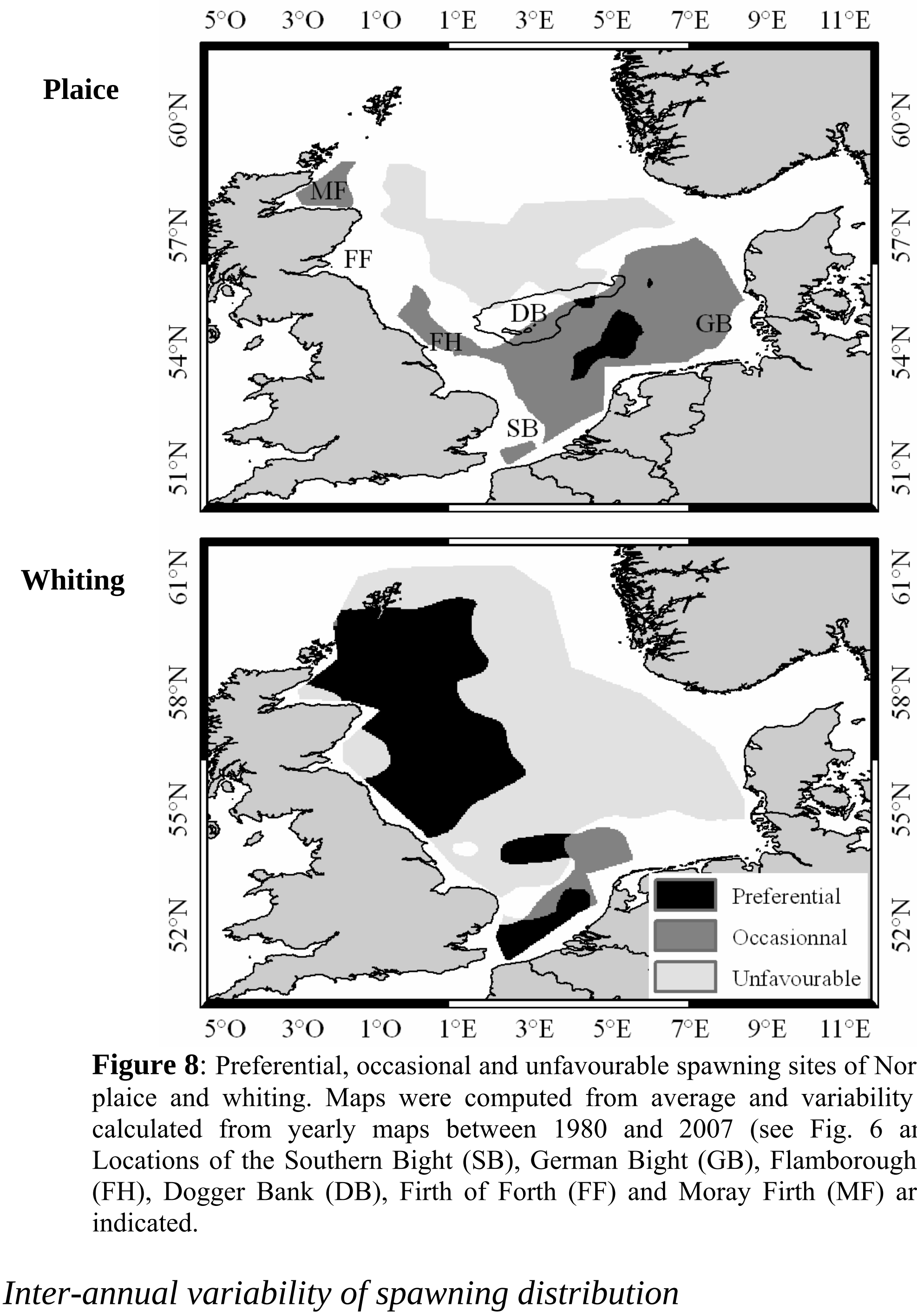

Figure 8: Preferential, occasional and unfavourable spawning sites of North Sea plaice and whiting. Maps were computed from average and variability maps calculated from yearly maps between 1980 and 2007 (see Fig. 6 and 7). Locations of the Southern Bight (SB), German Bight (GB), Flamborough Head (FH), Dogger Bank (DB), Firth of Forth (FF) and Moray Firth (MF) are also indicated.

Inter-annual variability of spawning distribution

Plaice

For plaice, results of the correspondence analysis are presented in figure 9. The first axis explained 18.9% and the second axis explained 9.4 % of the variability (Fig. 9A).

Years were mainly distributed along the first axis with the eighties on the left part of the first axis, the nineties in the middle part and the 2000's on the right part, as shown by the increase of the values of the scores along the years (Fig. 9B). Distribution and scores of the years along the second axis were less clear.

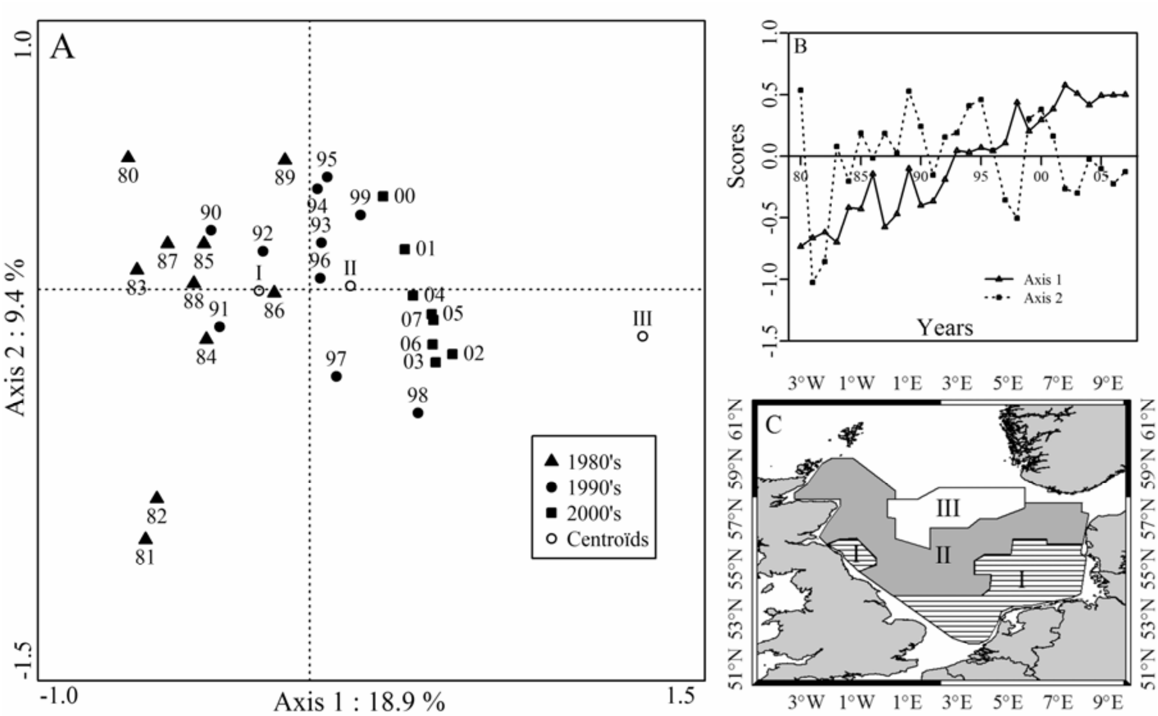

Figure 9: Plaice correspondence analysis performed on the 28 years (columns) and the 692 stations (lines). 9A, factorial plan of axes 1 and 2. The three groups of stations are indicated by their centroïds on the factorial plan. 9B, scores of the years along axes 1 and 2. 9C, location of the three groups of stations.

Three groups of stations were identified using cluster analysis. The first group gathered 240 stations located on the south-eastern part of the North Sea and along the east coast of Scotland (Fig. 9C). The centroïd of this group was located on the negative part of the first axis close to the eighties. The second group gathered 349 stations. The centroïd was close to the nineties and 2000's. These stations were located North to the first group of stations (Fig. 9C). The third group contained 103 stations that were located in the central part of the North Sea. The centroïd of this group was on the right part of the first axis.

Whiting

For whiting, results of the correspondence analysis are presented in Fig. 10. The first axis explained 26.4 % and the second axis explained 13.8 % (Fig. 10A). Distribution of years in the factorial plan showed an arch effect indicating a gradient along axis 1 and 2. Along axis 1, years 1980 to 1992 were located on the right part and years 1993 to 2007 on the left part. Scores of the years for the first axis showed a decrease in their value from 1980 to 2007 (Fig. 10B). Scores of the years for the second axis showed a cycle in their value with years 1980-1987 and 1993-1999 with negative scores and years 1988-1992 and 2000-2007 with positive scores.

Four groups of stations were identified through the cluster analysis with respectively 104, 232, 270 and 201 stations for group I, II, III and IV. These groups of stations were distributed along a Southeast-Northwest direction (Fig. 10C). Centroïds of theses groups were also distinct in the factorial plan with group I and II on the right part of the first axis, and group III and IV on the left part. These four groups were respectively close to years 1980-1984, 1985-1992, 1993-1999 and 2000-2007.

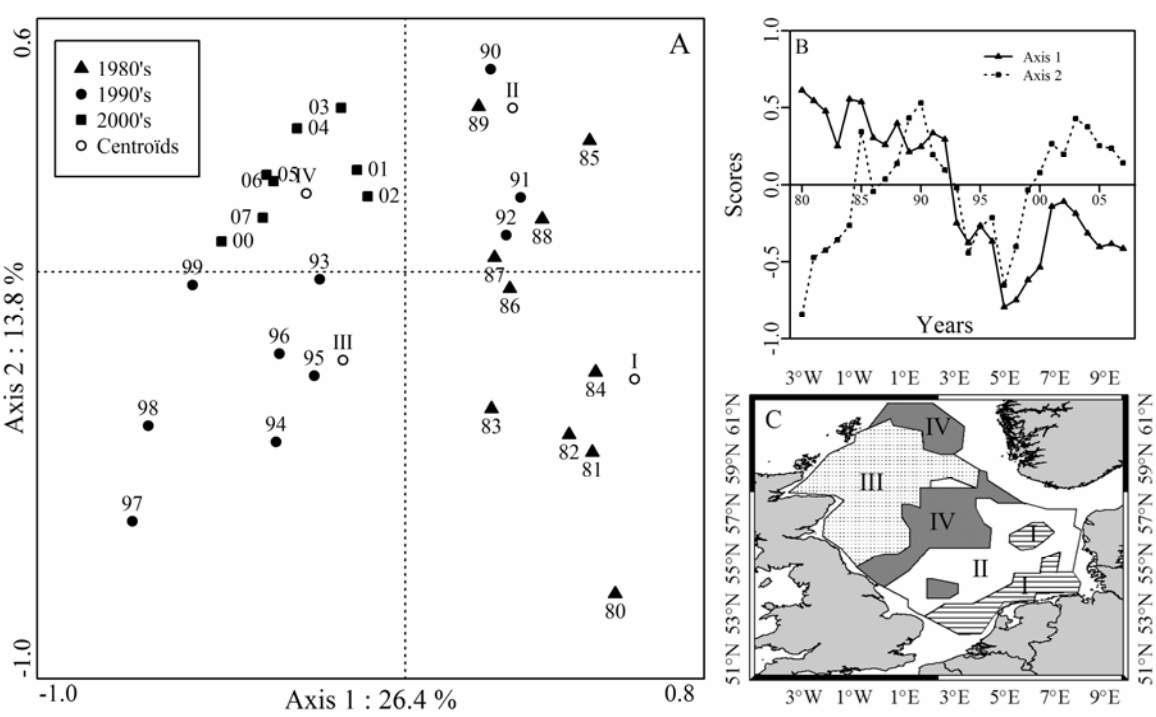

Figure 10: Whiting correspondence analysis performed on the 28 years (columns) and the 807 stations (lines). 10**A**, factorial plan of axes 1 and 2. The four groups of stations are indicated by their centroïds on the factorial plan. 10**B**, scores of the years along axes 1 and 2. 10**C**, location of the four groups of stations.

Discussion

Spatial distribution of spawning adults

Maps of the distribution of North Sea plaice spawning adults showed a clear separation between the central part and the southern and western parts of the North Sea. The areas of high abundances in the southern and western parts were characterised as preferential and occasional spawning sites and corresponded to the main spawning grounds that were described from eggs location (Harding et al., 1978), in the German Bight, in the Flamborough Head and Moray Firth. regions. Also, the proportions of spawning adults were higher in the southern part than in the western part which denotes a more important spawning activity in this area which is in good agreement with the location of the spawning activity described by Daan et al. (1990). Although the Southern Bight is known as an important spawning ground, it was not relevant each year in our observations. This might be due to the timing of IBTS survey, at the end of January, whereas the peak of spawning in the Southern Bight occurs earlier in January (Harding et al., 1978). Spawning adults were virtually absent each year in the central part of the North Sea. Therefore, this area did not seem currently in use.

Higher proportions of whiting spawning adults were found in the south than in the north of the North Sea which confirms that the latitude of spawning area varies along the spawning period, occurring in February-March in the English Channel and southern North Sea, and in April-June in the northern North Sea (Daan et al., 1990; Zheng et al., 2001). As IBTS surveys offer an incomplete view of the spawning activity of whiting in the northern area, it may only be used to depict its distribution at the beginning of its spawning period. However, high abundances of spawning adults were already observed both in the north and in the south. Theses areas were identified as recurrent spawning areas and corresponded to historical spawning grounds described in previous studies (Coull et al., 1998). Charrier et al. (2007) showed that these areas were occupied by two distinct sub-populations that could be genetically identified. They concluded that the Dogger Bank seemed to be a natural barrier which prevented the two populations from mixing and maintained genetic differentiation between them. As for plaice, spawning of whiting remained clearly absent in the central and eastern parts of the North Sea that were clearly identified as unsuitable spawning areas.

Plaice: Inter-annual variability of spawning distribution

The ratio of the spatial variance over the temporal variance exceeded 1 which indicates that the distribution of spawning plaice was more variable in space than in time. It seems that location of the spawning grounds in geographically well defined areas promotes this highly structured spatial distribution. Interpolated maps for each year revealed that the whole spatial structure of spawning plaice distribution remained stable at the end of the last century. This was also confirmed by location of the spawning grounds from eggs surveys (ICES, 2005). However, the large extent of the occasional spawning sites indicated a high variance between years inside the areas of high abundances, reflecting temporal variations in the observed abundance levels and in the extent of spawning areas. Similar behaviour between the spatial trend and the spawning stock biomass along years suggested an abundance-area relationship (Swain & Morin, 1996; Fisher & Frank, 2004; Blanchard et al., 2005). Individuals expanded their distribution at high level of population size and contracted it at low level. This forms the basic idea of the “Individual Free Distribution” (IFD, Fretwell & Lucas, 1970; Sutherland, 1983) and density dependent habitat selection (Rosenzweig, 1991; Shepherd & Litvak, 2004). Abundances and extent of spawning areas were higher for years of high spawning biomass which could suggest a “basin model” (McCall, 1990) as both areas and abundances varied according to the spawning biomass.

Correspondence analysis revealed a linear trend in the scores of years which was associated with a shift in stations’dominant typologies. Years of the period 1980-1992 were more associated with abundant spawning typical of southernmost areas of the North Sea whereas years of the period 1993-2007 were more dominated by less abundant observations typical of central areas. This change in the dominant type of spawning may have been the result of the contraction of plaice distribution due to the spawning stock biomass that started to decrease in 1992. For herring, it was shown that such a decrease in the size of the population could lead to a spatial shift or a loss of past spawning grounds (Corten, 2002). For plaice, it seemed that such an event had a more limited effect and may have been counterbalanced by the strong attachment of this benthic fish to its spawning site. Moreover there was no collapse in the plaice population during the study period; the spawning stock biomass returned to its original level which might have prevented too dramatic change in the distribution of spawning adults.

Whiting: Inter-annual variability of spawning distribution

For whiting as for plaice, the ratio of the spatial variance over the temporal variance exceeded 1 which indicates that distribution of spawning adults was more variable in space than in time. However, interpolated maps for each year showed temporal variations in observed abundances in the southern and northern areas, in particular a recent depletion in the southern area and a strong contraction of adults distribution in the northern area. The similar variation of the spawning stock biomass and the amount of spatial trend during the eighties followed by a disruption of this relationship in the later period may be explained in different ways.

Firstly, there might not be any density dependent control of whiting distribution,

Secondly a density dependent effect that was only partially captured by the present study,

Finally the SSB failed to reflect the current state of the population.

The second hypothesis suggested that the SSB may have reached a lower limit after the eighties where density dependence became a less important regulation factor than others.to explain these variations in the spatial distribution of whiting. Variations in sea surface temperature through the North Atlantic current (Zheng et al., 2002) and the spatial segregation between young individuals confined to shallow areas and old individuals in deeper areas (Zheng et al., 2001) have also been proposed to explain these variations

The last hypothesis is supported by Serchuk et al. (1996) who highlighted some discrepancies, especially for the last years, between the estimates of the spawning stock biomass coming from the VPA (Virtual Population Analysis) performed each year by the ICES (ICES, 2008) and the spawning stock biomass estimated from the IBTS data only. Also, considering the whiting population as one stock whereas two distinct populations have been genetically identified (Charrier et al., 2007) may lead to misinterpretation of the respective variation in time of their spawning biomass.

In the correspondence analysis, the scores of the years on the first axis allowed to distinguish between two distinct time periods : 1980-1992 and 1993-2007. The second period, being more correlated with stations located in the northern part of the north sea, suggested that the linear trend on the first axis highlighted a general decrease of the abundances of spawning adults in the Southern part between 1980 and 2007. On the second axis, the two periods could be split in two as indicated by the cyclic pattern. This illustrated that years were alternatively dominated by observations typical of the Southern and Northern part of the North Sea or observations typical of the central part of the North Sea. This revealed a temporal shift in typology of whiting spawning grounds during the study period towards the northern, less abundant type. This shift might be due to alternating period of extension and contraction of adult distributions in the Southern part and to the contraction of the distribution in the Northern part at the end of the study period.

Conclusion

Distribution of the spawning areas using spatial distribution of spawning adults were in agreement with location of historical spawning grounds that were described from past eggs surveys. This showed that distribution of spawning adults at the time of IBTS sampling was relevant to describe, map and model the spawning habitat of plaice during its peak of spawning and whiting at the beginning of its spawning period in the North Sea.

For both species, maps produced from geostatistical analyses emphasized that spawning adults were concentrated in geographically well defined areas whilst being nearly absent from others. This results in a high degree of spatial structure which supported that plaice and whiting tended to come back each year to the same spawning areas. Although the spatial distribution remained stable over the last thirty years at the scale of the North Sea, it also suffered of local temporal variations.

Whereas the two species were not spawning exactly at the same time and did not present a strong spatial concordance of their spawning habitat, multivariate analysis highlighted that for both species the study period could be split into the same two periods. Eighties were clearly separated from nineties and 2000’s. Although for plaice, a part of the variations may be explained by temporal variations of its spawning biomass, for whiting, the process involved remained unclear. Nevertheless, abundances of spawning adults may be used in future studies to explore the mechanisms that control the spatial distribution of spawning plaice and whiting.

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