Meso-scaled investigation of spatial distribution of the flatfish species dab, *Limanda limanda* (Linnaeus, 1758), within the German Bight: a geostatistical approach^{*}

Vanessa Stelzenmüller¹, Gerd-Peter Zauke^{1,**}, and Siegfried Ehrich²

¹ Carl von Ossietzky Universität, ICBM, D-26111 Oldenburg, Germany.
 ² Federal Research Centre for Fisheries, Institute for Sea Fisheries, Palmaille 9, D-22767 Hamburg, Germany.
 ** Corresponding author. E-mail: gerd.p.zauke@uni-oldenburg.de.

Abstract

In the context of planning and building offshore windfarms within the inner German Bight, this study tries to provide a method for evaluation of future long-term monitoring data in order to assess possible effects on fishes. Data collected by the German Small-scale Bottom Trawl Survey (GSBTS) during the summer cruises 1996-2000 in a small area of the inner German Bight were supplied by the German Institute of Sea Fisheries as an example data set for spatial analysis. Geostatistical tools were used to discover characteristics and persistence of spatial structures of two different size classes of the demersal fish species dab, Limanda limanda (Linnaeus, 1758), as a measure of natural variability. Spatial autocorrelation was detected in the catch data for both size classes, and spatial structuring was persistent throughout the time of investigation. Both size classes could be characterised by a moderate degree of spatial dependency within the catch rates. Furthermore, larger dab tend to aggregate in patches 3.2 km in diameter, whereas medium-sized dab aggregated in patches with average diameters of 1.1 km. The modelled structures were used to calculate the mean c.p.u.e. of dab within the survey area. This kriged mean was compared with the calculated arithmetic mean. Furthermore, the geostatistical variance of the arithmetic mean was compared to the 'classical' variance (neglecting the spatial structures). The contour plots of biomass index, estimated by kriging based on the models fitted to the mean structures for all years, displayed no locations with persistently increased fish biomass index for either size class throughout the years.

Key-words: dab, geostatistics, *Limanda limanda*, mean semivariogram, ordinary blockkriging, spatial structure

^{*} pre-print: Proceedings of the Second International Symposium on GIS/Spatial analyses in Fishery and Aquatic Sciences, Vol. 2 (Nishida, T., Kailola, P.J. & Hollingworth, C.E., Eds.), Fishery-Aquatic GIS Research Group, Kawagoe-city, Japan, 251-269 (2004).

1 Introduction

The inner part of the German Exclusive Economic Zone (EEZ) is a preferred area for constructing offshore windfarms. One of the questions is how to detect possible effects on fish populations after the windfarms have been put into operation. Classical methods to obtain quantitative information within fish assemblages and to detect possible changes over time are based on bottom trawl surveys, which are carried out under standard survey protocol conditions, including standard fishing gear and sampling strategies.

Stations randomly distributed over an area can yield unbiased estimates of the variable of interest only if the sampling-point observations are independent (Petitgas, 2001). When random sampling is carried out at an appropriate spatial scale, it effectively extinguishes any underlying spatial structure in the distribution of organisms. However, the scale of spatial distribution of the target species is usually unknown, and this factor may result in a bias in the calculation of estimates (Maynou, 1998). The presence of a spatial structure is indicated by spatial autocorrelation between pairs of samples, *viz*. the realisation of a regionalised variable (e.g. biomass of organisms) at one location influences the realisations at neighbouring locations. Thus, when samples are not taken independently of one another and when the population sampled is spatially structured, the computation of any variance requires a model of the spatial correlation in the population (Matheron, 1971). Spatial autocorrelation present in a data set can be analysed and modelled mathematically by geostatistics.

Geostatistics was initially developed for the mining industry to optimise the exploration of natural resources (Clark and Harper, 2001; Isaaks and Srivastava, 1989; Journel and Huijbregts, 1978). In the past 25 yr, applications of this methodology in ecology have increased continuously (Legendre, 1993; Robertson, 1987; Rossi *et al.*, 1992). In fisheries, geostatistics is used to optimise sampling strategies (Petitgas, 1996), to estimate catch data and corresponding variances, taking into account the existence of spatial structures (Conan *et al.*, 1992; Fernandes and Rivoirard, 1999; Maynou, 1998; Warren, 1997), as well as to map the estimated distributions and spatial patterns of organisms (Lembo *et al.*, 1999; Maravelias *et al.*, 1996). Therefore the geostatistical approach was employed to investigate the persistence and changes of spatial patterns with time. Additionally, the computation of unbiased estimates of the mean fish biomass within an area of interest can be achieved by this method.

The German Institute for Sea Fisheries provided for this study catch data from the German Small-scale Bottom Trawl Survey (GSBTS) sampled in an area of about the same size as an off-shore windfarm with approximately 200 windmills. The development of the spatial characteristics of the non-target flatfish species dab (*Limanda limanda*), the most common flatfish species in the North Sea, is described. Although this species carries out seasonal migrations between feeding and spawning areas, the spatial distributions of the fish in spring and summer are supposed to be stable (Rijnsdorp *et al.*, 1992). The objective of this study was the application of geostatistical tools for the assessment of spatial structures and the estimation and mapping of a demersal species. The advantages of a spatial analysis as a means of providing information on natural variability and possible effects of windfarms on the fish population were highlighted.

2 Methods

2.1 Survey area and fishing surveys

The data used for this analysis are from an area of the inner German Bight (box A, Figure 1), one of the eleven standard sampling areas of the GSBTS in the North Sea (Ehrich *et al.*, 1998). Sampling took place from 1996 to 2000 during summer. Catch data were assembled aboard the German research vessel "Walther Herwig III". Fishing was carried out under standard IBTS (International Bottom Trawl Survey) protocol using a standard net GOV (Chalut à Grande Ouverture Verticale), with a trawling time of 30 min at a trawling speed of 4 knots (1 knot = 0.514 m s⁻¹). The locations of sampling stations (21 to 24) as well as trawl directions were selected randomly within the area of investigation for each year of the survey. The trawl positions were taken as midpoint of the haul converted to an absolute measure in km (easting and northing) relative to $54^{\circ}27$ N and $6^{\circ}58$ E.

2.2 Biological categories considered

In order to explore spatial structures depending on biological categories, such as size (age) of fish (Fernandes and Rivoirard, 1999), the catch data for dab were separated into two size classes: 9.5-19.5 cm (2-7 yr old; referred to as d2) and > 19.5 cm (older than 7 yr; referred to as d3) following Heessen and Daan (1996). The size-class < 9.5 cm was excluded from the analysis as there were too few juveniles in the catches. The group d2 is supposed to be the most important one, because dabs will mature at a length of 13 cm (Rijnsdorp *et al.*, 1992).

2.3 Preparatory data analysis

Numbers per 30 min trawl time within each size class were converted into biomass (kg30min⁻¹ trawl time; c.p.u.e.) on the basis of the following length-weight relationship (unpublished data):

weight
$$[g] = a \cdot \text{length } [cm]^b$$
 with $a = 0.0074$ and $b = 3.113$ (1)

All catch data were tested for normality using the Shapiro-Wilk test (Royston, 1982). In cases of deviation from normality, c.p.u.e.s were log-transformed and the log-transformed data were used for further analysis. Catch data that had to be transformed were d2 and d3 in 1997, d3 in 1998 and d3 in 1999. Further linear and non-parametric regressions with one covariate (Bowman and Azzalini, 1997) (north and east co-ordinates) were carried out to investigate possible trends within the c.p.u.e.s (Kaluzny *et al.*, 1998). Significant linear trends within the catch data with east co-ordinates were detected for d2 in 1997 and 1998 and with north co-ordinates for d2 in 1999. These trends were taken into account for the subsequent spatial analysis.

2.4 Geostatistical analysis

2.4.1 Variography

First an experimental semivariogram was calculated to analyse the spatial structure of dab, followed by fitting of a theoretical variogram model. Using the spatial structure defined, ordinary blockkriging, a linear method of spatial prediction was used to estimate the annual mean c.p.u.e. within box A. For mapping predicted distributions of dab, ordinary pointkriging was employed. The structure of spatial variability of Z(x) (kg30min⁻¹ per size class) was assessed by an experimental covariance function. Experimental semivariograms $\hat{\gamma}(h)$ were used to describe the spatial structure of fish biomass. The semivariogram outlines the spatial correlation of data, measuring the half variability between data points as a function of their distance. In the absence of spatial autocorrelation among samples, the semivariance is equal to the variance of Z(x). A monotonic increase of the semivariance with increasing separation distance (*h*) of the sampling positions indicates the presence of spatial autocorrelation. When a linear trend was present, c.p.u.e.s were detrended (Kaluzny *et al.*, 1998). Only omnidirectional semivariograms were computed using the classical estimator (Matheron, 1971):

$$\hat{\gamma}(h) = \left\{ 1 / \left[2N(h) \right] \right\} \sum_{i=1}^{N(h)} \left[Z(x_i + h) - Z(x_i) \right]^2$$
(2)

and the robust estimator ("modulus"), which is supposed to be resistant against extreme values, introduced by Cressie and Hawkins (1980):

$$\hat{\gamma}(h) = \left\{ \left[1/[N(h)] \right] \sum_{i=1}^{N(h)} \left| Z(x_i + h) - Z(x_i) \right|^{0.5} \right\}^4 / \left[0.914 + 0.988 / N(h) \right]$$
(3)

where $Z(x_i)$ is the realisation of biomass (c.p.u.e.) of dab for one size class at station x_i , $Z(x_i + h)$ is another realisation separated from x_i by a discrete distance h (measured in km) and N(h) is the number of pairs of observations separated by h. Furthermore, to improve knowledge of spatial structures, for each size class, average semivariograms (survey years 1996-2000) were computed (Rivoirard *et al.*, 2000). The absolute average semivariogram represents the average of the different individual semivariograms, weighted by the number of pairs at each distance. It was thus assumed that the different spatial distributions can be described by the same ecological process.

In many cases a transformation of the data is recommended, since the structure of the transformed variable often is more regular than that of the untransformed variable (Rivoirard *et al.*, 2000). This would lead to a biased estimate of the raw structure. However, to allow ecologically sound interpretations and to establish the structure of the raw variable, an appropriate back transformation is required after performing the structural analysis. We used the following equation for the log-transformed data (Guiblin *et al.*, 1995):

$$\gamma(\mathbf{h}) = \left[\mathbf{m}^2 + \operatorname{var}(\mathbf{Z})\right] \left\{ 1 - \exp\left[\sigma^2 \gamma_{\mathbf{L}}(\mathbf{h}) / \operatorname{var}(\mathbf{L})\right] \right\}$$
(4a)

with

$$\sigma^{2} = \log \left[1 + \operatorname{var}(Z) / m^{2} \right]$$
(4b)

where *m* is the mean of Z(x), *L* is the logarithmic transformation of the variable and $\gamma_L(h)$ is the structure of the transformed variable. A simulation study described in Rivoirard et al. (2000) showed that the use of log-transformation, associated with a back transformation, provides an improved method for estimating variogram parameters and estimation variance. Subsequently, parameters (nugget, sill and range) of spherical and linear models were fitted automatically (Cressie, 1991), to reduce subjectivity and to ensure reproducibility of the fit (Fernandes and Rivoirard, 1999). Following Webster and Oliver (2001), firstly the types of models regarding the

general trends of the semivariogram curve (log back semivariograms) were selected, and then models were fitted using a weighted least-squares method with suitable weights. Least-squares methods are based on finding the model which is "visually" close to the semivariogram curve by minimising the sum of squares of the differences between the generic semivariogram estimator and a model (Chilès and Delfiner, 1999). Here a weighted least-squares procedure recommended by Cressie (1991) was employed, where more weight is given to the points near the origin, which is the crucial part in determining the variogram parameters:

$$\sum_{h} N(h) \left\{ \left[\hat{\gamma}(h) \right] / \left[\gamma(h) \right] \right] - 1 \right\}^{2}$$
(5)

where N(h) is the number of pairs used to compute the experimental semivariogram $\hat{\gamma}(h)$ and $\gamma(h)$ is the fitted model (spherical, exponential or linear). In order to assess the goodness-of-fit (*gof*) of the different models, for each fitting procedure an index recommended by Fernandes and Rivoirard (1999) was computed:

$$gof = \left\{ \sum_{h} \omega(h) \left[\hat{\gamma}(h) - \gamma(h) \right]^2 \right\} / \left\{ \sum_{h} \omega(h) \left[\hat{\gamma}(h) \right]^2 \right\}$$
(6)

where $\omega(h)$ is the number of pairs used to compute the semivariogram, $\hat{\gamma}(h)$ is the experimental semivariogram and $\gamma(h)$ is the fitted model. The closer the *gof* to zero, the better the fit. Furthermore, the strength of spatial dependence (*SpD*) was calculated (Robertson and Freckmann, 1995) as:

$$SpD = (1 - nugget / sill) \cdot 100 \tag{7}$$

This information was used to compare changes in the development of spatial autocorrelation in catch data with time and among size classes. The greater this value (ranging from 0 to 100), the greater the spatial dependence. Low spatial dependency indicates a high sampling and/or analytical error, or a spatial variability occurring at scales smaller than the minimum distance separating small sampling pairs (Robertson and Freckmann, 1995). Sokal and Oden (1978) related the diameter of an aggregation of a species to the modelled range. Therefore the effective range (eR) was compared for each model fitted, in order to detect characteristics and changes of spatial patterns with time. The effective range for spherical models is equal to the estimated range. In addition, the observed data were cross-validated by ordinary kriging, which provides a measurement of the reproduction of the data by the model defined and the kriging procedure. The results of this jack-knifing method are given by standardised errors. If the mean of this standardised error (*Zscore*) is zero and the standard deviation (*SD-Zscore*) approximately 1, then the model and the method employed provide an adequate reproduction of the data (Isaaks and Srivastava, 1989).

2.4.2 Ordinary kriging

Mapping of density surfaces of the predicted dab biomass index was carried out for both size classes with ordinary pointkriging. This method estimates the variable values at unsampled locations using the observed values $Z(X_i)$ in the surrounding neighbourhood as follows (Matheron, 1971):

$$\hat{Z}(X_0) = \sum_{i}^{n} \lambda_i Z(X_i)$$
(8)

where λ_i are charging weights attributed to each $Z(X_i)$ subject to $\sum_{i=1}$ in order to guarantee unbiased estimates (Cressie, 1991). The uncertainty of the estimation of ordinary pointkriging was expressed by mapping the kriging variance (Petitgas and Lafont, 1997). Mean catch rate estimates over box A for both size classes $\hat{Z}(X_0)$ of dab were obtained by ordinary blockkriging, a method used as a direct method of biomass assessment in fisheries (Maynou, 1998). The computerised algorithm requires the area to be finely discretised. The discretisation used here is a grid of 35 x 35 blocks, which was found to optimise speed and precision of the computation. Variances were expressed as coefficients of variation of the arithmetic mean (m) and were calculated using the classical estimator, which does not take into account the spatial autocorrelation within the sampled data:

$$CV_{class} = \left(s^2 / n\right)^{0.5} / m \tag{9}$$

with s^2 as data variance and *n* as number of stations. CV_{class} was compared with the geostatistical estimation variance of the arithmetic mean (Matheron, 1971):

$$CV_{geo} = \left(\sigma_{E}^{2}\right)^{0.5} / m \tag{10}$$

with σ_{E} as the global estimation variance (Petitgas and Lafont, 1997), which is influenced by the geographical position of the stations, the shape of the survey area and the model fitted.

Computations were done using R (version 1.7.1), a programming environment for data analysis and graphics (<u>http://www.r-project.org/</u>) and R-geo (<u>http://sal.agecon.uiuc.edu/csiss/Rgeo/ in-dex.html</u>), spatial data analysis (see also <u>http://www.est.ufpr.br/geoR/</u>).

3 Results

3.1 Spatial population structures

Semivariograms revealed that the two size classes of dab displayed different spatial structures during the time of investigation (Figure 2 - 3). For both size groups of dab, almost all spatial structures, including the mean structures (Figure 3), could be successfully described by spherical and linear models (1997, d2, d3). The parameters nugget, sill and range of the models fitted, the values of goodness-of-fit statistic, the measure of strength of spatial dependency (Equation 7), the effective range, as well as the results of the cross-validation, are compiled in Table 1, indicating valid models throughout the years and size classes.

Models fitted to the semivariograms showed values for the goodness-of-fit statistic (*gof*) close to zero for both size classes, pointing to reliable fitting procedures. For both size classes the effective ranges and values of spatial dependence peaked in 2000 (d2: 8.62, 78.09; d3: 6.94, 77.62; Table 1). On the average, d2 and d3 developed a medium strength of spatial dependency, indicated by the values of SpD (d2: 43.21; d3: 40.74) of the mean structures. Size class d3 tend to aggregate in patches with a diameter of 3.2 km, which is more than double the mean patch diameter of d2 (1.1 km).

3.2 Geostatistical estimation of biomass (mean catch in weight)

The biomass index (c.p.u.e., kg30min⁻¹) of d2 varied between 26.5 (1996) and 40.2 (2000), whilst c.p.u.e. of d3 ranged from 9.2 (1996) to 43.0 (1998) (Figure 4a, 4b). The c.p.u.e. of me-

dium-sized dab (d2) showed a slow increase from 1996 to 2000, whereas the biomass index of d3 increased from 1996 to 1998 and decreased in 1999 and 2000 (Figure 4a, 4b). The estimated geostatistical and arithmetic means were in good agreement. With one exception (1996, d3), the geostatistical estimation variance (CV_{geo}) was always smaller than the classical one (CV_{class}) (Figure 4a, 4b). The largest difference between the two coefficients of variation was found in 1997 for both size classes.

3.3 Geostatistical mapping

The patchiness of the distribution of both size classes was different in shape and size for each year. For both size classes, the estimated maps of fish biomass index showed no persistent area, with high density in box A throughout the years (Figure 5, 6). Similarities of the geographical locations of the patch centres between size classes were obtained for 1996, 1997 and 2000. The mapped uncertainties for the kriged biomass index demonstrate that the estimated locations, shapes and sizes of the patches are reliable.

4 Discussion

Although the structural analysis of the biomass index of dab was carried out at the limit for an application of geostatistics, due to the low numbers of sampling stations, the presence of spatial autocorrelation was discovered for both biological categories considered. A minimum of 30-50 sampling points is recommended by Legendre (1993), whereas here only 21 to 24 stations per survey were available. Hence data have been transformed, and also the classical and modulus estimator has been used, both leading to less erratic semivariograms. Finally, due to the modelling of the log-back transformed semivariograms and the results of the goodness-of-fit statistic and cross-validation, one can have confidence in the modelled structures (Table 1). Furthermore, by computing the mean semivariograms of the biomass indices of d2 and d3, derived from summer surveys in box A and based on the survey design applied, the persistence of spatial structures was obvious (Figure 3). Although the spatial structuring of d2 and d3 in the German Bight was only moderate, one has to take into account the presence of spatial autocorrelation when estimating the mean catch rate of dab or assessing variability. At least in part this may be due to the fishing gear used in this survey (GOV), which is not specifically designed for catching dab, so that the population structure of this species might not have been resolved completely.

In 2000, the strength of spatial autocorrelation in the catch rates of d2 and d3 were highest, also the greatest patch diameters (d2: 8.6 km; d3: 7 km) were detected, and throughout the investigation period, size class d3 aggregated in larger patches. This is consistent with the idea that larger fish may tend to form larger associations than smaller fish (Rivoirard *et al.*, 2000). An analysis of the length frequency within one size class showed that, in most cases, a length of 16.5 cm was predominant within the medium-sized class d2 and 19.5 cm was the dominant length in d3. The difference between the modal values of the length frequencies seems to be large enough to cause varying spatial patterns.

Distinguishing two size classes of a fish species in order to investigate different spatial structures is related to the idea that fish distribution depends on the size of the individuals rather than on their age (Fernandes and Rivoirard, 1999; Guiblin and Rivoirard, 1996). A further reduction of variability and an improved assessment of spatial structuring may be obtained when taking into account other biological categories such as sex. Furthermore, an improvement of a spatial analy-

sis when the c.p.u.e. of female and male dab are taken into account raises the question whether reproduction may cause the development of spatial patterns of fish density. This would be likely, because spawning occurs from Jan to Sep (Rijnsdorp *et al.*, 1992) and takes place in well-defined nursery areas situated in the south-eastern North Sea (Daan *et al.*, 1990). Other marine organisms, especially benthic ones, often develop patches, which could result from social behaviour or reproduction (Valiela, 1995). Patch formation of dab may be also caused by sediment composition (Ehrich, 1988), distribution of the prey species (epizoobenthos) and fish behaviour due to reproduction. Additionally, abiotic variables may also induce a spatial pattern, but salinity and temperature were more or less homogeneous within the study area.

Because of the persistence of spatial patterns found for both size classes of dab throughout the time of investigation, the models fitted to the mean structures were used for estimating the density maps (Figure 5, 6). The detected conformance of the locations of the patch centres in 1996, 1997 and 2000 could be explained by reproduction, when biomass indices of two size classes were almost identical with fractions of female and male dab. The variability of the location of high-density spots may be due to the fact that the area of investigation is homogeneous, and probably a preferred feeding site for dab does not exist.

During the time of investigation, the variability of the catch rates of d2 was small, whereas the c.p.u.e. of d3 varied by more than 30 kg30min⁻¹. This may be explained by increased fishing effort in 1999 or a weak recruitment. The geostatistical coefficient of variation in almost all cases showed lower values than the classical one, although differences between the two coefficients were small. The geostatistical variance depends on the model specified, sample locations, shape of investigation area and intensity of sampling (Petitgas, 1996, 2001). Therefore, the low number of sampling stations (21-24) of the surveys may have resulted in increased geostatistical variances.

The main focus of the present study was to develop a strategy to evaluate long-term monitoring data to assess possible effects of offshore windfarms on a fish population within a meso-scaled area. The main advantage of the procedure used was that the detected spatial autocorrelation within the catch data has been taken into account. Furthermore, additional information about the spatial characteristics of the species studied, which may be correlated with population dynamics (Warren, 1997), is provided. The species-specific aggregation within an area is an interesting measure of variability. With this method, the differentiation of natural and experimental variability is possible, after the sampling strategy has been optimised. Then the natural variability within an area may be explored and possible effects of offshore windmills on fish populations can be defined and evaluated, provided that an appropriate reference area is available.

5 Acknowledgements

This work is part of the PhD thesis of V. Stelzenmüller at the Carl von Ossietzky Universität, Oldenburg, Germany, supported by the Scholarship Program of the German Federal Environmental Foundation (Deutsche Bundesstifung Umwelt, Osnabrück; No. 20002/290).

6 References

- Bowman, A., and Azzalini, A. 1997. Applied Smoothing Techniques for Data Analysis. Oxford University Press, New York. 193 pp.
- Chilès, J.-P., and Delfiner, P. 1999. Geostatistics: Modelling Spatial Uncertainty. John Wiley & Sons, New York. 695 pp.
- Clark, I., and Harper, W.V. 2001. Practical Geostatistics 2000. Geostokos (Ecosse) Limited, Scotland. 342 pp.
- Conan, G.Y., Maynou, F., and Sardá, F. 1992. Direct assessment of the harvestable biomass from a stock of *Nephrops norvegicus*, seasonal and spatial variations. ICES CM, K:22: 24.
- Cressie, N., and Hawkins, D.M. 1980. Robust estimation of the variogram. Mathematical Geology, 12: 115-125.
- Cressie, N.A.C. 1991. Statistics for Spatial Data. John Wiley & Sons, New York. 900 pp.
- Daan, N., Bromley, P.J., Hislop, J.R.G., and Nielsen, N.A. 1990. Ecology of North Sea fish. Netherlands Journal of Sea Research, 26: 343-386.
- Ehrich, S. 1988. The influence of sediment on the distribution of bottom fish and the response of survey strategies here to. ICES CM, 1988: G:67. 9pp.
- Ehrich, S., Adlerstein, S., Götz, S., Mergardt, N., and Temming, A. 1998. Variation of meso scale fish distribution in the North Sea. ICES CM, J:25: 7.
- Fernandes, P.G., and Rivoirard, J. 1999. A geostatistical analysis of the spatial distribution and abundance of cod, haddock and whiting in North Scotland. *In* Geoenv II - Geostatistics for Environmental Applications, pp. 201-212. Ed. by J. Gomez-Hernandez, A. Soares, and R. Froidevaux. Kluwer Academic Publisher, Dordrecht.
- Guiblin, P., and Rivoirard, J. 1996. Spatial distribution of length and age for Orkney Shetland herring. ICES CM, D: 14. 23 pp.
- Guiblin, P., Rivoirard, J., and Simmonds, E.J. 1995. Analyse structurale de données á distribution dissymétrique: exemple du hareng écossais. Pages 137-159. Ecole des Mines de Paris, Paris.
- Heessen, H.J.L., and Daan, N. 1996. Long-term trends in ten non-target North Sea fish species. ICES Journal of Marine Science, 53: 1063-1078.
- Isaaks, E.H., and Srivastava, R.M. 1989. An Introduction to Applied Gesostatistics. Oxford University Press, Oxford. 561 pp.
- Journel, A.G., and Huijbregts, C. 1978. Mining Geostatistics. Academic Press, London. 600 pp.
- Kaluzny, S.P., Vega, S.C., Cardoso, T.P., and Shelly, A.A. 1998. S+ Spatial Stats User's Manual for Windows and UNIX. Springer-Verlag, New York. 327 pp.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology, 74: 1659-1673.

- Lembo, G., Silecchia, T., Carbonara, P., Acrivulis, A., and Spedicato, M.T. 1999. A geostatistical approach to the assessment of the spatial distribution of *Parapenaeus longirostris* (Lucas 1846) in the central-southern Thyrrenian Sea. Crustaceana, 72: 1093-1108.
- Maravelias, C.D., Reid, D. G., Simmonds, E.J., and Haralabous, J. 1996. Spatial analysis and mapping of acousting survey data in the presence of high local variability: geostatistical application to North Sea herring (*Clupea harengus*). Canadian Journal of Fisheries and Aquatic Sciences, 53: 1497-1505.
- Matheron, G. 1971. The theory of regionalized variables and their applications. Les cahiers du Centre de Morphologie Mathématique. Centre de Geostatistique, Fontainebleau, Paris. 212 pp.
- Maynou, F. 1998. The application of geostatistics in mapping and assessment of demersal resources. *Nephrops norvegicus* (L.) in the northwestern Mediterranean: a case study. Scienta Marina, 62: 117-133.
- Petitgas, P. 1996. Geostatistics and their applications to fisheries survey data. *In* Computers in Fisheries Research, pp. 113-141. Ed. by B.A. Megrey, and E. Moksness. Chapman & Hall, London.
- Petitgas, P. 2001. Geostatistics in fisheries survey design and stock assement: models, variances and applications. Fish and Fisheries, 2: 231-249.
- Petitgas, P., and Lafont, T. 1997. EVA2: Estimation Variance. Version 2. A geostatistical software on windows 95 for the precision of fish stock assessment surveys. ICES CM, Y:22: 22.
- Rijnsdorp, A.D., Verthaak, A.D., and Van Leeuwan, P.I. 1992. Population biology of dab *Limanda li-manda* in the south-eastern North Sea. Marine Ecology Progress Series, 91: 19-35.
- Rivoirard, J., Simmonds, J., Foote, K.G., Fernandes, P.G., and Bez, N. 2000. Geostatistics for Estimating Fish Abundance. Blackwell Science, Oxford. 206 pp.
- Robertson, G.P. 1987. Geostatistics in ecology: interpolating with known variance. Ecology, 68: 744-748.
- Robertson, G.P., and Freckmann, D.W. 1995. The spatial distribution of nematode trophic groups across a cultivated ecosystem. Ecology, 76: 1425-1432.
- Rossi, R.E., Mulla, D.J., Journel, A.G., and Franz, E.H. 1992. Geostatistical tools for modeling and interpreting ecological data spatial dependence. Ecological Monographs, 62: 277-314.
- Royston. P. 1982. An extension of Shapiro and Wilk's W Test for normality to large samples. Applied Statistics, 31: 115-124.
- Sokal, R.R., and Oden, N.L. 1978. Spatial autocorrelation in biology. 1. Methodology. Biological Journal of the Linnean Society, 10: 199-228.
- Valiela, I. 1995. Marine Ecology Processes. Springer Verlag, New York. 686 pp.
- Warren, W.G. 1997. Changes in the within-survey spatio-temporal structure of the northern cod (*Gadus morhua*) population, 1985-1992. Canadian Journal of Fisheries and Aquatic Sciences, 54: 139-148.
- Webster, R., and Oliver, M. 2001. Geostatistics for Environmental Scientists. John Wiley & Sons, New York. 271 pp.

Year	Group	Model	C ₀	С	а	Spd	gof	Zscore	SD-Zscore
1996	d2	Sph	132	46	3.9	25.8	0.06	0.00	0.96
1997	d2	Lin	8	12	n.a.	0.0	0.04	n.a.	n.a.
1998	d2	Nug	124	0	0.0	0.0	0.06	n.a.	n.a.
1999	d2	Sph	61	90	1.8	59.5	0.03	0.00	1.14
2000	d2	Sph	41	145	8.6	78.1	0.04	-0.01	1.28
Mean	d2	Sph	30	23	1.1	43.2	0.01	0.00	5.15
1996	d3	Sph	12	19	2.3	61.8	0.05	-0.01	1.09
1997	d3	Lin	10	8	n.a.	0.0	0.04	n.a.	n.a.
1998	d3	Sph	118	271	2.1	69.6	0.02	0.00	2.55
1999	d3	Sph	15	11	7.1	41.7	0.01	0.00	3.65
2000	d3	Sph	12	41	6.9	77.6	0.06	-0.01	1.15
Mean	d3	Sph	162	112	3.2	40.7	0.00	0.00	1.76

Table 1: Estimated parameters^a of spherical and linear semivariogram models fitted with a least-squares method to c.p.u.e. data for dab in the German Bight (sampling area box A, Figure 1).

^a Group: size groups d2 and d3; Sph: spherical; Lin: linear; Nug: pure nugget; C₀: nugget; C: sill (for linear models = slope); a: range ; SpD: spatial dependency (Equation 7); *gof*: measure of the goodness-of-fit (Equation 6); *Zscore*: mean standardised error of the crossvalidation; *SD-Zscore*: standard deviation of the standardised error (see Methods section for details).



Figure 1: Survey area "box A" within the German Bight, with locations of the sampling stations in 1996 as an example of the survey design.



Figure 2: Experimental semivariograms of c.p.u.e. catch data for dab size class d2 and d3 (1996-1999) with fitted spherical and linear (1997) models. Note that for the structural analysis in 1998 and 2000 of d3 the modulus estimator was used. Note: Figure 2 (f) varies in scale



Figure 3: Mean spatial structures (1996-2000) of dab size class d2 and d3 with fitted spherical models (model parameters in Table 1).



Figure 4: Arithmetic mean c.p.u.e., geostatistical mean c.p.u.e. of dab size class d2 (above, a) and d3 (below, b), estimated with oridinary blockkriging (OBK), and coefficients of variation CV_{class} (%) and CV_{geo} (%) (Equations 9, 10) of the arithmetic mean c.p.u.e. (see Methods section for details).



Figure 5: Density of c.p.u.e. biomass index for dab size class d2 within box A estimated with ordinary pointkriging (left panel) and estimated kriging variance (right panel) for the summer surveys 1996–1999 (a-e).



Figure 6: Density of c.p.u.e. biomass index for dab size class d3 within box A estimated with ordinary pointkriging (left panel) and estimated kriging variance (right panel) for the summer surveys 1996 –1999 (a-e).